Ecological and historical filters constraining spatial caddisfly distribution in Mediterranean rivers

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SUMMARY

1. Contemporary species distributions are determined by a mixture of ecological and historical filters acting on several spatial and temporal scales. Mediterranean climate areas are one of the world's biodiversity hotspots with a high level of endemism, which is linked to complex ecological and historical factors.

2. This paper explores the ecological and historical factors constraining the distribution of caddisfly species on a large regional scale. A total of 69 taxa were collected from 140 sampling sites in 10 Iberian Mediterranean river basins. Approximately 74% of taxa can be considered rare, with the southern basins (the Baetic–Riffian region) having greater endemism. The greatest richness, involving a mixture of northern and southern species, was found in the transitional area between the Baetic–Riffian region and the Hesperic Massif.

3. The historical processes occurring during the Tertiary (i.e. the junction of the Eurasian and African plates) explained 3.1% of species distribution, whereas ecological factors accounted for 20.7%. Only 0.3% was explained by the interaction of history and ecology. A set of multi-scale ecological variables (i.e. basin, reach and bedform characteristics) defined five river types with specific caddisfly assemblages. The commonest caddisfly species accounted for the regional distribution pattern, while rare taxa contributed to the explanation of subtle patterns not shown by common species.

4. Despite the importance of historical factors for biogeography and the large scale used in our study, ecological variables better explained caddisfly distribution. This may be explained by the length of time since the historical process we are considering, the high dispersion and colonisation capacity of many caddisfly species, and the strong environmental gradient in the area. Because of the historical and environmental complexity of Mediterranean areas, rare taxa should be included in ecological studies so that the singularity of these ecosystems is not missed.

Keywords: ecological factors, historical factors, Iberian Peninsula, Mediterranean rivers, species distribution, Trichoptera

Introduction

Organisms are patchily distributed in space and time rather than randomly or homogeneously, generating

spatial and temporal heterogeneity (Pringle *et al.*, 1988). Community ecology and biogeography seek to detect patterns in communities and to understand the processes that cause these patterns (Townsend, 1989). Ecologists have traditionally focused on external (i.e. abiotic environment) and intrinsic (i.e. biotic interactions) processes (Power *et al.*, 1988), whereas biogeographers emphasise the role of historical factors (see Myers & Giller, 1988; Cornell & Lawton, 1992).

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The presence and abundance of organisms at a site is the result of the action of several multi-scale filters, including both historical and ecological constraints ranging from landscape to micro-habitat scales (Poff, 1997). The relative effects of historical and multi-scale ecological factors may vary according to the spatial scale of the study. In a large-scale study, history may be more important than in local studies, in which patterns can be explained by environmental variables alone (Townsend *et al.*, 2003). Several studies have sought to identify the distribution of macroinvertebrate patterns in both large geographical areas (Wright *et al.*, 1984; Corkum, 1989; Quinn & Hickey, 1990; Marchant, Barmuta & Chessman, 1995; Kay *et al.*, 1999, 2001) and small ones (Ormerod & Edwards, 1987; Graça, Fonseca & Castro, 1989), revealing the strong relationship between aquatic biota and environmental variables. However, the historical factor has usually been overlooked.

The Mediterranean Basin's very complex history and environmental features have contributed to the high biodiversity and endemism currently found in these areas (Balletto & Casale, 1991). Therefore, both historical and environmental characteristics should be used to explain contemporary aquatic organism distribution. In the Iberian Peninsula, two historical factors are significant in defining present aquatic biota: (1) the lack of strong glaciations during the Quaternary, which played an important role in increasing biodiversity; and (2) the incorporation of part of the Baetic-Riffian Massif (south and southeast of Spain) with the Hesperic Massif at the end of the Miocene (Baetic ranges) (Rosenbaum, Lister & Duboz, 2002). This joining of the Eurasian and African plates enabled North-African species to enter the southeast of the Iberian Peninsula and neo-endemisms to develop there (Ribera *et al.*, 1996; Ribera, 2000).

The Trichoptera is a well-represented and highly endemic group in the Iberian Peninsula, with 390 species recorded (González, 2003). Because of the high endemism and diversity of species in the Iberian Peninsula and the low number of trichopterologists, knowledge of their larvae is incomplete (Vieira-Lanero, 2000). Given this, few studies have focused on the autoecology of immature stages (but see Puig *et al.*, 1981; Gallardo-Mayenco, Prenda & Toja, 1998), and no large-scale study has looked at the distribution of the species and factors involved in this distribution. However, some studies have been reported in other

European countries (Leuven, Vanhemelrijk & Van der Velde, 1987; Czachorowski, 1994; Wiberg-Larsen *et al.*, 2000), North America (Ross, 1963) and South Africa (de Moor, 1992).

The aims of the present study were: (1) to clarify the relative influence of historical and ecological factors constraining caddisfly distribution in the Mediterranean basins of the Iberian Peninsula; (2) to analyse the most relevant ecological factors acting at different scales; and (3) to establish the caddisfly assemblages that are representative of different combinations of environmental conditions. If historical events and ecological factors are important driving forces determining caddisfly distribution in Iberian Mediterranean basins, then we would expect to find significant contributions by both in explaining community variability. If species distributions are the result of the interaction of several multi-scale filters, we would expect caddisfly distribution to respond to a mixture of basin, reach, and bedform factors, and that different assemblages would be found in different combinations of environmental conditions.

Methods

Study area

The study covers almost 1000 km of the Iberian Mediterranean coast, on which several low and high mountain ranges are located, reaching at times over 2000 m.a.s.l. Overall, a thermal and pluviometric gradient is present, with annual precipitation ranging from less than 300 mm in the most arid areas in the southeast to over 800 mm in northern regions or in some mountain areas. Limestone and other sedimentary rocks and deposits are dominant, although some siliceous areas are also found in the Sierra Nevada, Pyrenees and Montseny ranges (Fig. 1). Sclerophyllous and evergreen trees and shrubs are dominant, although in some areas there are deciduous and coniferous forests. Because of Mediterranean climate conditions, rivers are characterised by high seasonality, with frequent torrential floods in autumn and spring and droughts in summer (Molina, Vidal-Abarca & Suárez, 1994).

Caddisflies were obtained from a total of 140 sampling sites visited on four occasions in 1999 (spring, summer, autumn, and winter). Sites belong to 10 river basins located along the eastern Spanish

Fig. 1 Basins sampled along the Mediterranean coast of the Iberian Peninsula in the GUADALMED Project. Mountain ranges and the approximate extension of the Hesperic Massif and the transitional and Baetic–Riffian areas are shown.

Mediterranean coast (Fig. 1): Besòs, Llobregat, Mijares, Turia, Júcar, Segura, Almazora, Aguas, Adra and Guadalfeo (an extensive description of the basins studied can be found in Robles *et al.*, 2002). In general, 15 sites per basin were selected, in an attempt to cover all river types present. Because of the very high pollution at some sites and the ephemeral nature of some others in summer, several sampling sites and seasons did not contain Trichoptera larvae, and therefore the data matrix was reduced to 372 samples (sites $\times$ seasons).

The biological data matrix

Macroinvertebrate samples were collected from all available habitats with a kick-net of 250 μ m mesh, following the GUADALMED Protocol (Jáimez-Cuéllar *et al.*, 2002). Samples were first examined in the field, and successive samples were taken until no more different families were found. Samples were preserved in 70% alcohol and sorted in the laboratory. Caddisfly taxa were identified to the maximum level possible (see Bonada *et al.* 2004a) for more information about the collected species), and rank of abundances for each taxon were recorded: 1 from one to three individuals, 2 from four to 10, 3 from 11–100 and 4 for more than 100 individuals. Because

of the large number of undescribed larvae in the Iberian Peninsula (Vieira-Lanero, 2000) and the small size of many individuals (first larval instars), we were not able to identify the species of all larvae with certainty. When possible, pupae and adults were collected in the field to ensure correct identification. In some cases, mature larvae were reared in the laboratory. Consequently, different taxonomical levels were mixed between sites and even within a single site, which may hinder the achievement of some objectives at the community level (Cuffney *et al.*, 2002). To minimise this problem, the caddisfly data matrix with all individuals identified at the maximum possible level (called ‘caddis-max’) was compared with the same matrix in modified form (called ‘caddis-mod’). This modified matrix was constructed as follows: the unidentified taxa were deleted from the analyses when they represented a small proportion of the sample, and most individuals were identified to species. In contrast, when most of the individuals remained unidentified because they were too small or too young or for taxonomical reasons, all individuals were clumped to genus or family level. Both matrices, caddis-max and caddis-mod, were compared using Mantel’s standardised correlation coefficient (r_M) tested by random permutations (999 runs) (Mantel, 1967).

The historical data matrix

To assess the effect of history on caddisfly distribution, we studied the effect of the joining of the Eurasian and African plates in south-eastern Spain during the Tertiary. The basins located below the Segura River Basin correspond to the African plaque and the join zone (i.e. Baetic ranges and the Baetic–Riffian internal zones – Ribera, 2000). A dummy variable, with a value of one if the site was located in the Baetic–Riffian region (Almanzora, Aguas, Adra and Guadalfeo Basins) or in the transitional area (Segura Basin), and a value of 0 if it was located elsewhere (Besòs, Llobregat, Mijares,

Turia and Júcar Basins), was included in the multivariate analysis to characterise the historical phenomenon. At the scale of this study, the effect of glaciations was not assessed because the sampled area of Iberian Mediterranean coast was little affected and was a refuge for many taxa (Stewart & Lister, 2001).

The ecological data matrix

At each site, 29 environmental variables at different scales (i.e. basin, reach and bedform – Townsend *et al.*, 2003) were measured (Table 1). Basin variables included geological basin characteristics and drainage

Table 1 Variables measured and used in the analysis, grouped at three spatial scales: basin, reach, and bedform

Scale	Variable	Code	Description
Basin	% Siliceous basin	%Sil	Percentage of siliceous materials in basin from each site
	% Calcareous basin	%Cal	Percentage of calcareous materials in basin from each site
	% Sedimentary basin	%Sed	Percentage of sedimentary materials in basin from each site
Reach	Basin area	Basin-area	Basin area drained in each site (km ²)
	Altitude	Altitude	Altitude of each site (m a.s.l.)
	Stream order	Str-Ordre	Stream order at 1 : 250 000
	Channel width	Chan-width	Channel width: up to 1 m (1); from 1 to 10 m (2); over 10 m (3)
	Channel shape	Chan-shape	Channel shape according to the QBR field sheet (Munné <i>et al.</i> , 2003)
	Temporality	Tempo	Number of seasons that the river was dry: (1) none; (2) one season; (3) two seasons
	Discharge	Discharge	Water discharge (l s ⁻¹)
	pH	pH	Water pH
	Temperature	Tempe	Water temperature (°C)
	Conductivity	Conductivity	Water conductivity at 25 °C (mS cm ⁻¹)
	NH ₄ ⁺	NH ₄ ⁺	Concentration of NH ₄ ⁺ (mg L ⁻¹)
	N–NO ₂ ⁻	NO ₂ -	Concentration of N–NO ₂ ⁻ (mg L ⁻¹)
	P–PO ₄ ³⁻	PO ₄ 3-	Concentration of P–PO ₄ ³⁻ (mg L ⁻¹)
	IBMWP	IBMWP	Biological index for water quality (Alba-Tercedor & Pujante, 2000)
	IASPT	IASPT	Relationship between IBMWP and number of families
	Riparian Cover	Rip-Cove	Proportion of riparian area covered by trees and shrubs
	Riparian Structure	Rip-Stru	Proportion of the riparian vegetation composed of trees and shrubs separately
	Riparian quality	Rip-qual	Absence of introduced species, garbage and other human impact on riparian vegetation
	Channel quality	Chan-qua	Human impact altering channel form
	Shade	Shade	A score running from not shaded to completely shaded
Bedform	Embeddedness	Embed	Percentage of embeddedness in riffles or sedimentation in pools
	Riffles vs. pools	R/L	Frequency of riffles in sampling reach: distance between riffles/stream width
	Substrate composition	Substrat	Types and abundance of substrates: % boulders and stones, pebbles and gravels, sand or silt and clay
	Flow and depth regimes	Flow-depth	Number of classes present in sampling reach: slow-depth, slow-shallow, fast-depth and fast-shallow
	Heterogeneity elements	Hetero	Percentage of leaf litter, presence of wood and branches, tree roots or natural dams
	Instream vegetation	Inst-veg	Types and abundance of different instream vegetation formations: % of plocon, pecton and macrophytes

Codes for their use in Table 3 and Figs 2 and 3 are shown.

area. Reach variables included physical and chemical variables (see methods in Toro *et al.*, 2002), riparian characteristics (see Munné *et al.*, 2003) and the biological IBMWP index (see Alba-Tercedor & Pujante, 2000) and the IASPT values (the ratio between IBMWP value and the number of taxa). Finally, bedform variables referred to habitat condition at the sampling site, and were those measured in the IHF index (Indice de Hábitat Fluvial) for habitat diversity (see Pardo *et al.*, 2002). Variables were tested for autocorrelation using the non-parametric Spearman correlation coefficient. Because most of the variables had a non-normal distribution (after a Shapiro–Wilk test) and some of them were highly skewed (e.g. conductivity, nitrites, ammonium), they were log-transformed prior to being included in the multivariate analysis.

Statistical analyses

To determine the relative influence of historical and ecological factors, a Variance Partition was conducted (Bocard, Legendre & Drapeau, 1992). Several canonical correspondence analyses (CCA) and partial canonical correspondence analyses (pCCA) were performed: (1) a CCA with the historical variable; (2) a CCA with the ecological variables; and (3) a pCCA with environment as variable and history as a covariable; or (4) a pCCA with history as a variable and environment as a covariable. The sum of canonical eigenvalues of each analysis compared with the sum of all eigenvalues (i.e. inertia) was retained to calculate the relative influence of both factors. Because the ecological data matrix included samples collected during different seasons, the effect of seasonality (measured as four dummy variables: spring, summer, autumn, and winter) was tested with a CCA. The relationship of this matrix with environmental variables was extracted with a pCCA. Finally, non-explained variability was also calculated.

To decide whether to use a linear or a unimodal ordination method, the gradient length was measured using a detrended correspondence analysis (DCA), detrending-by-segments and non-linear re-scaling of axes. Results of this analysis indicated that the first DCA axis has a gradient length of 5.70 standard deviation units, justifying the use of unimodal response models (Lepš & Šmilauer, 2003). Therefore, an indirect analysis of correspondence analysis (CA) using biological data was performed. To detect how

environmental variables determine organisms' patterns, direct ordination was used. A pCCA was performed instead of a simple CCA to extract the influence of temporal patterns, because significant differences between seasons in caddisfly communities were found after an Multi-Response Permutation Procedures (MRPP) test ($A = 0.003$; $P = 0.022$). Most significant environmental variables were selected by forward selection method and rare species were down-weighted to avoid bias in the final results in CA and pCCA analysis. Canonical axes obtained with pCCA ordination were tested for significance using a Monte Carlo permutation test (199 runs). Eigenvalues of CA were kept and compared with the ones obtained in pCCA to show whether the measured environmental variables used in the pCCA reflect the gradient shown by CA. Finally, Pearson correlations were calculated between the projections of samples in CA and pCCA axes, to decide the number of axes to be interpreted. The CANOCO program was used to compute all ordinations (ter Braak & Šmilauer, 1998).

To clarify the meaning of the canonical axes and to grasp which factors explained caddisfly distributions, correlations between the canonical axes and environmental variables were analysed. Several groups of samples with various caddisfly assemblages explained by different environmental variables were differentiated in the pCCA plots. To corroborate these groups in statistical terms, samples were clustered using their projections onto canonical axes with a k-means method in the SPSS program (SPSS, 1999). A stepwise discriminant analysis using the Wilks' Lambda method was used to select the most significant environmental variables that defined each k-means group in a hierarchical way. Finally, an Indicator value (IndVal) method (Dufrêne & Legendre, 1997) with 9999 runs determined which caddisfly taxa were the most representative of these k-means groups. The PCORD program (McCune & Mefford, 1999) was used to carry out this analysis.

Results

Taxa distribution

There was a high and significant correlation between the caddis-max and the caddis-mod matrix ($r_M = 0.9822$ and $P = 0.0101$), which indicated that similar information was provided by both matrices. Thus, the caddis-mod matrix was used to simplify the analysis

and the interpretation of results. Although this may result in a loss of historical and ecological signal, the caddis-mod matrix is more reliable because it rules out problems relating to taxonomy and a variety of organism sizes in one sample. A total of 69 taxa were obtained, although species richness was somewhat higher, because we grouped some species at the generic level (e.g. *Sericostoma*, *Wormaldia*). The Segura basin had the highest taxon richness (42), whereas in the Aguas and Mijares Basins fewer than 20 taxa were found. The rest of the basins had intermediate values of taxon richness (between 20 and 32 taxa).

Table 2 gives the maximum abundance of each caddisfly taxon in each basin and their frequency of appearance. The number of rare taxa found was high, with 73.9% in fewer than 5% of samples and only 10 taxa found in more than 10% of samples. *Hydropsyche* gr. *pellucidula* and *Hydroptila* sp. were found in all sampled basins. Many caddisflies were absent from only one basin (e.g. *Agapetus* sp., *Chimarra marginata* Stephens, *Mesophylax aspersus* (Rambur), *Hydropsyche exocellata* Dufour, *Polycentropus* sp. and *Tinodes* sp.). 26% of taxa were absent from northern basins, whereas 22% were absent from southern ones. The Segura Basin displayed a mixture of taxa widely distributed in northern and southern basins, such as *Hydropsyche siltalai* Döhler, *H. gr. instabilis*, *Chaetopteryx* sp., *Rhyacophila nevada* Schmid, *Hydropsyche infernalis* Schmid, *Setodes argentipunctellus* McLachlan and *Micrasema moestum* (Hagen). Some affinities were observed between the most northern and southern basins (Besòs/Llobregat and Adra/Guadalejo, respectively), which shared species such as *Potamophylax latipennis* (Curtis). In general, from the information of González *et al.* (1992), most of the caddisflies collected in the area had a wider distribution than just the Iberian Peninsula (W in Table 2). However, these species were more dominant in northern and central basins, whereas southern basins had species shared with North Africa (N in Table 2) (e.g. *Rhyacophila munda* McLachlan, *S. argentipunctellus*, *M. moestum*, *Cyrtus* cf. *montserrati*) and endemic species only distributed in the Baetic cordillera (Es) (e.g. *R. nevada*, *Hydropsyche fontinalis* Zamora-Muñoz & González, *H. infernalis*).

Relative effect of historical and environmental factors

The results of the Variance Partition analysis indicated that environmental variables accounted

for 21% of the variation in caddisfly distribution, whereas history accounted for only 3.4%. Interaction between the two groups of factors was weak, accounting for only 0.3% of total variability, which indicated that 20.7% was purely ecology and 3.1% was purely history. In addition, seasonality only explained 0.93% of all caddisfly distribution, and the interaction of seasonality and environmental variables accounted for 0.2%. Non-explained variability was 75.17%.

As environmental variables correlated poorly with each other when ρ -Spearman coefficients between pairs of variables were calculated (not shown), none of them was excluded from the analysis. Canonical axes from CA and pCCA analysis showed a low percentage of caddisfly variability in samples, with 7.4% in the first CA-axis and 5.8% in the first pCCA-axis. However, the results suggested that a high percentage of all caddisfly variability shown in the first CA-axis was explained by environmental variables (comparison of eigenvalues for each axis in CA versus pCCA: 78.3% for the first axis, 42.3% for the second, 33.8% for the third and 31.6% for the fourth). This indicates that the variables measured are among the factors that explain caddisfly distribution. Monte Carlo permutation tests (199 permutations) indicated that all canonical axes are significant in relation to the set of variables used ($F = 3.715$, $P < 0.010$). Some variables (i.e. nitrite, phosphate, discharge, temperature, channel shape, riparian quality, and riparian cover) were not significant (after applying the forward selection method in the CANOCO program) and so were not used in the analysis. Only the first three canonical axes were used because these showed the closest and most significant correlations between the CA and pCCA axes ($r = 0.979$ for the first, $r = 0.497$ for the second, $r = 0.578$ for the third and $r = 0.291$ for the fourth; all at $P < 0.050$).

The first axis (X_1) differentiated samples in good ecological conditions located in headwaters at high altitude from samples of lowland reaches with higher conductivity (Table 3 and Fig. 2). The second axis was positively related to ammonium, basin area, stream order, channel width and others, whereas it was negatively associated with high values of riparian and biological quality, several bedform characteristics and stream temporality (Table 3 and Fig. 2). Finally, the third axis was associated positively with stream order and sedimentary geology and negatively with ripar-

Table 2 Maximum abundance of each taxon recorded in each basin (1 = from one to three individuals; 2 = from four to 10; 3 = from 11 to 100; and 4 = over 100). Taxa are ordered according to their exclusivity from northern to southern basins.

Taxa	Distribution	% Occurrence	B	L	M	T	J	SE	AL	AG	AD	G
<i>Glyptotaelius pellucidulus</i>	W	0.8	2	0	0	0	0	0	0	0	0	0
<i>Synagapetus</i> sp.	–	0.8	3	0	0	0	0	0	0	0	0	0
<i>Odontocerum albicorne</i>	W	1.1	2	1	0	0	0	0	0	0	0	0
<i>Beraea maurus</i>	W	0.5	1	1	0	0	0	0	0	0	0	0
<i>Rhyacophila</i> gr. <i>tristis</i>	W	1.9	1	1	0	0	0	0	0	0	0	0
<i>Hydropsyche dinarica</i>	W	1.6	0	3	0	0	0	0	0	0	0	0
<i>Rhyacophila fasciata denticulata</i>	W	0.3	0	2	0	0	0	0	0	0	0	0
<i>Rhyacophila relicta</i>	Ep	0.5	0	1	0	0	0	0	0	0	0	0
<i>Allotrichia pallicornis</i>	W	0.5	3	0	0	0	2	0	0	0	0	0
<i>Psychomyia pusilla</i>	W	0.5	0	0	0	0	2	0	0	0	0	0
<i>Halesus radiatus</i>	W	2.9	2	1	2	2	3	0	0	0	0	0
<i>Wormaldia</i> sp.	–	1.1	3	0	0	1	1	0	0	0	0	0
<i>Rhyacophila dorsalis</i>	W	6.1	1	3	2	2	1	0	0	0	0	0
<i>Potamophylax cingulatus</i>	W	1.9	2	3	0	0	2	0	0	0	0	0
<i>Ecnomus</i> sp.	–	0.5	0	2	0	1	0	0	0	0	0	0
<i>Mystacides azurea</i>	W	2.9	2	2	2	1	1	2	0	0	0	0
<i>Chaetopteryx</i> sp.	–	1.9	1	1	0	2	1	1	0	0	0	0
<i>Lype reducta</i>	W	0.5	1	0	0	0	0	1	0	0	0	0
<i>Tinodes waeneri</i>	W	1.1	1	0	0	0	0	1	0	0	0	0
<i>Hydropsyche siltalai</i>	W	4.3	4	4	0	0	2	1	0	0	0	0
<i>Halesus digitatus</i>	W	0.8	2	1	0	0	0	0	1	0	0	0
<i>Stenophylax</i> sp.	–	2.6	1	0	0	0	1	3	1	0	0	0
<i>Limnephilus</i> sp.	–	6.6	4	2	3	2	3	0	0	1	0	0
<i>Hydropsyche</i> gr. <i>instabilis</i>	?	2.9	0	1	1	0	3	3	0	0	0	0
<i>Hydropsyche bulbifera</i>	W	1.3	0	0	2	0	0	3	0	0	0	0
<i>Hydropsyche brevis</i>	Ep	5.6	0	0	1	2	3	3	0	0	0	0
<i>Ithytrichia</i> sp.	–	2.4	0	0	0	2	2	1	0	0	0	0
<i>Ceraclea sobradieli</i>	Ep	1.1	0	0	0	0	1	1	0	0	0	0
<i>Cheumatopsyche lepida</i>	W	2.4	0	0	0	0	3	2	0	0	0	0
<i>Psychomyia</i> cf. <i>ctenophora</i>	Ep	0.3	0	0	0	0	1	0	0	0	0	0
<i>Allogamus</i> sp.	–	4	0	1	0	1	0	3	3	0	0	0
<i>Halesus tessellatus</i>	W	4.3	2	0	0	1	0	1	0	0	3	2
<i>Rhyacophila meridionalis</i>	W	2.7	2	3	0	0	0	2	2	0	2	0
<i>Agapetus</i> sp.	–	8.2	3	0	1	1	3	3	1	3	3	3
<i>Potamophylax latipennis</i>	W	4.3	1	3	0	0	0	0	0	0	3	2
<i>Polycentropus</i> sp.	–	15.4	3	3	0	2	2	3	3	2	2	2
<i>Sericostoma</i> sp.	–	10.4	2	3	0	1	2	3	0	0	1	2
<i>Plectrocnemia</i> sp.	–	4	1	2	0	0	1	2	0	0	1	1
<i>Philopotamus montanus</i>	W	2.9	3	1	0	0	0	1	0	0	1	2
<i>Hydropsyche instabilis</i>	W	19.4	3	2	3	3	0	3	3	0	3	3
<i>Hydropsyche exocellata</i>	W	27.4	4	4	3	3	4	2	3	0	3	1
<i>Mesophylax aspersus</i>	W	10.9	3	3	2	3	1	3	2	0	1	2
<i>Tinodes</i> sp.	–	8	1	1	1	1	1	1	2	1	0	2
<i>Hydropsyche</i> gr. <i>pellucidula</i>	W	31.9	3	3	3	3	3	3	2	3	3	3
<i>Hydroptila</i> sp.	–	43.6	3	4	2	3	4	3	3	3	2	2
<i>Chimarra marginata</i>	W	13.6	0	4	3	1	4	1	1	3	2	2
<i>Rhyacophila munda</i>	N	10.4	0	0	2	1	1	3	2	2	2	3
<i>Setodes argentipunctellus</i>	N	5.3	0	0	0	1	2	3	3	3	2	1
<i>Lasiocephala basalis</i>	W	9.3	0	0	0	1	3	2	0	0	1	3
<i>Orthotrichia angustella</i>	W	1.3	0	0	0	0	3	0	0	0	0	0
<i>Hydropsyche fontinalis</i>	Es	0.3	0	0	0	0	0	3	0	0	0	0
<i>Drusus bolivari</i>	W	1.3	0	0	0	0	0	2	0	0	0	0
<i>Metatype fragilis</i>	W	0.5	0	0	0	0	0	1	0	0	0	0
<i>Rhyacophila</i> cf. <i>munda</i>	N	0.5	0	0	0	0	0	1	0	0	0	0
<i>Micrasema minimum</i>	W	0.3	0	0	0	0	0	1	0	0	0	0

Table 2 (Continued)

<i>Adicella</i> sp.	–	0.8	0	0	0	0	0	1	0	0	0	1
<i>Calamoceras marsupus</i>	W	0.3	0	0	0	0	0	1	0	0	0	0
<i>Cyrrnus</i> cf. <i>montserrati</i>	N	0.5	0	0	0	0	0	1	0	0	0	0
<i>Oxyethira</i> sp.	–	1.6	0	0	0	0	0	2	2	3	0	0
<i>Micrasema moestum</i>	N	4.7	0	0	0	0	0	3	4	0	0	1
<i>Hydropsyche infernalis</i>	Es	4.3	0	0	0	0	0	3	1	1	2	2
<i>Rhyacophila nevada</i>	Es	10.9	0	0	0	0	0	3	3	0	1	2
<i>Athripsodes</i> sp.	–	7.2	0	0	0	0	0	0	3	1	1	2
<i>Anomalopterygella chauviniana</i>	W	2.9	0	0	0	0	0	0	0	0	1	2
<i>Rhyacophila</i> cf. <i>occidentalis</i>	W	2.1	0	0	0	0	0	0	0	0	1	2
<i>Glossosoma</i> sp.	W	0.5	0	0	0	0	0	0	0	0	0	1
<i>Hydropsyche tibialis</i>	Ep	0.3	0	0	0	0	0	0	0	0	0	1
<i>Brachycentrus</i> (O.) <i>maculatum</i>	W	0.5	0	0	0	0	0	0	0	0	0	1
<i>Micrasema longulum</i>	W	1.6	0	0	0	0	0	0	0	0	0	2

B, Besòs; L, Llobregat; M, Mijares; T, Turia; J, Júcar; S, Segura; AL, Almanzora; AG, Aguas; AD, Adra; G, Guadalfeo.

The distribution category of the species was taken from González *et al.* (1992), as follows:

W, species with a wider distribution than the Iberian Peninsula, extending North of the Pyrenees and reaching or not North Africa; E, Iberian endemic species (Es indicates exclusivity from the southern areas and Ep indicates endemicity but with a wider extension in the Iberian Peninsula); and N, species present in south-western Europe and North Africa.

? indicates distribution not known.

The percentage of taxa occurrence is also shown. Unidentified individuals of *Rhyacophila* sp. and *Hydropsyche* sp. were omitted.

Table 3 Pearson correlations (*r*) between environmental variables and the first three canonical axes in pCCA

Variable code	X ₁ -pCCA	X ₂ -pCCA	X ₃ -pCCA
Tempo	-0.017	-0.268**	-0.017
NH4+	0.322**	0.386**	-0.080
pH	-0.042	0.106*	0.025
Conductivity	0.641**	-0.035	0.062
IBWMP	-0.490**	-0.478**	-0.013
IASPT	-0.596**	-0.193**	-0.108
%Sil	-0.382**	-0.057	0.074
%Cal	0.454**	0.185**	-0.038
%Sed	0.395**	-0.018	0.326**
Basin-area	0.597**	0.370**	0.022
Altitude	-0.561**	-0.114*	0.055
Str-ordre	0.366**	0.227**	0.302**
Chan-width	0.176**	0.438**	0.019
Embed	-0.109*	0.057	-0.237**
R/L	-0.165**	0.240**	-0.235**
Substrat	-0.112*	0.211**	0.146**
Flow-depth	-0.227**	0.113*	-0.192**
Shade	-0.390**	-0.182**	-0.151**
Hetero	-0.416**	-0.157**	-0.098
Inst-veg	-0.089	0.125*	-0.208**
Rip-stru	-0.322**	-0.299**	-0.073
Chan-qua	-0.403**	-0.203**	-0.001

For explanation of codes, see Table 1.

P* < 0.05; *P* < 0.01.

ian and bedform characteristics (Table 3 and Fig. 2). Results from the pCCA analysis enabled five groups of sites to be identified by eye. This was corroborated

by applying a k-means cluster to all samples using the five predefined groups (Fig. 2a and 2b): (1) headwater samples at medium altitudes with high riparian structure and biological quality (bottom area of Fig. 2b); (2) headwater sites at high altitude, diverse bedform characteristics and siliceous basins (top-left from Fig. 2a); (3) low-altitude and temporary sedimentary samples with high conductivity (top-left in Fig. 2b); (4) middle parts of river sites located at medium altitudes (central area of second axis from Fig. 2b); and (5) low-altitude samples located in lowland reaches from medium to large rivers with poor biological and chemical quality (top-right from Fig. 2a).

A mix of basin (i.e. geology, basin area), reach (i.e. channel width, stream order, conductivity, riparian structure) and bedform (i.e. riffles vs. pools, substrate diversity, heterogeneity elements) variables significantly differed between k-means groups in a discriminant analysis (Fig. 3). Overall, our analysis revealed that the five groups of samples differed in geology and longitudinal zonation related variables. Thus, group 1 corresponded to calcareous/siliceous headwaters; group 2 to siliceous headwaters; group 3 to sedimentary-marls middle reaches (rambla type); group 4 to calcareous/sedimentary middle reaches; and group 5 to calcareous/sedimentary lowland rivers.

Fig. 2 pCCA plots representing sites and environmental variables on first (X_1) and second (X_2) axes on the left (a and c), and second (X_2) and third (X_3) on the right (b and d). Samples are labelled according to the results from the k-means analysis: 1k, 2k, 3k, 4k and 5k are the different k-means groups and include 39, 53, 97, 102 and 80 samples, respectively. Ellipses represent the extension of each group.

Caddisfly assemblages

The results from the IndVal analysis to detect caddisfly assemblages representative of each of the five k-means groups are shown in Table 4. Because of the low abundance and frequency of occurrence of many caddisflies, few taxa had indicator values higher than 25 (indicating that the species is present in at least 50% of one site group and that its relative abundance in that group reaches at least 50% – Dufrène & Legendre, 1997), although many were significant for each group ($P < 0.01$). Overall, species with the highest indicator value in each group were those with higher than 5% appearance in all samples, whereas rare species had low indicator value (Tables 2 and 4). Thus, *Sericostoma* sp. and *H. siltalai* were indicator taxa

from calcareous/siliceous headwaters located at medium altitude from northern basins (group 1), among other significant taxa. Some caddisflies characteristics of group 1 were shared by siliceous headwaters (group 2). Species such as *M. aspersus*, *R. munda*, *H. infernalis*, or *S. argentipunctellus* came solely from more sedimentary marl-type basins. Midstream reaches with a dominant calcareous geology (group 4) were significantly composed of *C. marginata*, *Hydropsyche brevis* Mosely, and *H. gr. pellucidula* among others. Other species presented in this group 4, such as *Rhyacophila dorsalis* (Curtis) and *Limnephilus* sp. (*guadarramicus* type), were also characteristic of headwaters with similar geology (group 1). In group 5, *H. exocellata* was the only significant indicator and occurs together with other exclusive but not

Fig. 3 Results from the discriminant analysis, with the most significant variables between k-groups. Mean and confidence intervals at 95% of log-transformed variables are shown. Plots are grouped according to the spatial scale of the variable (i.e. basin, reach and bedform). Inside each group, plots are ordered according to their weight in discriminant analysis (i.e. their Wilk's Lambda values).

Table 4 Indicator value results for each group of samples separately

	Indicator value	P-value
Calcareous/siliceous headwaters (group 1)		
<i>Sericostoma</i> sp.	44.1	0.001
<i>Hydropsyche siltalai</i>	35.4	0.001
<i>Limnephilus (guadarramicus)</i> sp.	22.1	0.001
<i>Halesus radiatus</i>	22	0.001
<i>Rhyacophila dorsalis</i>	20	0.001
<i>Potamophylax latipennis</i>	18.6	0.001
<i>Potamophylax cingulatus</i>	17.9	0.001
<i>Hydropsyche dinarica</i>	12.2	0.001
<i>Chaetopteryx</i> sp.	12	0.001
<i>Wormaldia</i> sp.	10.3	0.001
<i>Polycentropus</i> sp.	24.7	0.002
<i>Philopotamus montanus</i>	11.6	0.002
<i>Synagapetus</i> sp.	7.7	0.002
<i>Rhyacophila relictia</i>	5.1	0.01
<i>Mystacides azurea</i>	8.5	0.017
<i>Halesus digitatus</i>	4.9	0.019
<i>Plectrocnemia</i> sp.	10	0.02
<i>Rhyacophila meridionalis</i>	6.5	0.021
<i>Glyptotaelius pellucidus</i>	4.6	0.025
<i>Rhyacophila</i> gr. <i>tristis</i>	6.7	0.033
Siliceous headwaters (group 2)		
<i>Hydropsyche instabilis</i>	88.2	0.001
<i>Lasiocephala basalis</i>	58.8	0.001
<i>Rhyacophila nevada</i>	47.9	0.001
<i>Athripsodes</i> sp.	39.6	0.001
<i>Micrasema moestum</i>	21.7	0.001
<i>Halesus tessellatus</i>	21.4	0.001
<i>Rhyacophila</i> cf. <i>occidentalis</i>	14.8	0.001
<i>Anomalopterygella chauviniana</i>	11.1	0.001
<i>Micrasema longulum</i>	11.1	0.001
<i>Philopotamus montanus</i>	9.3	0.001
<i>Potamophylax latipennis</i>	10.5	0.005
<i>Sericostoma</i> sp.	14.6	0.008
<i>Glossosoma</i> sp.	3.7	0.014
<i>Brachycentrus</i> (O.) <i>maculatum</i>	3.7	0.028
<i>Rhyacophila meridionalis</i>	5.3	0.041
Sedimentary-marls midstreams (group 3)		
<i>Hydropsyche</i> gr. <i>pellucidula</i>	48.4	0.001
<i>Agapetus</i> sp.	24	0.001
<i>Mesophylax aspersus</i>	23.5	0.001
<i>Rhyacophila munda</i>	21	0.001
<i>Hydropsyche</i> sp.	12.8	0.001
<i>Hydropsyche infernalis</i>	11.5	0.001
<i>Setodes argentipectus</i>	11.4	0.001
Calcareous/sedimentary midstreams (group 4)		
<i>Hydroptila</i> sp.	41.9	0.001
<i>Hydropsyche</i> gr. <i>pellucidula</i>	27.1	0.001
<i>Chimarra marginata</i>	24	0.001
<i>Hydropsyche brevis</i>	15.2	0.001
<i>Limnephilus (guadarramicus)</i> sp.	10.5	0.001
<i>Cheumatopsyche lepida</i>	6.3	0.002
<i>Orthotrichia angustella</i>	4.9	0.003
<i>Rhyacophila</i> sp.	11.9	0.004

Table 4 (Continued)

	Indicator value	P-value
<i>Hydropsyche</i> gr. <i>instabilis</i>	6.7	0.004
<i>Polycentropus</i> sp.	14.4	0.017
<i>Rhyacophila dorsalis</i>	7	0.033
<i>Allogamus</i> sp.	5.1	0.034
<i>Ithytrichia</i> sp.	4	0.035
<i>Hydropsyche bulbifera</i>	2.6	0.048
Calcareous/sedimentary lowland rivers (group 5)		
<i>Hydropsyche exocellata</i>	95.6	0.001

Indicator values and the significance of the significant taxa in each group are shown.

Taxa are ordered according to their *P*-values.

significant species [*Ceraclea sobradieli* (Navás) and *Allotrichia pallicornis* (Eaton)].

Discussion

Current species distributions are the result of the interplay of several multi-scale factors in a spatial-temporal framework (Poff, 1997). Although this assumption entails a mixture of historical and ecological factors, historical events have been widely neglected in ecological studies. This is related to the difficulties of measuring them and to the lack of a complete phylogeny and phylogeography for the species (Ribera, 2000). Their relative weight depends on the extent of the geographical region used and the presence of strong environmental gradients (see Motzkin *et al.*, 2002). Our study examined caddisfly distributions over a large area in the Iberian Peninsula with high environmental variability (Robles *et al.*, 2002) and showed that the effect of historical aspects was not negligible.

Influence of historical events

Several authors working on aquatic invertebrates have pointed out that the southern European basins possess many species that are also distributed in North Africa (Margalef, 1983; González, García de Jalón & Terra, 1987; Bennis, Sáinz-Cantero & Ouarour, 2001; Ruiz, Salamanca-Ocaña & Ferreras-Romero, 2001; Luzón-Ortega, 2002). In some cases, a greater degree of similarity was found between the South of the Iberian Peninsula and North Africa than between the South of Iberia and more northern areas (Sáinz-Cantero & Aceituno-Castro, 1997; Sáinz-Cantero, Garrido &

Valladares, 1997; Ribera, 2000). The results of our study add to previous knowledge that caddisfly species composition in Mediterranean basins shifts from a dominance of Palearctic species in northern basins to an increasing presence of North African and endemic species in southern basins, with the Segura Basin's mix of species making it the richest of all. Vascular plant records from the Segura region also indicate that it is one of the most diverse regions in the Iberian Peninsula (Alcaraz *et al.*, 2000a,b). Similarly, studying aquatic Coleoptera and Heteroptera in the Segura Basin area, Moreno *et al.* (1997) noticed high richness of taxa with different biogeographical origins. Therefore, considerable evidence indicates the importance of historical factors that occurred at the coming together of Southern Europe and North Africa in explaining terrestrial and aquatic species distributions.

In a study comparing the richness of freshwater fishes in Western Europe and North America, Oberdorff, Hugueny & Guégan (1997) found that the distance from each river to the larger refuge area (a variable that is related to Pleistocene glaciation events) was significant, but explained only 1% of variance. Our study shows that history itself accounts for up to 3.1% of all variability in caddisfly distributions in the Iberian Mediterranean area. However, despite the relative importance of historical factors and the large scale used in our study, ecological variables better explained caddisfly distribution. There are three possible explanations: (1) contemporary species patterns may have faded with time, because the historical event we are considering occurred long ago and macroinvertebrates, especially many caddisflies, show high dispersion and colonisation capacities (Sheldon, 1984); (2) the effect of history could be masked by the strong environmental gradient in the area (see Robles *et al.*, 2002); and (3) some historical events may influence ecological variables, for example geology. However, although basin geology is related to paleogeographic origin, the result is usually a mixture of calcareous, siliceous and sedimentary materials. Thus, with the environmental variables used to measure basins' geological composition, we mostly distinguished between materials and not between regions. In addition, most of these environmental factors interact weakly with the historical event in explaining caddisfly distribution, as the fact that only 0.3% of variance is explained by the environment–history interaction shows.

Influence of ecological factors

Overall, our results indicated that Trichoptera on the Iberian Mediterranean coast were organised according to a set of environmental variables acting at different scales: basin, reach, and bedform characteristics. Combinations of all these significant variables resulted in five groups of sites with their corresponding caddisfly assemblages, which could be explained mainly by geology and longitudinal zonation. All basin variables but only half of the reach and bedform variables were significant in the discriminant analysis. In a study analysing the influence of basin, reach and bedform variables on macroinvertebrates, Townsend *et al.* (2003) found that large-scale variables were more important than local variables in explaining macroinvertebrate composition in a New Zealand river. In fact, the relative influence of large-scale variables compared with local ones depends on the range of human-modified and natural environmental conditions, the area of study and the predictor used to measure macroinvertebrate communities (e.g. assemblage attributes, relative abundance or presence/absence) (Weigel *et al.*, 2003).

Geology has been seen as an important factor in caddisfly patterns and diversity in other areas (e.g. in South Africa – de Moor, 1992), as it was in our case. However, some caddisflies seem unaffected by geology and were more dependent on stream longitudinal zonation. For example, *P. latipennis*, *Hydropsyche instabilis* (Curtis), *Sericostoma* sp., *Philopotamus montanus* (Donovan) and *Rhyacophila meridionalis* Pictet were shared between siliceous-calcareous headwaters (Legier & Talin, 1973; Viedma & García de Jalón, 1980; Zamora-Muñoz, Picazo & Alba-Tercedor, 1997); and *R. munda*, presented in sedimentary marls in our study area, was found in siliceous basins in other studies of the Iberian Peninsula (Viedma & García de Jalón, 1980; Ruiz *et al.*, 2001).

Longitudinal zonation in streams has been related to slope and bed stability, water temperature and current velocity, along with some other characteristics of stream hydraulics (Statzner & Higler, 1986). Several studies have reported changes in macroinvertebrate composition downstream, associated with altitude, stream order and channel width (Corkum, 1989; Marchant *et al.*, 1995; Wiberg-Larsen *et al.*, 2000). Marchant *et al.* (1995) suggested that altitude affects macroinvertebrates indirectly by changing other

environmental factors. In our study, altitude, channel width, stream order, and their related variables such as conductivity, macroinvertebrate community composition, riparian structure, and heterogeneity elements were more important than temperature, discharge or chemical parameters for explaining longitudinal zonation in Trichoptera.

Effects of rare species

Although caddisfly classification was mainly defined by geology and longitudinal zonation, several significant rare taxa in a group could explain peculiarities inside that group that were not explained by common species. For example, the significant presence of shredders and woody-cased caddisflies in group 1 [*Halesus* sp., *Chaetopteryx* sp., *Glyptotaelius pellucidus* (Retzius) and *Potamophylax* spp.] might characterise this group with a higher riparian structure than others in which these species were not significant. Similarly, in midstream reaches of group 4, the best indicator species jointly with those with significant but low indicator values [*Cheumatopsyche lepida* (Pictet) or *R. dorsalis*] distinguished different conditions of water quality because the species have differing degrees of tolerance to pollution (Bonada *et al.*, 2004b). In this study, other local factors such as ephemerality [one important characteristic of Mediterranean climate rivers – Gasith & Resh (1999) – not significant in our study] were associated with several species in the pCCA, such as *G. pellucidus* in group 1 or *S. argenti-punctellus* and *M. aspersus* in group 3, but at the same time these species were mixed with other species associated with perennial streams, such as *Hydropsyche dinarica* Marinkovic–Gospodnetic (Bonada *et al.*, 2004a) or *H. infernalis* (Ruiz *et al.*, 2001). These trends shown by rare species within the main classification suggest that they may respond to local and subtle factors particular to each group. Cao, Larsen & Thorne (2001) based this suggestion on a literature review, but its application to bioassessment was questioned by Marchant (2002).

Although not all organisms were classified at the species level, a great number of rare taxa were found in this study. Rare taxa are reported in a high proportion in most stream macroinvertebrate studies (Lenat & Resh, 2001). However, although our study included samples collected over four seasons, on calculating the percentage of rare species for each

season, the levels we found were much higher (a mean of about 12% higher) than those found in literature dealing with a large set of sites (Wiberg-Larsen *et al.*, 2000; Boyero, 2003). However, a large number of rare taxa may be possible in Mediterranean fauna because of the high diversity and endemism recorded there, making the area distinctive in biogeographical terms and one of the biodiversity hotspots of the world (Balletto & Casale, 1991; Cowling *et al.*, 1996; Blondel & Aronson, 1999; Myers *et al.*, 2000). In fact, the Iberian Peninsula hosts more caddisfly species than any other part of Europe (390 species in the Iberian Peninsula – González, 2003 – in comparison with, for example, the 198 recorded in the British Isles – Wallace, Wallace & Philipson, 1990; Edington & Hildrew, 1995), but has similar numbers to other countries around the Mediterranean Sea Basin (e.g. Italy, with 381 species – Cianficconi, 2002). However, although Austin & Greig-Smith (1968) found that the percentage of variability explained in principal components analysis dropped on increasing the number of rare taxa included, the numerous rare taxa found in our study did not imply a lower percentage of explained variability by measured environmental factors than in other studies (e.g. 34% of explained variability in Aguiar, Ferreira & Pinto, 2002). Furthermore, explained variability was higher than the values reported by Møller & Jennions (2002) (but see Peek *et al.*, 2003) in a meta-analysis study using published data from many different sources, in which it was found that the mean amount of variance explained by the factors used was 2.51–5.42%. This would imply that, in spite of the high number of taxa found, they respond to measured variables. Thus, studies involving many rare taxa should include as many environmental variables as possible to ensure good explanation of species variability, since the relationship between rare species and environmental factors is difficult to characterise (Marchant, 2002). In addition, factors such as interactions between organisms, dispersal abilities, or chance, are examples of factors not considered in our study that could reduce the amount of unexplained variability.

In summary, general patterns of caddisfly distribution in the Iberian Mediterranean area are driven by a trade-off between all measured descriptors acting at different scales. The historical factor occurring in the south of the Iberian Peninsula may be viewed as a significant filter for some species, but ecological

factors go further in explaining the current regional caddisfly distribution, as may be expected from ecosystems with high spatial and temporal variability like Mediterranean rivers. This variability is expressed by the presence of many rare species, which should be taken into account when attempting to preserve these highly diverse ecosystems.

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