

Detecting the structural and functional impacts of fine sediment on stream invertebrates

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ABSTRACT

Fine sediment is one of the major sources of stream physical and ecological impairment worldwide. We assessed the ecological effects of fine sediment in an otherwise undisturbed catchment (the Isábena, NE Spain). Using data from sites across the catchment we describe the spatial variability and nestedness of invertebrate assemblages and evaluate the effectiveness of compositional (taxon-based) and functional (trait-based) metrics for detecting sediment impacts on these assemblages.

Invertebrate assemblages were relatively taxon poor and had low densities in those locations with high fine sediment content. Assemblages showed significantly nested patterns, with those in sediment-rich locations consisting of a subset of those in locations with little fine sediment. A number of biological traits appeared to promote this nestedness, particularly those conferring resistance and resilience to fine sediment (polivoltinism, short live cycles and small body sizes).

Generalised Additive Models indicated that most metrics were able to detect ecological responses to sedimentation. Some taxon-based metrics (%EPT and evenness) performed less well, with values showing only a weak relationship with fine sediment. Results are consistent with previous studies which have highlighted the limitations of taxon-based metrics and suggest that indices of functional diversity are capable of detecting sediment related impairment.

Overall, the study suggests that fine sediment in the Isábena was selecting for specific life-history traits, and that this selection resulted in clear differences in assemblage structure across the catchment. The use of biological traits in studies of sediment related disturbance may help identify extinction-prone species (e.g. those with univoltine and/or long life-cycles), while trait-based monitoring and assessment metrics, because they reflect the ecological mechanisms underlying observed patterns, should prove useful to help guide management in catchments subjected to excessive fine sediment. More broadly, the study indicates that nestedness in assemblage structure can be driven by local habitat changes, and not only by large scale biogeographical processes.

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1. Introduction

Fine sediment (material <2 mm) has long been recognised as one of the major causes of impairment and ecological degradation affecting freshwaters globally (Hynes, 1970; USEPA, 2000; Harrison et al., 2007). While sediment plays an important functional role in river ecosystems, providing a substrate for biological and

chemical processes, excess quantities of fine material can cause a range of impacts (reviews by Graham, 1990; Peckarsky, 1984; Waters, 1995; Doeg and Koehn, 1994; Wood and Armitage, 1997; Bilotta and Brazier, 2008). Fine sediment accumulation smothers riverbed micro-topography and clogs interstitial space. It also affects bed stability, and hence disturbance regimes, as a function of changes in cohesion and entrainment thresholds (Hjulström, 1935; Grabowski et al., 2011). Such changes affect aquatic organisms across all trophic levels, through mechanisms that include: (1) modification of habitat availability and suitability for some taxa; (2) increases in turbidity and reduction of primary production; (3) impairment of feeding due to a reduction in the energetic value

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of periphyton and prey density; and (4) impairment of respiration due to low oxygen concentrations in sediment deposits.

Diversity indices or metrics have classically been implemented in ecology to identify and assess ecological impacts and evaluate the ecological integrity of aquatic ecosystems (Coleman et al., 1997; Pires et al., 2000). The most commonly used metric to detect changes and summarise assemblage composition has been taxonomic richness or the number of taxa found in a sample (α -diversity, Magurran, 1988). Other metrics also take into account the assemblage structure and incorporate a measure of the relative abundance of taxa, such as the Shannon index (Shannon and Weaver, 1949) and its associated evenness. While some studies have found these taxonomically based metrics to be useful for detecting anthropogenic disturbance (Robertson, 1981; Erman and Mahoney, 1983), others have reported a poor performance (Wood, 1977; Mouillot et al., 2006). A specific limitation is that they cannot necessarily differentiate the cause of the assemblage change or discriminate between natural and anthropogenic stressors (Reizopoulou et al., 1996; Mouillot et al., 2006; Gallardo et al., 2011).

To overcome the limitations of taxonomic-based methods, the incorporation of species biological traits into alternative metrics has increased in recent years. Biological traits refer to the functional attributes of the species (i.e. morphological, physiological, behavioural and ecological characteristics) and offer the main advantage that they can be applied broadly across biogeographic boundaries (McGill et al., 2006). Trait approaches are based on the habitat template model proposed by Southwood (1977), which states that habitat selects for characteristic life history traits through natural selection; species are expected to respond to environmental gradients and we should therefore find a correlation between species traits and habitat characteristics over an evolutionary time period (Poff et al., 2006). Trait patterns can be indicators of the source of impairment because anthropogenic disturbances will select for well adapted species and, as a result, only those possessing relevant adaptive traits are likely to remain (Statzner et al., 2004).

Trait-based approaches have proved useful in understanding environmental change and have been widely applied in biological monitoring and restoration (Gayraud et al., 2003; Statzner et al., 2007). Pollard and Yuan (2010) studied the consistency of the response of trait- and taxon-based measures and found a better performance of the former, regardless of the geographic location and spatial scale considered. Bêche and Resh (2007) also reported consistent patterns in trait diversity and richness over time, despite high taxonomic turnover.

In parallel with the use of trait-based metrics, the assessment of nestedness in species composition has developed to provide insights into the effects of environmental stressors on patterns of species loss. The term *nestedness* was first described for insular faunas to describe patterns of species composition within continental biotas and among isolated habitats such as islands and landscape fragments (Darlington, 1957; Patterson, 1987; Atmar and Patterson, 1993). Perfect nesting occurs where rare species are exclusive to species-rich locations, while reduced nesting occurs where rare species are distributed more evenly (Wright et al., 1998). Species distribution patterns in naturally fragmented habitats often exhibit nested patterns as a result of colonisation and extinction processes over long time scales, while they can also be a consequence of human disturbance and habitat alteration (Fernandez-Juricic, 2002).

Few studies have compared the sensitivity of taxonomic, trait-based and nestedness metrics to fine sediment impacts (Angradi, 1999; Relyea et al., 2000; Zweig and Rabeni, 2001). The limited published work has been contradictory. For example, Angradi (1999) found a weak correlation between taxonomic metrics and

deposited sediment, while Zweig and Rabeni (2001) reported a strong relationship between them. Studies have generally been based either on experimental sediment additions (Suren and Jowett, 2001; Vasconcelos and Melo, 2008; Larsen et al., 2011; Reid et al., 2011) or were carried out in catchments with a high human impact (Leana et al., 2001; Suren et al., 2005; Kreutzweiser et al., 2005), where sedimentation is often associated with multiple stressors (e.g. nutrients, pesticides, alteration of thermal regimes), which result in complex ecological responses and a difficulty in disentangling individual effects.

The present study aimed to assess evidence of patterns in the structure of invertebrate assemblages and functional traits related to fine sediment, and evaluate the extent to which a number of metrics were able to detect these patterns. It is based on data collected in the river Isábena (Central Pyrenees, NE Spain), where naturally high sediment transport rates occur as a result of the presence of highly erodible badland formations in some of its tributaries. Specific objectives of the paper are to (i) describe the invertebrate assemblages across the entire Isábena catchment and assess whether nested assemblages were associated with high sediment loads, (ii) examine the trait composition of assemblages to test whether sites impacted by high sediment loads show a distinct trait structure, and (iii) assess the ability of a set of taxonomic and trait-based metrics to detect the impacts of fine sediment on invertebrate assemblages.

2. Methods

2.1. Study area

The river Isábena is a mesoscale mountainous catchment located in the Central Pyrenees (NE Iberian Peninsula). It belongs to the Ebro basin and occupies an area of 445 km² (Fig. 1). The basin is characterised by a strong heterogeneity in relief, vegetation and soil characteristics, with elevations ranging from 450 m to 2720 m.a.s.l. in the northern parts. Woodland occupies the major part of the catchment, with agriculture (on floodplains) and urban areas comprising only 13% and 1% of its area, respectively. An assessment of the physical and chemical habitat conditions in the Isábena was undertaken by the Ebro Water Authorities (United Research Services – URS, 2002). Overall, the river was classified as largely unaffected by human activities, with more than 71% of the reaches they studied classified as having physical and chemical conditions that were “good” or “very good” and none classified as “bad” or “deficient”.

The hydrology and sediment dynamics of the Isábena have been described in numerous studies (e.g. Verdú, 2003; Francke et al., 2008; López-Tarazón et al., 2009, 2010). Hydrology is characterised by a rain-snow fed regime with flows showing a marked seasonality, although the river has never dried up within the period of record. Floods typically occur in spring as a result of rainstorms, which tend to be scarce in summer and variable in autumn and winter. Mean annual discharge at the basin outlet is 4.1 m³/s, with minimum flows (~0.20 m³/s) typically occurring in summer and maximum flows recorded during autumn (e.g. 290 m³/s on 9th November of 1966, 192 m³/s on 18th December 1997).

Miocene continental sediments (marls, sandstones and carbonates) make up the western and middle parts of the catchment, leading to the formation of badlands. Although they represent less than 1% of the total area of the basin, badland areas, being highly erodible, have proven to be the major source of sediment, contributing more than 95% of the annual sediment load of the catchment. In addition, these areas are very well connected to the drainage network, facilitating sediment delivery to the channel. As a consequence, suspended sediment concentrations (hereafter SSCs) show great variability (they can span five orders of magnitude

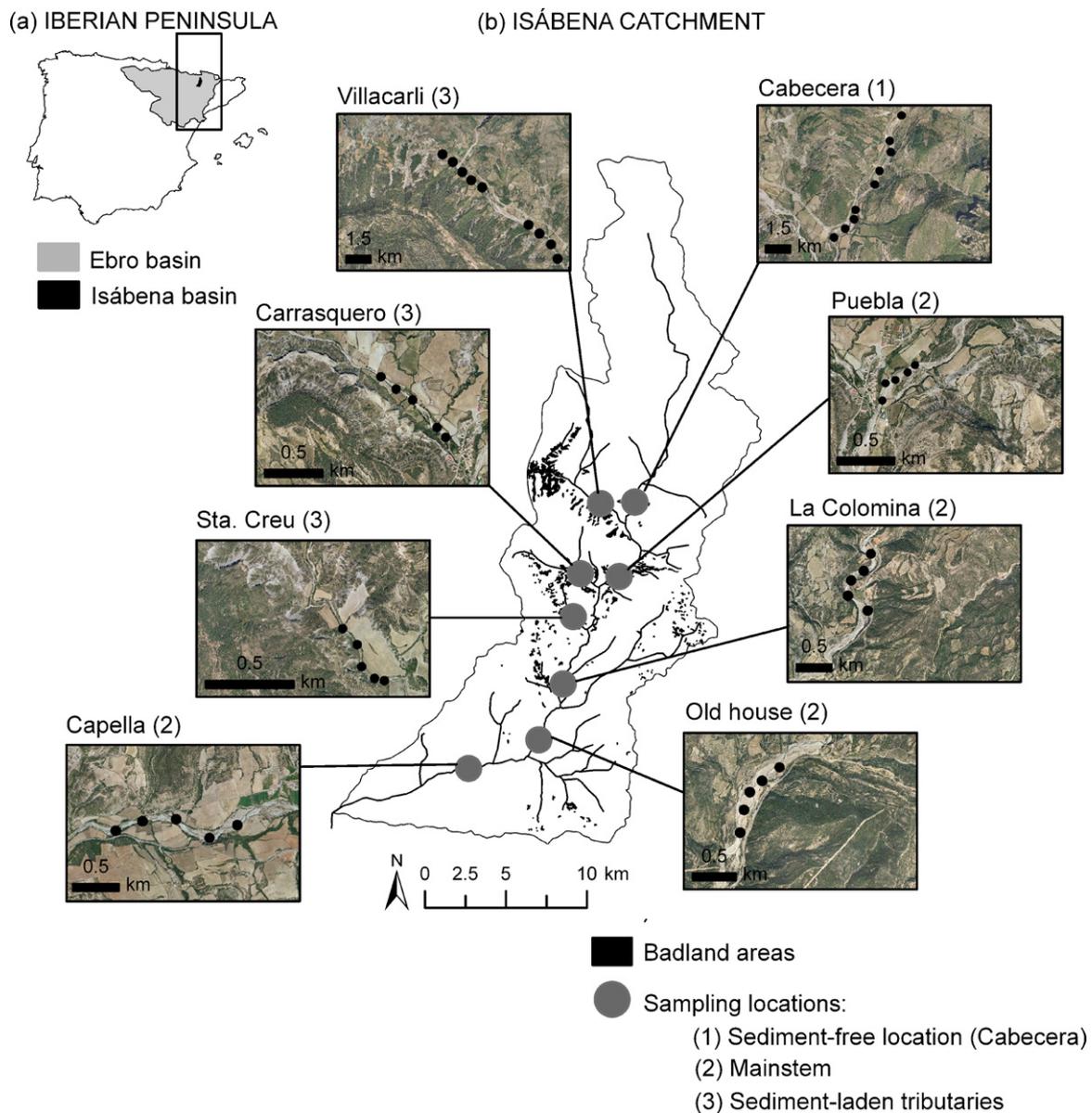


Fig. 1. Location of the Isábena catchment in the Iberian Peninsula (a) and sampling sites (b). Badlands are shown as black areas in the map.

for the same discharge) and may reach maximum instantaneous values above 300 g/l (López-Tarazón et al., 2009).

The relative location of badland areas gives rise to a wide range of sedimentary conditions along the river channel. In some headwater areas where badlands are virtually absent, fine sediment accumulation in the channel is minimum, whereas in areas with extensive badlands, it is extremely high. These contrasts, together with the fact that the river is not hydrologically regulated and shows limited human impact on landcover, make this catchment a suitable location for assessing the effects of fine sediment.

2.2. Sampling design

2.2.1. Sampling locations

In order to account for the spatial variability in both macroinvertebrate assemblage composition and fine sediment accumulation, eight reaches were selected across the Isábena (Fig. 1). One reach was located in the headwaters of the catchment (Cabecera) where badlands are virtually absent and thus represents an area free from fine sediment. Three reaches were located in the sediment-laden

tributaries in the western and northern parts of the catchment (Villacarli, Carrasquero and Sta. Creu). The other four reaches (Puebla, La Colomina, Old house and Capella) were located along the mainstem, to detect any downstream change in invertebrate assemblages associated with increasing distances from the sediment sources. To minimise inter-habitat variability, all reaches were pool-riffle morphologies, with all invertebrate samples being collected from riffles. In most reaches 5 samples were collected, with a sample taken from a randomly allocated point within each riffle. In two reaches (Cabecera and Villacarli), 10 samples were collected. This increased number was due to the fact that these two tributaries occupy a larger area than the others, provide the majority of the runoff and sediment to the catchment (Verdú, 2003) and, in the case of Cabecera, provides a reference free from fine sediment influences. Upstream catchment characteristics for each reach, as well as summary hydrologic information and suspended sediment concentrations, are given in Table 1. Sampling was completed under stable, base-flow conditions within 1 week (August 2010); which minimised sedimentary and geomorphic differences related to flow change.

Table 1

Summary information on study reaches. Landcover statistics were determined using GIS and are for the total area upstream from each reach. %Bad (percentage of badlands in the catchment), %Wood (percentage of catchment area occupied by badlands), %Agr (percentage of agriculture) and %NP (percentage of non-productive land, includes all those areas which are not under agriculture, e.g. urban areas).

Reach	Area (km ²)	%Bad	%Wood	%Agr	%NP	SSC ^a (g/l)	Vel ± SD (m ³ /s) ^b	Depth (m) ^b	Q (m ³ /s) ^c
Cabecera	146	<0.01	97.7	0.8	1.4	0.005	0.65 ± 0.02	0.15	4.1
Villacarli	40	6.7	81.2	4.3	14.5	0.007	0.61 ± 0.11	0.17	0.7
Sta. Creu	10	4	83.8	12	4.25	0.039	0.03 ± 0.01	0.11	0.2
Carasquero	25	2	86	10.5	3.5	0.009	0.47 ± 0.08	0.15	0.4
Puebla	215	1.3	93.8	2.8	3.4	0.006	0.56 ± 0.03	0.13	3.2
La Colomina	270	1.5	92.7	4.4	2.8	0.003	0.82 ± 0.04	0.15	5.9
Old house	309	1.5	91.9	5.4	2.6	0.025	0.68 ± 0.04	0.17	5.5
Capella	395	1.2	87.5	10.3	2.1	0.011	0.58 ± 0.02	0.14	6.2

^a Values of SSC are for the day of sampling.

^b Depth and velocity data are based on measurements taken at each of the invertebrate sampling locations ($n = 10$ in Villacarli and Cabecera, $n = 5$ at the remainder).

^c Discharge for each reach was calculated empirically using depth and velocity data collected on the day of invertebrate sampling.

2.2.2. Invertebrate sampling

The combined total of 50 benthic samples was collected using a standard surber sampler (300 μ m mesh size, 0.09 m² area). Invertebrates were preserved in 4% formaldehyde for later analysis. In the laboratory, they were sorted and identified to genus level according to Tachet et al. (2002). Diptera and Oligochaeta were identified as far as possible according to the key (subfamily or tribe level).

2.2.3. Fine sediment determination

Deposited fine sediment was assessed in the patches of bed immediately adjacent (laterally) to where invertebrates had been collected, using the re-suspension technique first proposed by Lambert and Walling (1988). This technique had been previously used in the Isábena to estimate fine sediment storage in the main-stem channel (López-Tarazón et al., 2011a,b) and in a preliminary study of fine sediment effects on benthic invertebrates (Buendia et al., 2011). Full details of this methodology can be found in these papers. Briefly, a metal cylinder (0.5 m diameter, and 0.6 m height) was carefully pushed into the river to delimit the sampling area. The surface 10 cm of the river bed were vigorously disturbed using a rod to resuspend deposited fine sediment. Two 500 mL water samples collected just after the disturbance to provide a mean of the suspended sediment concentration in the cylinder and calculate the volume of fines contained in the gravel-bed matrix isolated by the cylinder.

2.3. Data analysis

2.3.1. Spatial patterns in invertebrate assemblages

Non-metric Multidimensional Scaling (NMDS, Kruskal, 1964) using Sorensen's coefficient (Heino et al., 2003) was used to examine patterns in invertebrate assemblage composition. This ordination method calculates a distance matrix (D) and visualises this matrix in a low dimensional configuration (2 or 3 dimensions). It has advantages over other ordination techniques in that it makes few assumptions about the nature of the data and allows the use of any distance measure (McCune and Mefford, 1995). Stress was used to judge the goodness of fit (i.e. how well the ordination summarises the observed distances among the samples), as it indicates the degree of correspondence between the distances among points in the ordination plot and the original distances measured. Sorensen's distance values were used for the NMDS. Scree plots (i.e. stress by dimension) were used to select the dimensionality of the analysis. A vector representing fine sediment was fitted to the final plot to help interpretation of the ordination. Squared correlation coefficients (r^2) for the vector and the significance of these values were assessed by 1000 permutations of the sediment values.

To test the significance of patterns of clustering found in the NMDS, a Multi-Response Permutation Procedure (MRPP) was run using the Sorensen's distance values. MRPP is a nonparametric procedure for testing the hypothesis of difference between two or more pre-defined groups (Zimmerman et al., 1985). Chance-corrected within group agreement (A) was used to describe within group heterogeneity. Values of A range from 0 to 1, showing lower values when the groups are formed by identical items. The significance of the null hypothesis of no difference among groups was assessed using a Monte-Carlo permutation procedure ($n = 1000$).

The nestedness temperature of presence-absence matrices was used to quantify the level of nestedness in invertebrate assemblages across the Isábena catchment. The temperature method was proposed by Atmar and Patterson (1993) and is based on a measure of the order and disorder apparent in the nested patterns. It uses Euclidean distances of unexpected species absences and presences in individual locations from the isocline (or extinction curve) which separates presences from absences in a perfectly nested matrix. The isocline is a curvature of maximum packing, given the species-by-site matrix size and fills, and does not depend on the structure of the data (Atmar and Patterson, 1993). In a perfectly nested matrix, all presences will be in the upper left corner of the theoretical isocline and the matrix temperature will be 0° (cold systems where extinction order does not change). The maximum value of this metric is 100° and corresponds to systems with a high influence of random processes acting on populations, which therefore are less predictable. These "hot" systems are represented by a matrix with many unexpected absences above the isocline and unexpected presences below the line.

Nestedness analysis used the BINMATNEST algorithm developed by Rodríguez-Girones and Santamaría (2006). This algorithm has been argued to be more robust and efficient than others (Azeria and Kolasa, 2008; Larsen and Ormerod, 2010). BINMATNEST re-orders rows and columns from the presence-absence matrix to minimise unexpectedness and maximise nestedness and calculates the matrix temperature (T). In order to test the statistical significance of the maximised nested matrix (i.e. that the observed T is not lower than expected by chance), the observed T was compared with that of null models generated by randomising the original matrix in 400 Monte-Carlo simulations. Following Larsen and Ormerod (2010) the null model III was used, as it is less sensitive to species richness and occurrences and, thus, is considered the most conservative and reliable. Moreover it has been shown to perform better (smaller type I error) than the other null models available (Rodríguez-Girones and Santamaría, 2006). This model calculates the proportion of presences for each row (ρ_{ri}) and column (ρ_{ci}), and, for every random matrix, the probability of a cell being filled is set equal to the average probabilities of occupancy of its row and column $(\rho_{ri} + \rho_{ci})/2$ (Bascompte et al., 2003).

Spearman-rank correlations were used to test whether nested patterns observed could be driven by the fine sediment content of the riverbed and by the biological traits of the assemblages. For this, the ranking of sites in the maximally packed matrix was related to the proportions of each trait category (as per Larsen and Ormerod, 2010). A significant correlation would suggest that assemblages are packed in a particular order due to fine sediment influences and the selection of certain traits in sediment-rich (most nested) locations.

2.3.2. Biological trait data

Information on 12 traits (Table 2) was collected for a total of 47 taxa, using databases for European rivers (Tachet et al., 2002; Statzner et al., 1994, 2007). For some taxa (i.e. Oligochaeta), information on biological traits was not available and these were excluded from the analysis.

A fuzzy coding procedure (Chevenet et al., 1994) was used to quantify the affinity of each taxon for each trait category. Scores ranged from 0 (indicating no affinity) to 3 or from 0 to 5, depending on the number of categories within each trait. This approach provides information on the possible differences among functional characteristics of species belonging to the same genus and the possible variation of some habits throughout the different life stages of a species (Chevenet et al., 1994; Usseglio-Polaterra, 1991). To give the same weight to each taxon and each trait, affinity scores were rescaled so that the sum of a given taxon and a given trait equalled one (Doledec and Statzner, 2008; Van der Linden et al., 2012). Trait categories were then multiplied by the $\log(x + 1)$ abundance of each taxon at each site to obtain values used to create a site \times trait abundance matrix (Larsen and Ormerod, 2010; Feio and Doledec, 2012). Principal Component Analysis (PCA) on the covariance matrix of the fuzzy coded data was performed to determine patterns of functional trait composition of the invertebrate assemblages.

All statistical analyses were performed using the following packages within the R environment (R Development Core Team, 2009): *vegan* v2.0-3 (Oksanen et al., 2012) for MMS, MRPP and PCA and *bipartite* (Dormann et al., 2008) for the nestedness analysis.

2.3.3. Metrics

Invertebrate density (number of individuals per unit area) and six taxon-based diversity metrics were calculated for each invertebrate sample. The diversity metrics included taxon richness (total number of taxa), diversity (Shannon's index; Shannon and Weaver, 1949) and evenness (calculated as the ratio of observed diversity to maximum diversity; Pielou, 1966). These metrics were selected because they have a long history of use in aquatic ecology, with each summarising key properties of the assemblage (Magurran, 1988). In addition, three EPT metrics were computed to assess their ability to detect fine sediment impacts: EPT density (combined abundance of Ephemeroptera, Plecoptera and Trichoptera per unit area), EPT richness (number of EPT taxa) and %EPT (proportion of the assemblage consisting of EPT taxa). These metrics have been widely used in detecting human impacts, as EPT taxa are considered to be relatively sensitive to disturbance (Angradi, 1999; Zweig and Rabeni, 2001; Kaller and Hartman, 2004; Larsen et al., 2009, 2011).

Two trait-based metrics were computed for each sample to assess the functional attributes of invertebrate assemblages. Trait richness was calculated as the number of trait categories present. Functional diversity (FD) was calculated as the Rao diversity coefficient, following the methodology developed by Champeli and Chessel (2002). This index takes into account the dissimilarity in the trait space among species and each species' abundance in the quantification of functional diversity (i.e. by weighting the pairwise species dissimilarity by the product of relative abundances of the two species):

$$FD = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j$$

Table 2

Invertebrate traits and categories considered in this study. Codes were used as labels in Fig. 5.

Trait	Categories	Code
(A) Maximal size	<0.25	A.1
	0.25–0.5	A.2
	0.5–1	A.3
	1–2	A.4
	2–4	A.5
	4–8	A.6
	>8	A.7
(B) Life cycle duration	<1 year	B.1
	>1 year	B.2
	<1	C.1
(C) Potential generations per year	1	C.2
	>1	C.3
	Aquatic passive	D.1
(D) Form of dissemination	Aquatic active	D.2
	Aerial passive	D.3
	Aerial active	D.4
	Egg	E.1
	Larva	E.2
(E) Aquatic stage	Nymph	E.3
	Adult	E.4
	Ovoviviparity	F.1
	Isolated eggs, free	F.2
	Isolated eggs, cemented	F.3
(F) Reproduction	Clutches, fixed	F.4
	Clutches, free	F.5
	Clutches, in vegetation	F.6
	Clutches, terrestrial	F.7
	Asexual reproduction	F.8
	Eggs, statoblasts	G.1
	Coccons	G.2
	Housing	G.3
(G) Resistance forms	Diapause	G.4
	No resistance forms	G.5
	Microorganisms	H.1
	Detritus <1 mm	H.2
	Plant detritus >1 mm	H.3
(H) Food	Living macrophytes	H.4
	Living microphytes	H.5
	Dead animal <1 mm	H.6
	Living microinv.	H.7
	Living macroinv.	H.8
	Vertebrates	H.9
	Absorber	I.1
	Deposit feeder	I.2
	Shredder	I.3
(I) Feeding habits	Scraper	I.4
	Filter feeder	I.5
	Piercer	I.6
	Predator	I.7
	Parasite	I.8
	Tegument	J.1
(J) Respiration	Gill	J.2
	Plastron	J.3
	Spiracle (aerial)	J.4
	Hydrostatic vesicle (aerial)	J.5
	Flier	K.1
(K) Locomotion	Surface swimmer	K.2
	Full water swimmer	K.3
	Crawler	K.4
(K) Locomotion	Burrower	K.5
	Interstitial	K.6
	Temporarily attached	K.7
	Permanently attached	K.8
	Flag/boulders/cobbles/pebbles	L.1
	Gravel	L.2
	Sand	L.3

Table 2 (Continued)

Trait	Categories	Code
(L) Substrate	Silt	L.4
	Macrophytes	L.5
	Microphytes	L.6
	Branches rots	L.7
	Organic detritus littler	L.8

with ρ_i being the proportion of the i th species, d_{ij} the dissimilarity of species i and j , and S the total number of species or taxa in the assemblage. Rao's diversity coefficient for each sample was determined using the package FD, which uses the species-by-species Euclidean distance matrix for the computation of the index (Laliberté and Legendre, 2010).

Following the approach used by Gallardo et al. (2011), the relations between metric values and fine sediment were assessed using Generalised Additive Models (GAMs). This method uses smoothing curves to model the relationship between response and explanatory variables and is suitable for modelling non-linear relationships. The model for all response variables (i.e. metrics) had the general form:

$$Y_i = \alpha + f(\text{sediment}_i) + \varepsilon_i$$

where Y_i is the value of the metric in sample i , sediment_i is the value of deposited fine sediment in sample i , ε_i is the residual for sample i and α the population intercept. The function $f()$ is the population smoothing function, with cubic regression splines used in all models to estimate the smoothed relationship between response variable and predictors. For count data (EPT richness and taxon richness) a Poisson distribution was selected to model the residual variation, while a binomial distribution was used for proportion data (%EPT) and a Gaussian distribution for continuous variables (invertebrate density, EPT density, Shannon, evenness and functional diversity). The percentage of deviance explained by the fitted model was used to assess its goodness-of-fit; inspection of residual plots confirmed modelling assumptions. Analyses were performed using the package mgcv (Wood, 2011) within the R environment (R Development Core Team 2009), which allows the application of Generalised Cross Validation (GCV) to automatically select the degrees of freedom of the smoothers (i.e. amount of smoothing).

3. Results

3.1. Fine sediment

Mean values of fine sediment stored in the channel of the Isábena ranged from 90 g/m² at those sites without the influence of badlands to 400 g/m² in the mainstem and up to 1000 g/m² in those tributaries where badlands comprised a relatively large proportion of their catchment area (Fig. 2). Maximum individual values were found in Villacarli, where fine sediment reached 1800 g/m². ANOVA and Tukey's HSD indicated that fine sediment values differed significantly between the three groups of sites shown in Fig. 2 ($p < 0.001$), but that there were no differences between sites within each group (mainstem p -value = 0.09; tributaries p -value = 0.1).

3.2. Assemblage structure and trait composition

NMDS produced a 2-axis ordination (Fig. 3) with a final stress value of 0.18, which indicates a satisfactory solution (stress values > 2 indicate unreliable and poor solutions; Clarke, 1993). The direction of the vector for fine sediment shows the sediment gradient (increasing from left to right), with the length of the arrow being proportional to the correlation between the variable and the ordination. Fine sediment proved to be highly correlated with the

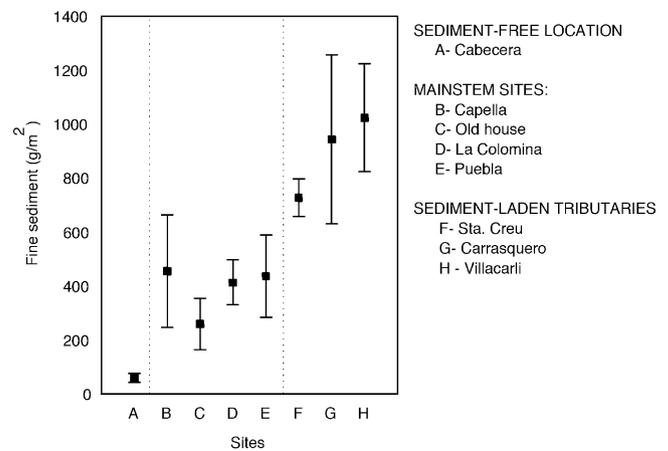


Fig. 2. Mean values of fine sediment content on the river bed. Bars represent the 95% confidence intervals.

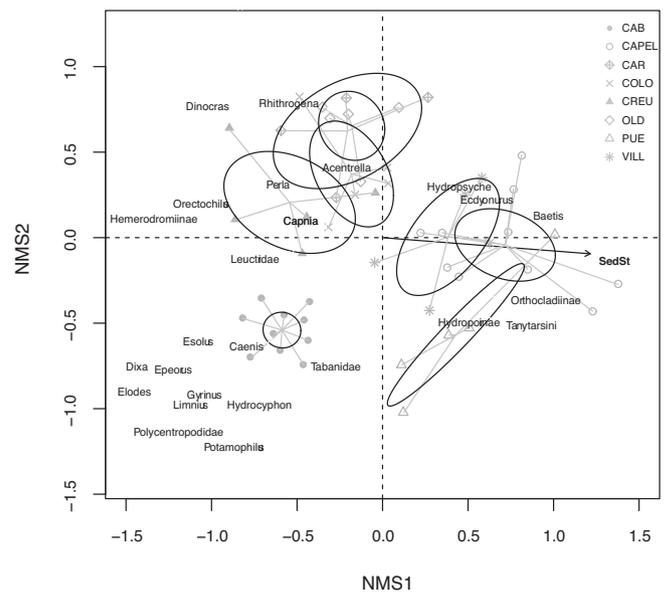


Fig. 3. NMDS ordination plot for the invertebrate data. Lines were drawn connecting each sample and the centroid of the group they belong to. 95% confidence ellipses around class centroids were also drawn. The overlapping of these ellipses indicate that classes are not significantly different at level $p < 0.05$. For clarity of the representation, those species with low NMS1 scores (< 0.3) were removed from the plot.

first axis of the ordination ($r^2 = 0.45$, p -value < 0.001). Three major groups are evident, each formed by a cluster of ellipses. Chance-corrected within group agreement (A) from the MRPP was 0.2, indicating a lower heterogeneity within the three groups identified than expected by chance (McCune and Grace, 2002). The groups were clearly spread along axis 1. Cabecera (sediment-free site, located in the right hand side of the plot) was separated from the rest, indicating marked differences between its invertebrate assemblages and those at locations downstream. Samples from the sediment-laden tributaries (Carrasquero, Villacarli and Sta. Creu) formed another group located at the positive end of the ordination axis. This group sat very close to the group formed by the samples from the mainstem, indicating some similarities between their faunas. No clear spatial pattern was evident within the group formed by sites along the mainstem, suggesting no major longitudinal changes in assemblage composition.

Ordination of taxa highlighted invertebrates typical of sites with high sedimentation, as well as those most sensitive to fines. EPT

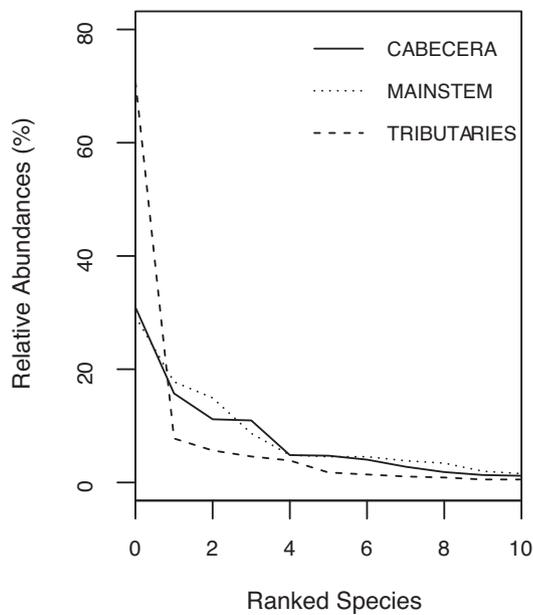


Fig. 4. Ranked-abundance plots for the three main groups defined from the NMDS ordination. Change in species relative abundances is more gradual in Cabecera and the mainstem, with a more evenly distribution of individuals between the taxa than in the tributaries.

taxa showed a variety of responses to the sediment gradient. Some mayfly and stonefly genera such as *Baetis*, *Ecdyonurus* and the caddis *Hydropsyche* were aligned with the group formed by the tributaries, indicating their predominance in these locations. Other EPT genera were inversely correlated to fine sediment values, such as the mayfly *Epeorus*, the plecopterans *Dinocras* and to a lesser extent *Perla*, *Capnia* and *Leuctridae*. In general, coleoptera genera such as *Gyrinus*, *Dryops* and *Elodes*, as well as the dragonfly *Onychogomphus*, proved to be sensitive to fines as they were consistently weighted towards the negative end of NMDS axis 1.

Density and taxon richness differed significantly between the three groups of sites [ANOVA: $F(8, 47) = 27.86$ and 45.40 respectively; $p < 0.001$]. Cabecera showed the highest mean values (2700 ind/m^2 and 42 taxa), while the lowest means were found in the tributaries, particularly in Sta. Creu river (100 ind/m^2 and 4 taxa). Sites on the mainstem showed intermediate values of richness (5–11 taxa) and density ($370\text{--}500 \text{ ind/m}^2$). In general, assemblages at all sites were dominated by EPT taxa, with ephemeropterans being the most abundant. The most common taxon at all sites was *Baetis*, comprising approximately 30% of the total abundance in Cabecera and the mainstem and 70% in the tributaries. Fig. 4 shows the ranked-abundance diagrams for the groups defined in the NMDS ordination. Cabecera and the mainstem showed a more equitable distribution, with a larger proportion of taxa with intermediate abundances (i.e. *Esolus*, *Hydropsyche*, *Ecdyonurus*). Conversely, one taxon (i.e. *Baetis*) was clearly dominant in the tributaries, with the remainder being uncommon (e.g. *Cheumatopsyche*, *Acentrella*, *Rhyacophila*).

PCA (Fig. 5) identified major patterns in biological traits present among sites. Both axes were correlated with fine sediment ($r^2 = 0.3$, $p\text{-value} = 0.001$), implying that overall trait distribution patterns were influenced by sedimentary conditions. Cabecera and the group formed by the tributaries draining badland areas corresponded to the extremes in the fine sediment gradient and were clearly separated in the ordination space. Samples from sites along the mainstem were widely dispersed on the PCA rather than forming distinct site clusters. The same applied to samples from sites in the tributaries. The proximity of the mainstem and tributary sites

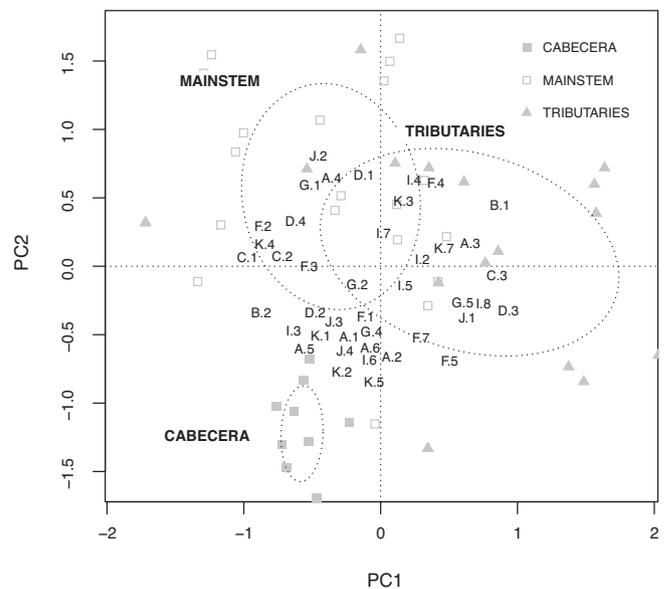


Fig. 5. PCA ordination showing the position of sites described in terms of their trait (i.e. functional) composition. 95% confidence ellipses around centroids were plotted around each group. Codes for the trait data are described in Table 2. The first two axes explained 47% of the variance in the trait data.

(specifically the overlap of their 95% confidence ellipses around group centroids) suggested a similar set of traits in their invertebrate assemblages.

Traits responsible for the major differences between sites were mainly related to the reproductive potential of organisms (i.e. number of generations per year) and the duration of their life cycle. Results indicated that multivoltine taxa (>1 generation per year) with short life-cycle durations (<1 year) were favoured in those locations with high volumes of fine sediment. Forms of locomotion seemed to respond differently to sedimentation. Unlike swimmers and temporarily attached taxa, crawlers and burrowers were particularly sensitive and were absent from the sediment laden tributaries. Assemblages in sediment-free locations were characterised by a more diverse set of maximum size categories, with animals ranging from very small (<0.25 mm) to large (4–8 mm) body sizes, while only small sizes (0.5–1 mm) were frequent in the tributaries. No resistance forms seemed to be selected by fine sediment. To a lesser extent, sedimentation also appeared to favour certain feeding groups (deposit feeders and scrapers), as well as aerial forms of dissemination and tegumental respiration. There were no major patterns related to general substrate affinities or aquatic stages (i.e. categories of these traits showing low component loadings in the PCA analysis).

The temperature of the maximally packed matrix indicated a significantly nested pattern in taxon distribution across the Isábena (Fig. 6, $T = 10.47$; $p < 0.01$). The nested rank order of taxa was significantly correlated with fine sediment content on the river bed ($r_s = 0.35$, $p = 0.008$). Therefore, those found in taxon-poor locations were subsets of those found in the taxon-rich, sediment-free ones. This suggests that the sequential removal of taxa across the catchment was driven by sedimentary conditions, with only common species persisting in fine sediment-rich locations. Results from Spearman's rank correlations between trait categories and the site ranking in the matrix indicated that certain traits appeared to be driving the nested patterns (see Table 3). The least nested locations, which had less fine sediment content, were mainly characterised by long-lived taxa with longer life cycles, larger sizes, a higher representation of shredders and deposit feeders and taxa with abdominal gill placement. Conversely, locations at the nested end of the matrix

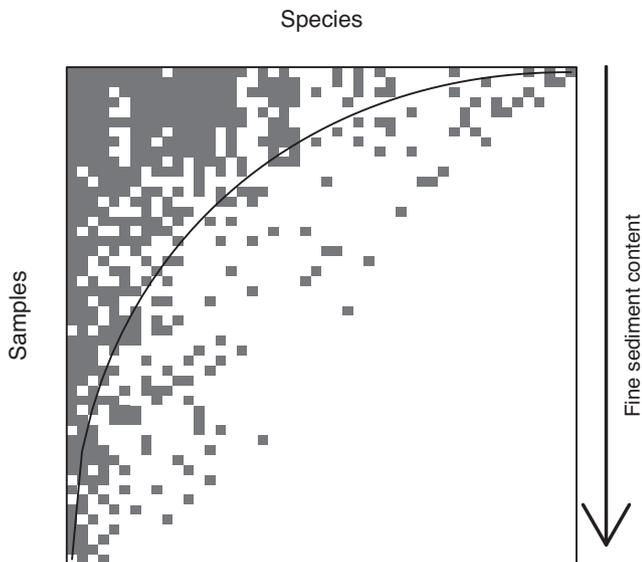


Fig. 6. Maximally packed matrix from the nestedness analysis. Filled squares indicate the presence of a particular species in a specific patch. The isocline reflects the curvature of maximum packing or perfect order.

Table 3

Spearman correlation coefficients (r_s) between trait categories and the ranking of sites from the maximally packed matrix. Note that only those traits with categories showing significant values are shown.

Trait	Category	Spearman, r_s	p -Value
Maximal size	0.25–0.5	–0.65	<0.0001
	0.5–1	0.34	0.014
	1–2	0.41	0.003
	2–4	–0.46	0.0006
	4–8	–0.44	0.001
Life-cycle duration	<1 year	0.69	<0.0001
	>1 year	–0.69	<0.0001
Potential generations per year	<1	–0.51	0.0035
	1	–0.29	0.0001
	>1	0.48	0.0004
Feeding habits	Shredder	–0.53	<0.0001
	Scraper	0.43	<0.0001
	Filter feeder	–0.55	<0.0001
	Deposit feeder	0.23	<0.0001
Respiration	Gills	0.45	0.0008
Locomotion	Swimmer	–0.58	<0.0001
	Crawler	–0.35	0.01
	Burrower	–0.49	<0.0001

held short-lived taxa with smaller body sizes, a larger number of potential generations per year and a higher representation of scrapers, deposit feeders and burrowers.

3.3. Responsiveness of metrics to fine sediment

Fig. 7 shows the values of the metrics for the study sites. All metrics showed lower values in the mainstem and particularly the sediment-laden tributaries, suggesting an inverse response of these metrics to fine sediment content across the study catchment. %EPT was the exception, with a higher EPT to all taxa ratio in locations with larger values of fines. The deviance in metric values explained by the fitted GAMs (goodness-of-fit) varied from 22 to 91% (Table 4). The density metrics (invertebrate density and EPT density) were those best explained by fine sediment content (deviance values above 80%). Conversely, %EPT and evenness had poorer model fits (deviance values of 43% and 22% respectively). Metrics based on

Table 4

Deviance explained and p -value (significance of the smoother) for each GAM fitted to metric and fine sediment values.

Metric	Deviance explained (%)	p -Value
Invertebrate density (ind/m ²)	91.7	<0.001
Taxon richness	75.3	<0.001
EPT density (ind/m ²)	81.9	<0.001
EPT richness	71.9	<0.001
%EPT	43.4	<0.001
Evenness	22	0.01
Shannon	57.4	<0.001
Trait richness	53.7	<0.001
Functional diversity	68.8	<0.001

biological traits also performed well, particularly functional diversity, with almost 70% of its deviance explained by variation in fine sediment.

4. Discussion

In-channel fine sediment constitutes an important component of sediment transfer through river systems, and thus plays an important role in the sediment budget of drainage basins (Wilson et al., 2004). López-Tarazón et al. (2011a,b) studied in-channel surface fine sediment storage in the Isábena and reported a mean value of 990 g/m² for their study sections, with a maximum of 8400 g/m². Larsen et al. (2009) reported values for in-channel fine sediment in the river Usk (where human activities have negligible impact) ranging from 2 to 147 g/m². Comparison of these values helps emphasise the extremely high fine sediment content of the riverbed in parts of the Isábena. Nonetheless, some sections of the Isábena are relatively sediment free, due to an absence of badland areas in their catchments. Such contrasts within this one, otherwise undisturbed catchment provided a basis for assessing differences in assemblages related to fine sediment. The consistency of the results of the NMDS and trait-based analyses provide strong evidence of sediment related patterns in invertebrate assemblages across Isábena. Sites with high values of deposited sediment were taxonomically depauperate and functionally homogeneous, with spatial patterns reflecting sample site position relative to the badland areas (i.e. sediment sources). An important point that should be borne in mind when interpreting these results is that our study assessed the overall effects of sedimentation on assemblages. Thus, it is not possible from our data to disentangle effects of the direct physical impacts of fine sediment on invertebrates (e.g. clogging of gills, reduction of interstitial space) from physico-chemical changes (e.g. low oxygen concentrations, changes in pH) which may be occurring within the bed as a consequence of sedimentation (Ryan, 1991).

4.1. Structural and functional effects of fine sediment

Small increases in deposited sediment can cause a decrease in invertebrate densities due to a reduction in habitat availability and quality, even though there may be little or no change in assemblage structure (Rabeni et al., 2005). With greater amounts of deposited sediment, densities of sediment-tolerant species may increase and alterations in assemblage structure may occur. In our study, sediment accumulation was associated with reduced invertebrate density and taxon richness, with the most impoverished sites located in the sediment laden tributaries draining badlands (some sites supported as little as 4 taxa and 100 individuals/m²). Invertebrate assemblages were generally homogeneous along the mainstem of the river. This homogeneity indicates that there was no clear downstream ecological recovery gradient related to distance from headwater sediment sources. Despite the distance from these

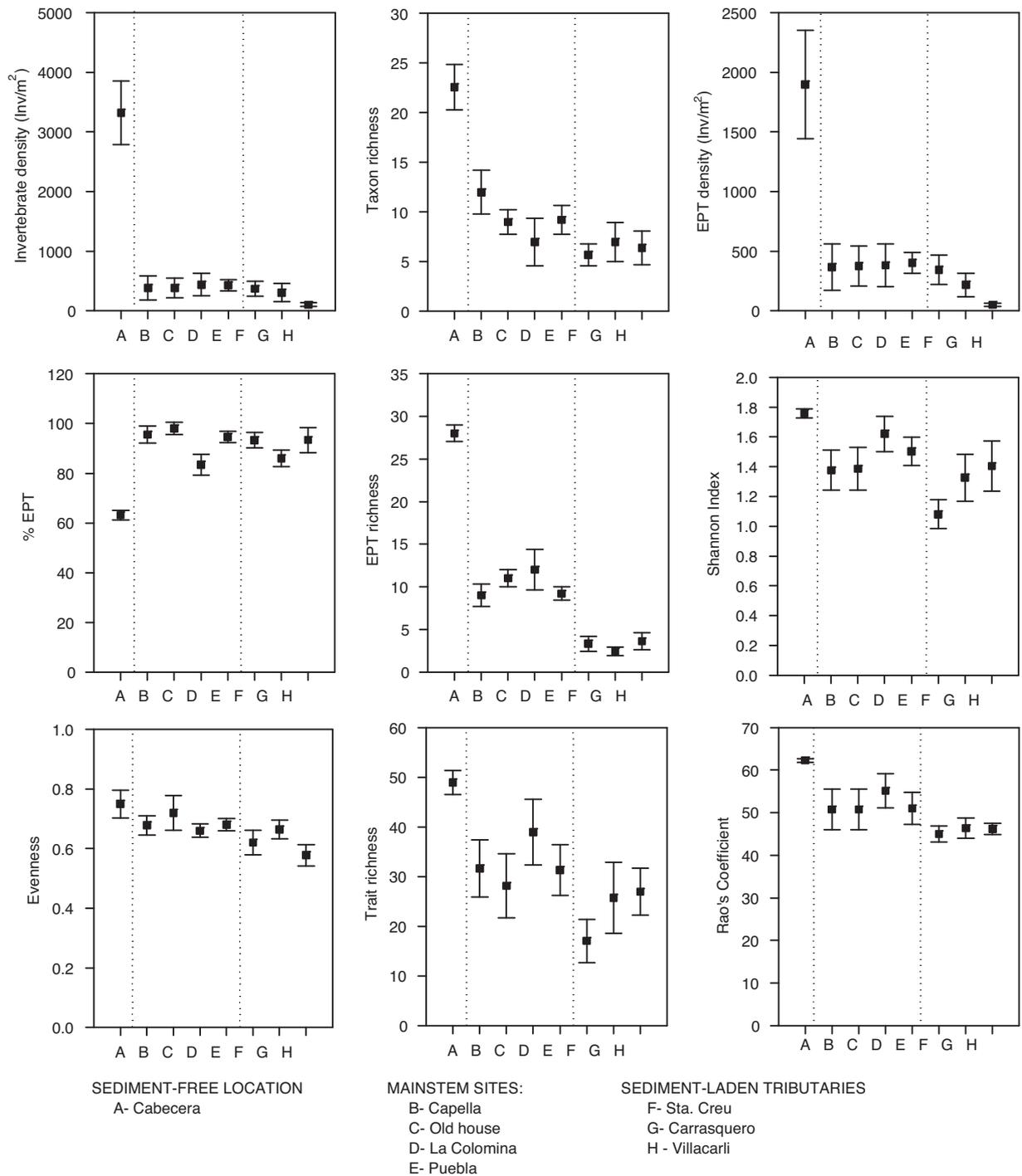


Fig. 7. Mean values and 95% confidence intervals of the metrics computed for each sampling location.

sources, large accumulations of fines were found along the main channel at the most downstream study sites, providing a plausible explanation for observed patterns of assemblage composition. The presence of such large accumulations of fine materials here indicates that fine sediment input exceeds the transport capacity of the river mainstem. This situation is typical of rivers draining highly erodible materials where sediment production is high (Walling and Amos, 1999; López-Tarazón et al., 2010).

Previous studies of the implications of fine sediment inputs to streams indicate that, in the longer term, assemblage structure changes from one comprising a range of Ephemeroptera, Plecoptera and Trichoptera to one dominated by animals such as

Oligochaeta, Chironomidae and Bivalva, taxa adapted to burrowing (Wood and Armitage, 1997). However, this shift was not observed in the Isábena, where EPT taxa were dominant and other genera (e.g. *Gyrinus*, *Potamophilus*, *Polycentropodidae*) were common only in those locations with low volumes of fines. The Ephemeroptera seems to be an important invertebrate Order to consider in fine sediment impact studies as it contains taxa responding in markedly different ways to sedimentation. For example, *Acentrella*, *Epeorus* and *Rhithrogena* have been reported to be fine sediment intolerant or moderately intolerant while *Baetis*, *Ephemerella* and *Paraleptophlebia* appeared to be tolerant taxa (Relyea et al., 2000; Wallace and Gurtz, 1986). In the Isábena, assemblages in sediment impacted

sites were clearly dominated by *Baetis* (which made up more than 50% of the assemblages) and *Hydropsyche*.

As predicted by the habitat template model (Southwood, 1977), changes in habitat in the Isábena appeared to select for certain biological and ecological traits. Changes in trait profiles reflect changes in the ability of invertebrates to cope with disturbances, as only those traits conferring resistance and resilience are selected (Statzner and Bêche, 2010). Results from the Isábena are in accordance with other studies which have indicated that modified habitats may show shifts in trait structure as those taxa with sensitive traits are filtered out (Peru and Dolédec, 2010; Feio and Doledéc, 2012). Across the Isábena, the representation of short life cycles, small sizes, deposit feeders and tegumental respiration increased as fine sediment storage increased. Life history was clearly the trait most affected by sedimentation, with polivoltinism being favoured in sediment-rich locations. Fine sediment, once deposited on the river bed, can easily be re-suspended even during relatively low flow conditions (López-Tarazón et al., 2009). The selection of polivoltinism and short life cycles to the detriment of merovoltine or bivoltine organisms and long-lived taxa, reflects a selection of organisms capable of rapid colonisation and adaptation to such low stability habitats, where fine sediment is frequently mobilised (Larsen et al., 2011). In addition, deposited sediment fills interstices and reduces porosity, affecting the larger organisms which require larger interstitial space (Larsen and Ormerod, 2010).

The habit trait group, which indicates invertebrate locomotion and attachment, also proved to be a responsive measure to sedimentation. In the Isábena only crawlers and swimmers responded markedly to fines: while crawlers rapidly disappeared with increasing sedimentation, swimmers appeared to be the most tolerant group. This positive correlation of swimmers with fine sediment may result from the ability of these organisms to move out of the most impaired areas; crawlers move slowly and thus may not be able to escape from areas experiencing sedimentation.

Feeding activities have been reported to be affected by deposited sediment in a variety of ways. For example, Rabeni et al. (2005) studied changes in functional feeding groups associated with sedimentation and found a greater proportion of gatherers and a lower proportion of filterers and scrapers. They also concluded that trophic or feeding groups were more sensitive to deposited sediment than the habit group. Contrary to these results, trophic composition in the Isábena did not show such a strong relationship with sedimentation. Certain feeding groups, such as deposit feeders, were apparently favoured by deposited sediment. Filterers appeared to be the most sensitive group, while the other groups did not show marked changes in their frequencies across the fine sediment gradient. Filterers have been considered the most intolerant group, as respiration structures are clogged by fine particles (Lemly, 1982; Wood and Armitage, 1997). Scrapers, which feed on periphyton attached to the substrate and need clean surface on which to graze, have usually been found to be intolerant (Wasserman et al., 1984; Rabeni et al., 2005; Oliver et al., 2012). A decrease in this group was not seen in the Isábena, and in fact there was a slight increase in their representation in sediment-rich locations. Published work on trophic composition is rather contradictory, with several studies reporting that functional feeding groups are not useful in detecting ecological impairment. For example, Culp and Davis (1983) reported that feeding groups did not change significantly throughout the year between sediment impacted and unimpacted sites. Duncan and Brusven (1985) also found similar proportions of feeding groups in logged and unlogged streams. However, these results may be attributable to the dominant influence of other abiotic controls, such as bed scour and flow hydraulics, leaving changes in food resources of secondary importance (Rejyea et al., 2000). Overall, the results for feeding were ambiguous and less clear cut in the Isábena than for other functional traits.

The reduction of the availability and quality of the habitat in the Isábena led to a sequence of non-random species loss which strongly depended on ecological and biological traits. The systematic drop-out of species over the sediment gradient promoted nested patterns across the catchment, with rare taxa limited to areas with low volumes of fines. In particular, trait categories conferring resilience (i.e. small size, short generation time and polivoltinism) increased in frequency in sediment-rich locations. The same trait selection and nested patterns were found in the experimental study conducted by Larsen et al. (2011) and in the sediment-rich sites over larger areas studied by Larsen and Ormerod (2010). Results from the Isábena provide further evidence that nestedness is a consequence of a non-random colonisation–extinction pattern driven by the selection of pre-adapted generalist species.

Benthic invertebrates play an important role in ecosystem functioning, as they serve as a food source and convert allochthonous and autochthonous plant material into energy for higher order organisms. In the Isábena, high sedimentation levels appeared to promote changes in invertebrate trait proportions. Such changes have potential implications for secondary production, biomass and metabolism and litter decomposition (Duncan and Brusven, 1985). Assessment of such implications would help develop more fully our understanding of the effects of fines on river ecosystem function and, in turn, provide the basis for more holistic and effective stream integrity assessment tools (Feio and Doledéc, 2012).

4.2. Performance of the diversity metrics

Invertebrate diversity metrics calculated for the Isábena samples differed in their sensitivity to fine sediment content. Taxon richness and invertebrate density decreased markedly with increasing fine sediment content of the river bed. Previous studies have reported declines in abundance of certain invertebrate groups following an increased input of fine sediment, most notably plecopterans (Culp and Davis, 1983). Even though invertebrate density and taxon richness may be useful in distinguishing between unaffected sites and highly impacted ones (i.e. sites showing abundant assemblages or very poor ones respectively), they may not be useful in distinguishing intermediate levels of disturbance. This may be due to the fact that fine sediment favours some taxa at the expense of others, and, since these indices do not take into account any measure of differing relative abundances, they may fail to detect more subtle ecological changes.

Metrics that incorporate measures of equitability or the relative abundance of taxa have long been used to detect differences between impacted and unimpacted streams (Letterman and Mitsch, 1970). Shannon's index values in the Isábena decreased as fine sediment content increased, a result consistent with that of Sarver (2003). This index can also be used as a heterogeneity measure as it takes into account species' relative abundance. Shannon index values indicated a homogenising effect of fine sediment on invertebrate assemblages in the Isábena, with sites where the largest accumulations occurred being dominated by a small number of taxa (Fig. 7). However, values of evenness did not show a marked response to fine sediment accumulation. Kilgour et al. (2004), who assessed the sensitivity of several diversity metrics to different stressors, also found evenness to be less sensitive than taxon richness and Shannon's index. Larsen et al. (2011) concluded from their experimental studies that deposited sediments did not affect diversity index values. They attributed this to the loss of rare taxa at greater sediment cover, which led to fewer taxa that had an even distribution of individuals between them. Additionally, as pointed out by Peru and Dolédec (2010), natural assemblages rarely have a perfectly even distribution of taxa; this adds a degree of uncertainty to the use of metrics which are based on the assumption of the evenness of undisturbed systems.

EPT metrics are frequently used in bioassessment. In the Isábena, EPT density and EPT richness decreased as the fine sediment content of the sampled patches of bed increased, as found by Gray and Ward (1982) and Waters (1995). These taxa are expected to respond to changes in substrate composition and to show lower values of abundance and richness in streams with large volumes of deposited sediment (Pollard and Yuan, 2010). Nevertheless, in our study the %EPT metric did not respond in this way, but instead showed a weak positive relationship with fine sediment. This finding is in line with Relyea et al. (2000), who could not discriminate among streams with varying levels of fine sediment using %EPT. The pattern in %EPT values in the Isábena was due to the fact that while invertebrate assemblages at sites with high values of fine sediment comprised only a small number of individuals, these were often dominated by EPT taxa (notably *Baetis* and *Hydropsyche*). This led to the increased values of the %EPT metric with increasing sedimentation. Previous studies have indicated that some EPT taxa are relatively tolerant of fine sediment. For example, Angradi (1999) and Kaller and Hartman (2004) reported a positive correlation between the metric % Baetidae of Ephemeroptera and fine sediment. Ulfstrand (1975) reported that several groups of mayflies (i.e. Baetidae and Heptagenidae) have certain properties that confer resilience (i.e. less specialised feeding habits, high fecundities and short generation times). Thus, the specific ecologies of these animals need to be borne in mind when drawing conclusions from EPT metrics, particularly %EPT.

Taxon-based metrics, because they only take into account the presence/absence and relative abundances of species, may fail to detect functional changes occurring in response to habitat modification (Peru and Dolédec, 2010). The use of trait-based metrics should help overcome such problems. Some studies have pointed to functional diversity as being the most versatile metric as it provides an indication not only of species number and dominance but their functional role in the assemblage (Gallardo et al., 2011; Mouillot et al., 2006). A high proportion of the variability in functional metrics values computed for the Isábena could be accounted for by variability on fine sediment (Table 4). Rao's coefficient was indicated by Lêps et al. (2006) to be a good candidate for an efficient functional diversity index and our results support this assertion.

4.3. Fine sediment and flow regimes

The Mediterranean climate is relatively predictable, with marked floods occurring mainly during spring and autumn. Streams in this region are physically, chemically and biologically shaped by sequential, predictable, seasonal patterns of flooding and drying (Gasith and Resh, 1999). Floods will affect channel morphology of the stream, and depending on their magnitude, may impact reach scale morphology and local grain-size distributions. The erosion of fine sediments from badlands and their transport to river channels is not just controlled by rainfall intensity, but many other factors (e.g. vegetation cover, slope, connectivity). In the case of the Isábena, event-based observations in an experimental badland show that freeze-thawing processes in winter eventually loosen the materials and increase the sediment supply in subsequent rainfall events. Therefore, these processes control variability in fine sediment stored in the channel over the annual scale and consequently bed grain size distributions within stream reaches (López-Tarazón et al., 2011a).

As well the transport and deposition of fine material, changes to flood magnitude and frequency may facilitate or interfere with colonisation by invertebrates (Kochersberger et al., 2012). In the case of the Isábena, colonisation and recovery following episodes of fine sediment deposition may be impeded by the baking of exposed sediment which occurs during the hot summer months.

Fine sediment present across the channel is exposed as flows drop and, once dried, the bed is likely to become impenetrable, preventing exchange between surface and groundwaters, inhibiting the use of interstitial refugia by invertebrates and affecting the dissolved oxygen levels in the surface and shallow hyporheic zones. Even once rewetted by subsequent flow events, baked (cohesive) sediment may not be immediately removed because of its relatively high entrainment threshold. Such cohesion will likely perpetuate the ecological effects of episodes of sedimentation, although this has yet to be studied. Similarly, the effects of longer term (seasonal, annual) changes in patterns of sedimentation in the Isábena remain unknown.

5. Conclusions

The aim of this study was to assess the effects of naturally occurring fine sediment on an otherwise relatively undisturbed catchment. We examined invertebrate assemblage taxonomic structure and functional traits and assessed the ability of a set of commonly used biodiversity metrics to detect fine sediment impacts. Overall, results were in line with those of studies of sedimentation effects in anthropogenically modified catchments, with a decline in species richness, total density and trait diversity with increasing fine sediment content on the river bed.

Functional traits proved to be useful to understand the mechanisms responsible for observed patterns in the abundance and distribution of macroinvertebrates in the Isábena. Life history traits that conferred resilience to populations in sediment-rich locations were influencing the nested patterns observed across the catchment. Results help support the argument that nested patterns can result from fragmentation of the habitat due to changes in its quality, and not only as a consequence of larger-scale biogeographical processes (Hylander et al., 2005; Larsen and Ormerod, 2010).

Climate change, habitat modification, fragmentation and loss are leading to unprecedented rates of diversity loss. Even though efforts are being made to detect and identify the causes of impairment and the organisms at risk, there is still limited understanding of which the types of organisms should be targeted for protection. The study of trait responses and nested patterns could have considerable significance for the identification of sensitive species and hence their conservation (Larsen and Ormerod, 2010). The present study provides further support for the view that habitat change and fragmentation associated with excessive fine sediment loads are resulting in the elimination of species with sensitive traits, and that this is promoting nested patterns.

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References

- Angradi, T.R., 1999. Fine sediment and macroinvertebrate assemblages in appalachian streams: a field experiment with biomonitoring applications. *J. N. Am. Benthol. Soc.* 18, 49–66.
- Atmar, W., Patterson, B.D., 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96, 73–382.

- Azeria, E.T., Kolasa, J., 2008. Nestedness, niche metrics and temporal dynamics of a metaassemblage in a dynamic natural model system. *Oikos* 117, 1006–1019.
- Bascompte, J., Jordano, P., Melian, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* 100, 9383–9387.
- Bilotta, G.S., Brazier, R.E., 2008. Understanding the effects of suspended solids on water quality and aquatic biota. *Water Res.* 42, 2849–2861.
- Bêche, L.A., Resh, V.H., 2007. Biological traits of benthic macroinvertebrate in California Mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundam. Appl. Limnol.* 169, 1–23.
- Buendia, C., Gibbins, C.N., Vericat, D., López-Tarazón, J.A., Batalla, R.J., 2011. Influence of naturally high fine sediment loads on aquatic insect larvae in a montane river. *Scott. Geogr. J.* 127, 315–334.
- Champeli, S., Chessel, D., 2002. Measuring biological diversity using Euclidean metrics. *Environ. Ecol. Stat.* 9, 167–177.
- Chevenet, F., Doledec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biol.* 31, 295–309.
- Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in assemblage structure. *Aust. J. Ecol.* 18, 117–143.
- Coleman, N., Gason, A.S.H., Poore, G.C.B., 1997. High species richness in the shallow marine waters of south-east Australia. *Mar. Ecol. Prog. Ser.* 154, 17–26.
- Culp, J.M., Davis, R.W., 1983. An assessment of the effects of streambank clear-cutting on macroinvertebrate assemblages in a managed watershed. Canadian Technical Report for Fisheries and Aquatic Sciences, Ottawa, ON, Canada.
- Darlington, P., 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley and Sons, New York.
- Doeg, T.J., Koehn, J.D., 1994. Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *Regul. Rivers: Res. Manage.* 9, 263–278.
- Doledec, S., Statzner, B., 2008. Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. *Freshwater Biol.* 53, 617–634.
- Dormann, C.F., Gruber, B., Frund, J., 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8 (2), 8–11.
- Duncan, W.F.A., Brusven, M.A., 1985. Benthic macroinvertebrates in logged and unlogged low-order southeast Alaskan streams. *Freshwater Invert. Biol.* 4, 125–132.
- Erman, D.C., Mahoney, D.L., 1983. Recovery after clogging in streams with and without buffer strips in northern California. Contribution 186, California Water Resources Center.
- Feio, M.J., Doledec, S., 2012. Integration of invertebrate traits into predictive models for indirect assessment of stream functional integrity: a case study in Portugal. *Ecol. Indic.* 15, 236–247.
- Fernandez-Juricic, E., 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia* 131, 269–278.
- Francke, T., López-Tarazón, J.A., Schroder, B., 2008. Estimation of suspended sediment concentration and yield using linear models, random forests and quantile regression forests. *Hydrol. Processes* 22, 4892–4904.
- Gallardo, B., Gascón, S., Quintana, X., Comín, F.A., 2011. How to choose a biodiversity indicator—redundancy and complementarity of biodiversity metrics in a freshwater ecosystem. *Ecol. Indic.* 11, 1177–1184.
- Gasith, A., Resh, V.H., 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annu. Rev. Hydrol.* 30, 51–81.
- Gayraud, S., Statzner, B., Bady, P., Haybach, A., Scholl, F., Usseglio-Polatera, P., Bacchi, M., 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biol.* 48, 2045–2064.
- Graham, A.A., 1990. Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentrations in suspension. *Hydrobiologia* 199, 107–115.
- Grabowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: the importance of sediment properties. *Earth-Sci. Rev.* 105, 101–120.
- Gray, L.J., Ward, J.V., 1982. Effects of sediment releases from a reservoir on stream macroinvertebrates. *Hydrobiologia* 96, 177–184.
- Harrison, E.T., Norris, R.H., Wilkinson, S.N., 2007. The impact of fine sediment accumulation on benthic macroinvertebrates: implications for river management. In: Proceedings of the 5th Australian Stream Management Conference, Albury, New South Wales, 21–25 May 2007, pp. 139–144.
- Heino, J., Muotka, T., Mykka, H., Paavola, R., Hamalainen, H., Koskeniemi, E., 2003. Defining macroinvertebrate assemblage types of headwater streams: implications for bioassessment and conservation. *Ecol. Appl.* 13, 842–852.
- Hjulström, F., 1935. Studies on the morphological activity of rivers as illustrated by the River Fyris. *Bull. Geol. Inst.* 25, 54–61.
- Hylander, K., Nilsson, C., Jonsson, B.G., Gothner, T., 2005. Differences in habitat quality explain nestedness in a land snail meta-assemblage. *Oikos* 108, 351–361.
- Hynes, H.B.N., 1970. The Ecology of Running Waters. Liverpool University Press, Liverpool.
- Kaller, M.D., Hartman, K.J., 2004. Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate assemblages. *Hydrobiologia* 518, 95–104.
- Kilgour, B.W., Somers, K.M., Barton, D.R., 2004. A comparison of the sensitivity of stream benthic assemblage indices to effects associated with mines, pulp and paper mills, and urbanization. *Environ. Toxicol. Chem.* 23, 212–221.
- Kochersberger, J.P., Burton, G.A., Custer, K., 2012. Short-term macroinvertebrate recruitment and sediment accumulation: a novel field chamber approach. *Environ. Toxicol. Chem.* 31, 1098–1106.
- Kreutzweiser, D.P., Capell, S.S., Good, K.P., 2005. Effects of fine sediment inputs from a logging road on stream insect assemblages: a large scale experimental approach in a Canadian headwater stream. *Aquat. Ecol.* 39, 55–66.
- Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29, 115–129.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Lambert, C.P., Walling, D.E., 1988. Measurements of channel storage of suspended sediment in a gravel-bed river. *Catena* 15, 65–80.
- Larsen, S., Vaughan, I.P., Ormerod, S.J., 2009. Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater Biol.* 54, 203–219.
- Larsen, S., Ormerod, S.J., 2010. Combined effects of habitat modification on trait composition and species nestedness in river invertebrates. *Biol. Conserv.* 143, 2638–2646.
- Larsen, S., Pace, G., Ormerod, S.J., 2011. Experimental effects of sediment deposition on the structure and function of macroinvertebrate assemblages in temperate streams. *River Res. Appl.* 27, 257–267.
- Leana, D., Zweig, C.D., Rabeni, C.F., 2001. Biomonitoring for deposited sediment using benthic macroinvertebrates: a test on 4 Missouri streams. *J. N. Am. Benthol. Soc.* 20, 643–657.
- Lemly, A.D., 1982. Modifications of benthic insect assemblages in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia* 87, 229–245.
- Lêps, J., Bello, F., Lavorel, D., Berman, S., 2006. Quantifying and interpreting functional diversity of natural assemblages: practical considerations matter. *Preslia* 78, 481–501.
- Letterman, R.D., Mitsch, W.J., 1970. Impact of mine drainage on a mountain stream in Pennsylvania. *Environ. Pollut.* 17, 53–73.
- López-Tarazón, J.A., Batalla, R.J., Vericat, D., Francke, T., 2009. Suspended sediment transport in a highly erodible catchment: the River Isábena (Southern Pyrenees). *Geomorphology* 109, 210–221.
- López-Tarazón, J.A., Batalla, R.J., Vericat, D., 2010. Rainfall, runoff and sediment transport relations in a mesoscale mountainous catchment: the River Isábena (Ebro basin). *Catena* 82, 23–34.
- López-Tarazón, J.A., Batalla, R.J., Vericat, D., 2011a. In-channel sediment storage in a highly erodible catchment: the River Isábena (Ebro Basin, Southern Pyrenees). *Z. Geomorphol.* 55, 365–382.
- López-Tarazón, J.A., Batalla, R.J., Vericat, D., Francke, T., 2011b. The sediment budget of a highly dynamic mesoscale catchment: the River Isábena. *Geomorphology* 138, 15–28.
- Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, NJ.
- McCune, B., Mefford, 1995. PCORD. Multivariate Analysis of Ecological Data, Version 2.0. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- Mcgill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding assemblage ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185.
- Mouillot, D., Spatharis, S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A., Chi, T.D., 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water assemblages. *Aquat. Conserv.: Mar. Freshwater Ecosyst.* 16, 469–482.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2012. Vegan: Assemblage Ecology Package. R package, version 2.0-3. <http://CRAN.R-project.org/package=vegan>
- Oliver, A.A., Bogan, M.T., Herbst, D.B., Dahlgren, R.A., 2012. Short-term changes in stream macroinvertebrate assemblages following a severe fire in the Lake Tahoe, California. *Hydrobiologia* 694, 117–130.
- Patterson, B.D., 1987. The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* 1, 323–334.
- Peckarsky, B.L., 1984. Do predaceous stoneflies and siltation affect the structure of stream insect assemblages colonizing enclosures? *Can. J. Zool.* 63, 1519–1530.
- Peru, N., Dolédec, S., 2010. From compositional to functional biodiversity metrics in bioassessment: a case study using stream macroinvertebrate assemblages. *Ecol. Indic.* 10, 1025–1036.
- Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13, 131–144.
- Pires, A.M., Cowx, I.G., Coelho, M.M., 2000. Benthic macroinvertebrate assemblages of intermittent streams in the middle reaches of the Guadiana Basin (Portugal). *Hydrobiologia* 435, 167–175.
- Poff, N.L., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P., Kondratieff, B.C., 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *J. N. Am. Benthol. Soc.* 25, 730–755.
- Pollard, A.I., Yuan, L.L., 2010. Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. *Freshwater Biol.* 55, 1420–1429.
- R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN: 3-900051-07-0 <http://www.R-project.org/>
- Rabeni, C.F., Doisy, K.E., Zweig, L.D., 2005. Stream invertebrate assemblage functional responses to deposited sediment. *Aquat. Sci.* 67, 395–402.
- Reid, D.J., Chiaroni, L.D., Hewitt, J.E., Lohre, D.M., Matthaei, C.D., Phillips, N.R., Scarsbrook, M.R., Smith, B.J., 2011. Sedimentation effects on the benthos of streams and estuaries: a cross-ecosystem comparison. *Mar. Freshwater Res.* 62, 1201–1213.

- Reizopoulou, S., Thessalou-Legaki, M., Nicolaidou, A., 1996. Assessment of disturbance in Mediterranean lagoons: an evaluation of methods. *Mar. Biol.* 125, 189–197.
- Relyea, C.D., Minshall, G.W., Danehy, R.J., 2000. Stream Insects as bioindicators of fine sediment. In: *Watershed Management Conference Proceedings*. Water Environment Federation Speciality Conference, Vancouver, BC, 9–12 July 2000, pp. 663–686.
- Robertson, D.J., 1981. Effects of clearcutting on lotic invertebrate assemblages in the central Appalachian Mountains. Ph.D. Dissertation, University of Pittsburgh, Pittsburgh, PA.
- Rodriguez-Girones, M.A., Santamaria, L., 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. *J. Biogeogr.* 33, 924–935.
- Ryan, P.A., 1991. Environmental effects of sediment on New Zealand streams: a review. *N. Z. J. Mar. Freshwater Res.* 25, 207–221.
- Sarver, R., 2003. Semi-quantitative macroinvertebrate stream bioassessment. Missouri Department of Natural Resources, Air and Land Protection Division, Jefferson City, Environmental Services Program.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Statzner, B., Resh, V.H., Dolédec, S. (Eds.), 1994. Ecology of the Upper Rhône River: A Test of Habitat Templet Theories. *Freshwater Biology (Special issue)*, 31, pp. 253–554.
- Statzner, B., Dolédec, S., Hugué, B., 2004. Biological trait composition of European stream invertebrate assemblages: assessing the effects of various trait filter types. *Ecogeography* 27, 470–488.
- Statzner, B., Bonada, N., Dolédec, S., 2007. Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate assemblages: a case for a collective public database. *Biodivers. Conserv.* 16, 3609–3632.
- Statzner, B., Bêche, L.A., 2010. Can biological traits resolve effects of multiple stressors in running waters? *Freshwater Biol.* 55, 80–119.
- Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies. *J. Anim. Ecol.* 46, 337–365.
- Suren, A.M., Jowett, I.G., 2001. Effects of deposited sediment on invertebrate drift: an experimental study. *N. Z. J. Mar. Freshwater* 35, 725–737.
- Suren, A.M., Martin, M.L., Smith, B.J., 2005. Short-term effects of high suspended sediments on six common New Zealand stream invertebrates. *Hydrobiologia* 548, 67–74.
- Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2002. *Invertebres d'Eau Douce*. CNRS, Paris, France, 588 pp.
- Ulfstrand, S., 1975. Diversity and some other parameters of Ephemeroptera and Plecoptera assemblages in subarctic running waters. *Fundam. Appl. Limnol.* 76, 499–520.
- United Research Services (URS), 2002. Estudio de la calidad ecológica integral de los tramos fluviales más importantes del río Cinca, vol. X, río Isábena. Confederación Hidrográfica del Ebro. Available from: <http://www.chebro.es/contenido.visualizar.do?idContenido=8025>
- Usseglio-Polatera, P., 1991. Representation graphique synthétique de la signification écologique d'un peuplement, Application aux macroinvertebres du Rhone a Lyon. *Bull. Ecol.* 22, 195–202.
- USEPA (U.S. Environmental Protection Agency), 2000. *Atlas of America's Polluted Waters*, EPA 840-B-00-002. Office of Water (4503F). United States Environmental Protection Agency, Washington, DC.
- Van der Linden, P., Patricio, J., Marchini, A., Cid, N., Neto, J.A., Marques, J.C., 2012. A biological trait approach to assess the functional composition of subtidal benthic assemblages in an estuarine ecosystem. *Ecol. Indic.* 20, 121–133.
- Vasconcelos, M.C., Melo, A., 2008. An experimental test of the effects of inorganic sediment addition on benthic macroinvertebrates of a subtropical stream. *Hydrobiologia* 610, 321–329.
- Verdú, J., 2003. *Análisis y modelización de la respuesta hidrológica y fluvial de una extensa cuenca de montaña mediterránea (río Isábena, Pre-Pirineo)*. Unpublished Ph.D. Thesis. Universitat de Lleida, Lleida.
- Wallace, J.B., Gurtz, M.E., 1986. Response of Baetis mayflies (Ephemeroptera) to catchment logging. *Am. Midl. Nat.* 115, 25–41.
- Walling, D.E., Amos, C.M., 1999. Source, storage and mobilisation of fine sediment in a chalk stream system. *Hydrol. Processes* 13, 323–340.
- Wasserman, L.J., Cederholm, C.J., Salo, E.O., 1984. The impact of logging on benthic assemblage structure in selected watersheds of the Olympic peninsula, Washington. University of Washington, Fisheries Research Institute, Seattle, WA. Contribution to the Final Report FRI-UW-8403.
- Waters, T.F., 1995. *Sediment in Streams Sources, Biological Effects and Control*. American Fisheries Society, Maryland, USA.
- Wilson, A.J., Walling, D.E., Leeks, G.J.L., 2004. In-channel storage of fine sediment in rivers of southwest England. In: Golosov, V., Belyaev, V., Walling, D.E.D.E. (Eds.), *Sediment Transfer Through the Fluvial System*, Proceedings of the Moscow Symposium. IAHS Publication, 288, Moscow, pp. 291–299.
- Wood, J.R., 1977. The aquatic insects of Rainy Creek with special reference to caddisflies (Trichoptera). M.S. Thesis, Central Washington State College, Ellensburg, WA.
- Wood, P.J., Armitage, P.D., 1997. Biological effects of fine sediment in the lotic environment. *Environ. Manage.* 21, 203–217.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Roy. Stat. Soc. Ser. B* 73, 3–36.
- Wright, D.H., Patterson, B.D., Mikkelsen, G.M., Cutler, A., Atmar, W., 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia* 113, 1–20.
- Zimmerman, G.M., Goetz, H., Mielke Jr., P.W., 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66, 606–611.
- Zweig, L.D., Rabeni, C.F., 2001. Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *J. N. Am. Benthol. Soc.* 20, 643–657.