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Research Paper

Diversity patterns and food web structure in a Mediterranean intermittent stream

key words: community, drought, macroinvertebrates, Functional Feeding Groups, Shannon-Wiener's index, Simpson's index

Abstract

In this work we present the results of a one-year study on the macroinvertebrate community in an intermittent stream in southern Spain. We have studied the taxonomic composition, diversity and food web monthly in order to consider temporal variability in these parameters. More than 60 macroinvertebrate taxa have been recorded in the stream, but they do not cohabit at the same time. Many of them join the community at the beginning of the wet period. Afterwards, some new taxa incorporate but some others disappear. This leads to huge fluctuations in the diversity of the community and in the food web of different sampling dates. These variations are linked to environmental disturbances, mainly to flow peaks and minimums. From a relatively well structured, but simple, food web at the beginning of the wet period, it can be seen how several trophic levels disappear with time, and how several organisms change or extend their trophic function within it. We relate these variations to the intermediate disturbance hypothesis and discuss the resilience of the community of this intermittent stream.

1. Introduction

Ecological drought may be defined as a shortage of water causing stress on ecosystems, adversely affecting the life of plants and animals (TALLAKSEN and VAN LANEN, 2004). Streams in Mediterranean climates are influenced by a sequence of regular and often extreme drought periods and floods. They determine the temporal and spatial dynamics of these systems, in which drying results in gradual increases in environmental and biological (*e.g.* predation, competition) controls in structuring biological communities (GASITH and RESH, 1999; BOIX *et al.*, 2010). The influence of drying may be even more intense in streams that lack a marked seasonality. This is the case of some intermittent streams with supra-seasonal drought, in which the absence of periodicity may greatly affect organisms' development and behaviour, and determine the primary and secondary production of these ecosystems. As the drought continues, habitat reduction becomes severe, changes in water quality occur, and intra-specific and inter-specific interactions may intensify or even develop *de novo* (LAKE, 2011). As pointed out by LAKE (2011), drought could act as a major force for regulating

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species diversity not only directly due to the stress of water absence, but also indirectly by altering the availability of resources. In streams, floods, as a type of natural disturbance, have been studied in relation to diversity, but less is known about the effect of drought in the diversity patterns of flowing waters. Thus, a better knowledge of the variations in the community composition of temporary streams throughout the wet period is needed to understand the functioning of these ecosystems.

The dominant community of temporary streams is composed by macroinvertebrates. Among them, Plecoptera and Odonata are poorly represented; particularly well suited to these habitats are Ephemeroptera, Hemiptera, Coleoptera, Trichoptera and Diptera (WILLIAMS, 2006). Within the latter, Tipulidae and Chironomidae are the dominant taxa in temporary waters. Many of these taxa have particular strategies to deal with drought (LAKE, 2003). These adaptations vary depending on the predictability of the environment. They include refuge use [see, for instance, the classification in BOULTON, (1989) or in ROBSON *et al.*, (2008)], resting stages in their life cycle, such as diapause or quiescence, rapid growth, and active dispersal to other water bodies (WILLIAMS, 2006). If perennial pools are present in the stream even cohort-splitting could be a successful strategy (ROBSON *et al.*, 2011). This strategy would allow some individuals to develop faster and others to develop slowly. So, if drought period begins early, at least some individuals would have completed their development and would leave descendants for the next year. The appearance and disappearance of organisms due to these strategies (for instance, due to the presence of resting stages) conditions the food webs that develop in these kinds of streams.

Food webs in temporary waters are poorly studied (WILLIAMS, 2006). The great majority of studies analyse together data from several months, so depicting an unrealistic food web that does not take into account significant temporal variations (CLOSS and LAKE, 1994; WOODWARD *et al.*, 2005). Typically, they are relatively short, omnivory is relatively common, and many are detritus-based, increasing their resistance and resilience to environmental disturbance (CLOSS and LAKE, 1994). In many cases, trophic complexity is related to temporal heterogeneity and the number of trophic levels seems to depend on the rate of availability of primary and secondary production, which is likely influenced by habitat stability and predictability (MENGE and SUTHERLAND, 1976; WILLIAMS, 2006). Though structural changes linked to the temporal variability in temporary waters must be accompanied by functional changes in the community, very few quantitative attempts have been made to address the latter issue (WILLIAMS, 2006).

Thus, the main aims of this work are: 1) to study how the diversity patterns vary with time throughout a whole year in an intermittent stream from a Mediterranean-climate region, and 2) to analyse how the trophic web structure is and how it changes with time in relation with the variable abiotic conditions of this ecosystem. In this sense we would expect a higher diversity some months before the end of the wet period, when abiotic conditions stabilize and a more complex trophic web when the diversity is higher.

2. Methods

The study was conducted in a tributary of the Arroyo de las Perdices (Sierra de Huétor, Granada, southern Spain, coordinates: N 37°17'38.2" W 3°28'57.9"; 1384 m a.s.l.), a Mediterranean intermittent stream that dries out unpredictably and whose flow may persist for several years. The stream source is 500 meters upstream of the study site and is fed by groundwater in some parts of its channel. It joins the Arroyo de las Perdices stream a few meters downstream from the study site. The channel is very narrow (less than 1.5 m wide) and very shallow (less than 30 cm deep). The substrate is composed mainly by sand and gravel, and submerged vegetation (mosses) is scarce. In the study site, the stream is surrounded by Juncaceae, *Rubus* sp., *Fraxinus* sp., *Pinus* sp. and *Retama* sp.

This study was carried out from September 2009, when the stream began to carry water to June 2010, when it dried out again. The stream was visited regularly each month throughout the year.

Macroinvertebrates were sampled quantitatively using a Surber sampler (0.1 m² area and 250 µm mesh size). Six samples were collected in different microhabitats (*i.e.* rapid flow, slow flow, gravels, sands), one per microhabitat, in order to collect organisms from all these microhabitats and so to have a proper representation of the community. Macroinvertebrates were preserved in 4% formaldehyde. In each sampling month, conductivity, dissolved oxygen and pH were measured with a VWR Symphony multiparametric probe (VWR International Eurolab S.L., Spain) and discharge was recorded with a Global Water flow meter (Global Water Instrumentation, USA) (Fig. 1). In October and November the low discharge in the stream did not allow measuring this variable. During the whole study period, a datalogger (iBCod, Eclo, Portugal; accuracy = 0.5 °C) was placed in the streambed to get a continuous measure of temperature (Fig. 1). In two occasions the datalogger remained exposed to the air due to a decrease in the water level and temperatures below zero were recorded. In these cases the value of temperature was substituted by a mean between the value of temperature of the day before and the value of temperature of the day after these records.

Macroinvertebrates were identified to the lowest possible level and counted in the laboratory. Gut contents of individuals of all the collected taxa were studied using the transparency method of BELLO

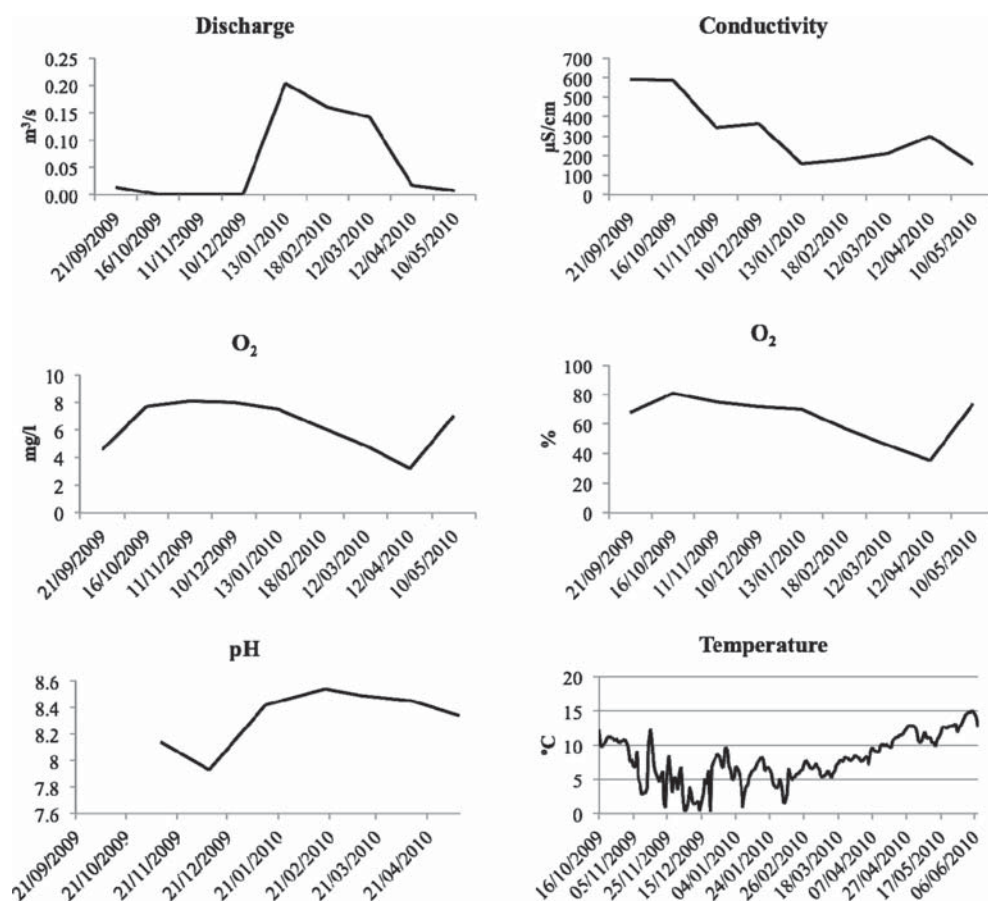


Figure 1. Variation of the recorded physicochemical parameters throughout the study period in the tributary of the Arroyo de las Perdices.

and CABRERA (1999), as in other articles on macroinvertebrate feeding (e.g. FENOGLIO *et al.*, 2009; LÓPEZ-RODRÍGUEZ *et al.*, 2009). For this, individuals of the same taxa from different dates were used in order to account for possible changes in diet with time. These individuals were introduced in a vial with Hertwig's liquid and heated in an oven at 65 °C for approximately 24 h (depending on the size of the animals, this time was shorter or longer). This treatment allows a clear view of the gut contents. Subsequently, individuals were placed in a slide with a cover on and examined under the microscope at 40× and 400× magnification. The gut content study was used to assign each taxon to its Functional Feeding Group (FFG, MERRITT and CUMMINS, 1996). For Hemiptera (that are fluidophagous and no gut content can be identified) and Ceratopogonidae Leptoconopinae (in which the only one individual collected had no gut content) we used the main FFG assigned to them by TACHET *et al.*, (2010).

For the whole community, we calculated both the Shannon-Wiener's diversity index $\left(\text{as } H' = \sum_{i=1}^S \rho_i \ln \rho_i \right)$ and the Simpson's inverse dominance index $\left[\text{as in KINDT and COE (2005), i.e. } D = \sum \rho_i^2 \right]$, using the

lower possible taxonomic resolution for taxa included in the analyses, as mentioned before. The Shannon-Wiener's index weights more the rare taxa, while the Simpson's index weights more the common ones.

Data from the gut content analyses were used to construct the food web diagrams. When some species shared common feeding relations in a date but they fed on different resources in previous dates, they were included in different boxes. Nevertheless, for food web analyses they were considered together. To study the trophic web, several characteristics were calculated following STEVENS (2009): nodes (trophospecies), as a set of organisms that share similar feeding relations; links, or feeding relations, as the connection between nodes, both directed (actual) and undirected (potential, not confirmed relations); connectance, as the proportion of possible links realized, both directed and undirected; top trophospecies, as those nodes that are fed upon by nothing; intermediate trophospecies, as those that feed on other species but are also fed upon by others; basal trophospecies, as those that feed on no other species; and top, intermediate and basal taxa, as the number of taxa included in top, intermediate and basal nodes.

Statistical analyses were computed using R ver. 2.14.0 (R Development Core Team 2011). The package BiodiversityR (KINDT and COE, 2005) was used for the calculation of the diversity indexes.

3. Results

Physic-chemical characteristics of the stream varied largely throughout the year (Fig. 1). Discharge was very low during the major part of the sampling period, but it increased drastically in winter, with a peak in January. After it, discharge decreased until the drought period. In the year when this study was carried out, almost no water flowed in the stream during October and November. Temperature ranged from almost 0 °C in winter to about 15 °C before summer. Oxygen content and pH also varied greatly during the sampling period. Conductivity was maximal at the beginning of the wet period and it decreased subsequently until the end, with a little increase in April.

Macroinvertebrate community in the tributary of the Arroyo de las Perdices was composed of Oligochaeta, Gastropoda, Collembola, Ephemeroptera, Odonata, Plecoptera, Heteroptera, Megaloptera, Trichoptera, Coleoptera and Diptera (Table 1). The most abundant taxa within them were *Centropilum* sp., *Nemoura* sp., *Baetis* sp., Tanypodinae, Prodiamesinae, Lumbricidae, Lumbriculidae, Prosimulini and Chironominae (Table 1). All the other taxa had very low total densities during the whole sampling period (lower than 100 ind/m²). New taxa incorporated to the community with time, ranging from less than 20 taxa at the beginning of the wet period to almost 70 before the summer drying. In terms of diversity patterns, there were huge fluctuations both in the Shannon-Wiener's and the Simpson's inverse indexes (Fig. 2). There was also a great variability in the FFG composition of the community with time (Fig. 3). Collector-gatherers were the most abundant throughout the sampling period, and they reached their maximum densities in October and latter in April (Fig. 3). Scrapers and shredders were very scarce at anytime, but shredders increased both in density and

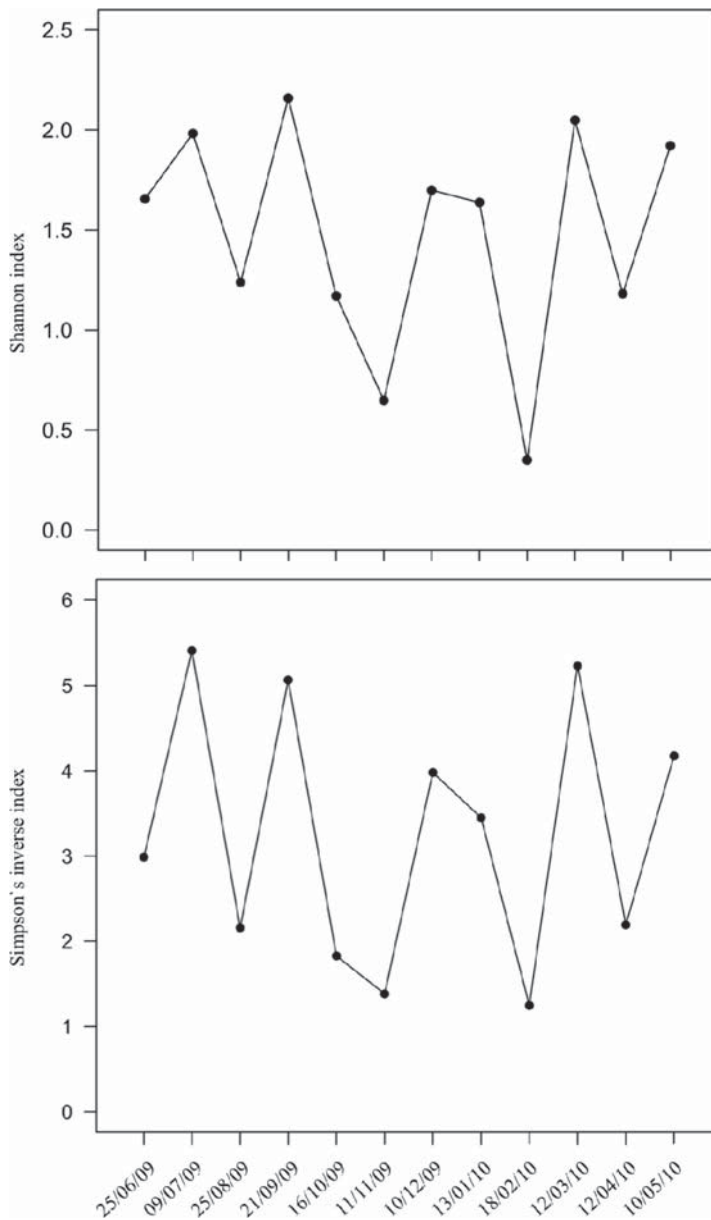


Figure 2. Diversity and dominance indexes in each of the sampling dates in the tributary of the Arroyo de las Perdices.

proportionally after the autumn. Filterers were more important at the beginning of the wet period and at the end, the last month before the drought. The proportion of predators was relatively important during all the months, but they had a maximum density peak in October, as had collector-gatherers. Predators and collector-gatherers had a similar density trend almost the whole sampling period (Fig. 3).

Table 1. Composition of the macroinvertebrate community of the tributary of the Arroyo de las Perdices with total densities of each taxon (as the sum of densities of all the sampling dates). FFG = Functional Feeding Group; C-G = collector-gatherer; F = filterer; Sc = scraper; Sh = shredder; P = predator.

Taxa	Density (ind/m ²)	FFG	Taxa	Density (ind/m ²)	FFG
OLIGOCHAETA			TRICHOPTERA		
Lumbricidae	415.00	C-G	<i>Rhyacophila</i> sp.	1.67	D + C-G
Lumbriculidae	278.33	C-G	<i>Agapetus</i> sp.	2.50	C-G
GASTROPODA			<i>Allotrichia</i> sp.	1.67	Sc
<i>Viviparus</i> sp.	1.67	Sc	<i>Hydropsyche</i> sp.	22.51	P + C-G
Planorbidae	1.67	Sc	<i>Polycentropus</i> sp.	5.00	P
<i>Ancylus</i> sp.	2.50	Sc	<i>Plectrocnemia</i> sp.	4.17	P
<i>Lymnaea</i> sp.	1.67	Sc	<i>Tinodes</i> sp.	1.67	Sc + C-G
COLLEMBOLA			<i>Stenophylax</i> sp.	32.50	C-G + Sh
<i>Podura aquatica</i>	1.67	C-G	<i>Sericostoma</i> sp.	3.34	Sh
EPHEMEROPTERA			DIPTERA		
<i>Ephemera danica</i>	16.67	C-G	Tipulidae	28.35	Sh + C-G
<i>Heptagenia</i> sp.	5.84	C-G	Limoniini	1.67	C-G
<i>Caenis</i> sp.	1.67	C-G	<i>Dixa</i> sp.	23.34	C-G
<i>Baetis</i> sp.	1168.33	C-G	Anophelinae	28.34	C-G
<i>Centroptilum</i> sp.	3020.00	C-G	Prosimulini	226.66	F
<i>Torleya major</i>	2.50	C-G	Chironominae	122.49	C-G
<i>Paraleptophlebia</i> sp.	17.50	C-G	Prodiamesinae	683.33	Sh + C-G
<i>Habrophlebia</i> sp.	13.33	C-G	Tanypodinae	895.00	P + C-G
PLECOPTERA			Ceratopogoninae	16.67	C-G
<i>Rhabdiopteryx christinae</i>	11.66	C-G	Leptoconopinae	1.67	C-G
<i>Nemoura</i> sp.	1586.67	C-G	Hemerodromiinae	15.01	P
<i>Protonemura</i> sp.	3.34	C-G	Empididae (undet.)	3.33	C-G
<i>Capnia bifrons</i>	6.67	C-G	<i>Chrysopilus</i> sp.	1.67	Sh + C-G
<i>Capnioneura libera</i>	5.00	C-G	Tabanidae	38.33	P
<i>Hemimelaena flaviventris</i>	3.33	P + C-G	<i>Atherix</i> sp.	51.68	P + C-G
ODONATA			<i>Atrichops</i> sp.	1.67	C-G
<i>Calopteryx</i> sp.	3.33	P	Diptera (undet.)	5.00	—
<i>Cordulegaster</i> sp.	1.67	P	COLEOPTERA		
HETEROPTERA			<i>Agabus</i> sp.	40.01	C-G
<i>Mesovella</i> sp.	5.00	P	<i>Agabus</i> sp. (adult)	3.34	C-G
<i>Notonecta</i> sp.	1.67	P	<i>Deronectes</i> sp.	11.67	P
Heteroptera (undet.)	1.67	P	<i>Deronectes</i> sp. (adult)	3.33	P
MEGALOPTERA			<i>Hydroporus</i> sp. (adult)	3.33	P
<i>Sialis nigripes</i>	4.17	P + C-G	<i>Stictonectes</i> sp.	21.67	C-G
			<i>Stictonectes</i> sp. (adult)	5.00	C-G
			<i>Elmis</i> sp.	12.50	C-G
			<i>Oulimimus</i> sp.	5.00	C-G
			<i>Hydraena</i> sp. (adult)	5.01	C-G
			<i>Dryops</i> sp.	1.67	C-G
			<i>Dryops</i> sp. (adult)	1.67	C-G
			<i>Laccobius</i> sp. (adult)	1.67	C-G
			<i>Anacaena</i> sp.	1.67	C-G

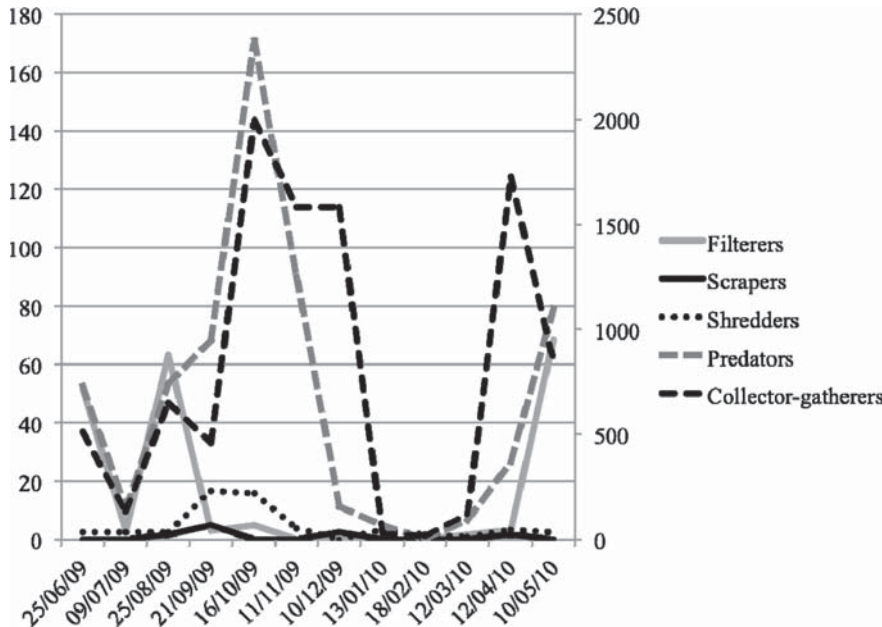


Figure 3. Densities of the FFGs during the sampling period in the tributary of the Arroyo de las Perdices. Due to differences in densities, collector-gatherers are represented using the right-Y axis scale, while the remaining FFGs are represented using the left-Y axis scale.

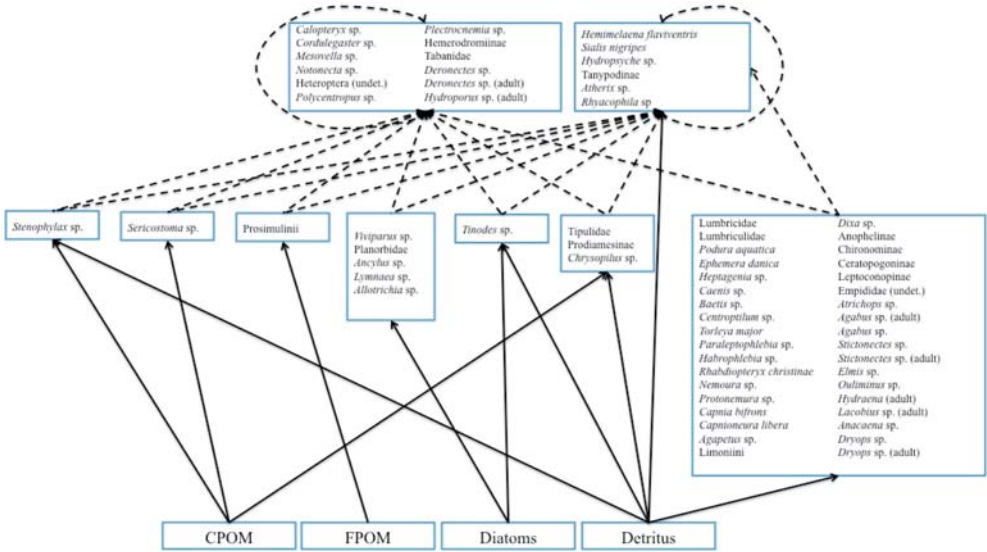


Figure 4. Potential food web diagram of the macroinvertebrate community in the tributary of the Arroyo de las Perdices. CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter in the water column. Dashed lines indicate undirected links and continuous lines indicate directed links.

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Table 2. Food web characteristics of the potential food web of the tributary of the Arroyo de las Perdices and the actual food webs in three sampling dates: at the beginning of the wet period (25/06/09), after the maximum discharge (18/02/10), and just before the drought period (10/05/10).

	Potential	25/06/09	18/02/10	10/05/10
Nodes (trophospecies)	9	5	2	2
Directed links	11	5	3	2
Undirected link	16	9	0	2
Connectance (directed)	0.14	0.20	0.75	0.50
Connectance (undirected)	0.44	0.90	0.00	2.00
Intermediate trophospecies	2	2	0	1
Basal trophospecies	7	3	2	1
Intermediate taxa	18	6	0	5
Basal taxa	48	11	2	14

The potential food web, *i.e.* the food web that could occur if all the organisms recorded during the whole study were present at the same time, was relatively simple (Fig. 4), with two main groups of predators (those strictly predators and those that incorporated also detritus to their diet sometimes during the sampling period), one large group of potential prey that fed on detritus, another group that fed on diatoms and some smaller groups of taxa that fed on coarse particulate organic matter (CPOM), either alone or in combination with detritus, and fine particulate organic matter (FPOM). This food web had a low directed connectance, but a medium to low undirected connectance (Table 2) as a consequence of the higher number of undirected links.

At the beginning of the wet period (in June) the food web was composed by a big group of detritivorous, two groups of predators (one exclusively predator and one that fed on detritus too), and two taxa that fed on FPOM one, and CPOM and detritus the other (Fig. 5). No taxa fed on diatoms. The directed connectance was low, but the undirected connectance was very high (Table 2). After the maximum discharge period, in February, a detritivorous group and a group that fed both on detritus and CPOM composed the food web (Fig. 5). In this date there were only directed links, and the directed connectance was relatively high (Table 2). In the last month of the wet period (May) the food web was composed by a big group of detritivorous, several small groups of detritivorous taxa that before had also another trophic role, and a small group of predators, whose taxa acted also as detritivorous (Fig. 5). Though directed connectance was low, undirected connectance was relatively high (Table 2). In none of the studied trophic webs there were top trophospecies.

4. Discussion

Abiotic conditions in the tributary of the Arroyo de las Perdices are very variable. Flow in this stream is extremely unpredictable and it is not entirely synchronized with the rainfall patterns due to the influence of the underlying aquifer. This is an important factor determining community structure, as many macroinvertebrates are very sensitive to discharge changes and pulse flow, and abrupt increases in it may wash them downstream and so alter the community stability (*e.g.* HYNES, 1970; ALLAN and CASTILLO, 2007).

Colonization of temporary waters may occur from “outside”, *i.e.* by organisms coming from nearby water bodies, including those that move upstream or downstream when the stream connects to others, and/or from “inside”, *i.e.* from resting stages of organisms

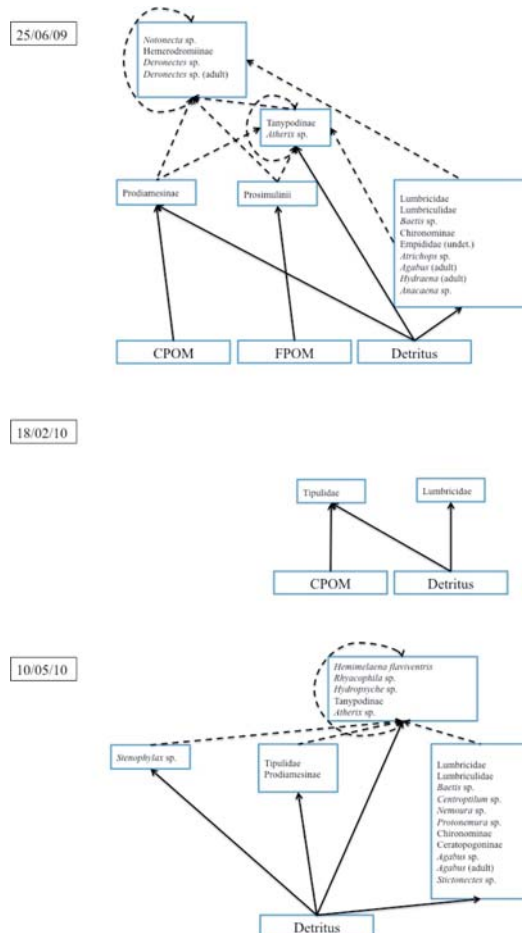


Figure 5. Food web diagram of the macroinvertebrate community in the tributary of the Arroyo de las Perdices in three sampling dates: at the beginning of the wet period (25/06/09), after the maximum discharge (18/02/10), and just before the drought period (10/05/10). CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter in the water column. Dashed lines indicate undirected links and continuous lines indicate directed links. Note: in the last trophic web, *Stenophylax* sp. and Tipulidae and Prodiamesinae are in separated boxes to indicate that they belonged previously to other trophospecies.

that have survived in the streambed or in the hyporheic zone (see WILLIAMS, 2006). In the tributary of the Arroyo de las Perdices both types are represented. In the first month of the wet period, the organisms that appeared in the stream (e.g. Lumbricidae, Lumbriculidae, *Baetis* sp., etc.) probably survived in the streambed during the dry period. Others, such as the beetles *Hydraena* spp., *Agabus* sp., or the heteropteran *Notonecta maculata*, which were caught as adults the first wet month, may come from neighbour streams. In fact, Coleoptera, Heteroptera and Diptera Simuliidae are among the early colonizers of water bodies (ROBSON *et al.*, 2011). Taxa such as blackflies (Simuliidae) have drought resistant eggs from which they hatch once flow resumes in ephemeral streams, while others, as Coleoptera and Heteroptera, use to come from other aquatic ecosystems as adults (ROBSON *et al.*, 2011).

Several insect species (including odonates and coleopterans) that require perennial surface waters have been observed to display positive rheotaxis, so that when the stream dries up, they move upstream to perennial headwaters (LYTLE *et al.*, 2008), and after the drought they return to the stream. In the tributary of the Arroyo de las Perdices, both kinds of organisms incorporate to the community to a relatively constant rate, even at the end of the wet period, probably coming from downstream (as upstream the stream is dry). The fact that two sources of organisms (the streambed and other nearby streams) influence the colonization process of this tributary is supported by the presence of some taxa not typical from temporary waters, such as the mayfly *Ephemera danica*. Particularly this species has a long nymphal development period [see LÓPEZ-RODRÍGUEZ *et al.*, (2009) for a study on this species in the same river basin]. Due to its burrowing habits, the nymphs of *E. danica* could remain within the substrate and rest there until the favourable conditions return to the stream, or could arrive even from downstream, where the species is known to be present.

Though we identified more than 60 taxa, only nine of them dominate in terms of density. All the others are found in very low numbers. This pattern has also been found in other temporary streams. For instance, Otermin *et al.* (2002) found that the most abundant taxa made up at least 85% of the total invertebrate density in a first-order stream after a drought period.

Maximum values of diversity are found in the mid-months, but fluctuations in diversity values occur all the year. Environmental disturbances are one major factor affecting diversity at a small or local scale, and in small streams (as the tributary of the Arroyo de las Perdices) highly variable and/or unpredictable discharge acts as a disturbance of variable frequency and intensity (POFF and ALLAN, 1995). Thus, communities submitted to disturbances exist in a non-equilibrium state, and so competitive equilibrium among organisms is prevented and best competitors do not dominate (KREBS, 2009). Several studies indicate that disturbances reduce benthic invertebrate density and diversity, but both may recover quickly (*e.g.* DEATH and WINTERBOURN, 1995). In fact, the intermediate disturbance hypothesis (GRIME, 1973; HORN, 1975; CONNELL, 1978) predicts that intermediate levels of physical disturbances maximizes biodiversity, while extreme events would reduce it drastically, leading to either the physical extinction of many taxa or to the dominance of the best competitors due to competitive exclusion. This hypothesis has been widely applied in lotic studies (DEATH and WINTERBOURN, 1995; WARD and STANFORD, 1983), and our results support it, as in the tributary of the Arroyo de las Perdices minimum values of diversity are found just after a great disturbance (the period of minimum flow, in November, and the peak of flow, in February).

Fluctuations in the community as shown by the diversity indexes are also reflected in the variability of the FFG's in the stream throughout the wet period. Collector-gatherers are always the dominant group, as they use to be early colonizers in streams (*e.g.* GORE, 1982; OTERMIN *et al.*, 2002). Shredders show their maximum proportion after the leaf-fall period, in January, when leaves are probably preconditioned by bacteria and fungi and are more palatable, but they are not very abundant the rest of the year. As pointed out by WILLIAMS (2006), the number of leaf-shredding species is lower in temporary waters than in permanent waters. Predators are present all the months but one, as prey are available every time, but also show slight oscillations in proportion to other groups. Their density varies together with that of collector-gatherers, sometimes in an asynchronous manner, but collector-gatherers are much more abundant throughout the year. BOULTON and LAKE (1992) also found this predominance of collector-gatherers in two intermittent streams of Australia. As no fishes are known to reach this stream, predation by macroinvertebrates is the main factor controlling prey populations.

Considering the potential food web we realize that the particular food web that actually develops each month of the wet period is quite simplified. In the first month the food web has different trophic sources, such as CPOM, FPOM, detritus and prey species, with several links among nodes. There are some cases of omnivory, such as those of Tanypodinae and *Atherix* sp., that act both as predators and detritus feeders, or Prodiamesinae, that feed on

CPOM and detritus [though this is not considered omnivory by some authors, *e.g.* STEVENS (2009)]. Thus, the beginning of the wet period is the phase in which a more complex food web develops. After a disturbance (as it is the peak of flow in January) the food web remains extremely simplified, coinciding with a reduction in the diversity of the community. At the end of the wet period, before the drought, the food web relies mainly on detritus and five taxa of predators are present, which also act as detritus feeders probably due to the adverse conditions in this period. As shown in several studies (*e.g.* BRIAND, 1983), food webs in variable or fluctuating environments seem to be less connected than those of more constant environments. Despite this little connectance, redundant species (*i.e.* those that are ecologically equivalent but differ in their responses to environmental factors) may strengthen both resistance and resilience in drought. Thus, although species are lost, ecological function remains, albeit reduced (LAKE, 2011). Nevertheless, species reduction or elimination may reduce the efficiency of resource utilization and productivity, and this reduction appears to be dependent on the identity of the species that are lost (*e.g.* CARDINALE *et al.*, 2006). In the tributary of the Arroyo de las Perdices, resilience seems to be relatively high, as shown by the structure of the food web after the drought period and also by the high values of diversity in comparison with other months of the wet period.

As observed from the diversity patterns throughout the wet period and the variability of the food web with time, abiotic factors, mainly flow fluctuations, determine the macroinvertebrate community structure in this intermittent stream. Thus, this community shows a certain degree of resilience, as shown by the food web and the diversity of taxa at the beginning of the wet period, providing these organisms with the capacity to cope with unpredictable conditions.

5. Acknowledgements

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