



RESEARCH PAPER

Anthropogenic flow intermittency shapes food-web topology and community delineation in Mediterranean rivers

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Abstract

Anthropogenic flow intermittency is considered a severe disturbance for benthic macroinvertebrates with largely unknown impacts on the organization of benthic communities and their food webs. We analysed the community composition (as taxonomic composition and relative abundance of taxa) and food webs of the macroinvertebrates inhabiting the pools and riffles of two Mediterranean streams with contrasting perennial and anthropogenic intermittent flow regimes. Our analyses comprised monthly measurements in two pools and two riffles of the community composition, food-web topology (the pattern in which specific links are arranged within the network) and food-web complexity indexes (the number of nodes and links regardless of their identity or arrangement) over 1 year. The food webs revealed a significant annual variation in size, complexity, and diversity within pools and under perennial flow (e.g., number of nodes, number of links, link density). Multivariate analysis showed strong differences in the composition and relative abundance of taxa and food-web topology of assemblages inhabiting pools and riffles. However, differences between communities inhabiting pools and riffles varied during the year; periods of great similarity were followed by periods in which communities were very different. This annual sequence of differences between pools and riffles was compressed under the anthropogenic flow intermittency regime. The anthropogenic intermittent flow studied here might represent a moderate stressor for Mediterranean communities well-adapted to dry conditions. Still, the reported deviation of the community composition and food-web topology from the reference status reflect the detrimental effect of this stressor on the benthic community.

KEYWORDS

drought, ecological networks, intermediate disturbance hypothesis, macroinvertebrates, trophic organization

1 | INTRODUCTION

Intermittent streams and rivers encompass around 30% of the total length and discharge of the global river network (Datry, Bonada, &

Boulton, 2017; Tooth, 2000). Furthermore, the number and length of intermittent rivers are expected to increase globally due to climate change and water abstraction (Jackson et al., 2001; Larned, Datry, Arcsott, & Tockner, 2010). In addition to naturally intermittent rivers,

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water abstraction and impoundment have caused many formerly perennial rivers to become intermittent in recent years (Datry, Larned, & Tockner, 2014). The shift from a perennial to an intermittent flow regime under natural circumstances is a “ramp disturbance” that gradually increases in intensity over time (Lake, 2003). In contrast, intermittency caused by anthropogenic factors is a severe disturbance for aquatic biota because it happens more rapidly (Datry, Larned, Fritz, et al., 2014), resulting in potentially powerful impacts on the organization of stream communities and the topology and dynamics of their food webs (Ledger, Brown, Edwards, Milner, & Woodward, 2013). Flow decreases result in habitat reductions, declines in water quality, and an intensification of existing interactions between organisms (Lake, 2011). Thus, reduced flow is a major stress factor for freshwater communities (López-Rodríguez et al., 2012). Flow intermittency may have different impacts on the stream communities depending on the mesohabitat that they live in (Boulton, 2003). For example, two typical mesohabitats in streams, pools and riffles, have very different flow conditions and form a natural sequence of lotic and lentic conditions at the reach-scale (Frissell, Liss, Warren, & Hurley, 1986; Gregory, Gurnell, Hill, & Tooth, 1994). Riffles are shallow, characterised by high flow velocity and the accumulation of relatively coarse material, whereas pools are deeper mesohabitats containing fine material on the channel bed (Richards, 1976). The substrate composition and flow are important environmental drivers in streambed ecology that might determine the distribution pattern of streambed macroinvertebrates to a greater extent than macroclimate conditions (Xuehua, Zhaoyin, Mengzhen, & Zhang, 2009). Consequently, pools and riffles house distinctive communities, which differ in trait composition and trophic structure (Bossley & Smiley, 2019; Brown & Brussock, 1991; Giller & Malmqvist, 1998) with important implications for ecosystem ecology, conservation and biomonitoring (Herbst, Cooper, Medhurst, Wiseman, & Hunsaker, 2018). Communities inhabiting riffles are generally characterised by higher richness, diversity, and biomass than those in pools (Brown & Brussock, 1991; Jones & Lim, 2005; Kobayashi & Kagaya, 2002; Logan & Brooker, 1983). However, pools are less variable habitats in which seasonal disturbances related to high flows and droughts might be partially buffered. As a result, pools can also act as a refuge for individual benthic organisms during drought (Hill & Milner, 2018) and host many organisms that have drifted from their preferred riffle habitats during floods (Brown & Brussock, 1991). Thus, the degree to which communities inhabiting pools and riffles differ may oscillate seasonally during the year.

An ecological community is a group of organisms inhabiting a particular habitat, which quantitatively differs from other groups (Eichhorn, 2016). Thus, delineating ecological communities and addressing their sensitivity to disturbances, implies studying the taxonomic composition and the biotic and abiotic interactions that take place in it. Food-web analyses provide integrated measurements of the community topology (the pattern in which specific links between consumer and resource nodes are arranged within the network), trophic interactions between organisms, and energy flow through different trophic levels (Bascompte, 2009). Food-web analyses are increasingly

used to examine the ecological implications of water flow intermittency on benthic communities (e.g., Ledger et al., 2013; Lu et al., 2016; McMeans, McCann, Humphries, Rooney, & Fisk, 2015). In particular, food-web metrics, such as the distribution and the strength of links within stream communities, are very sensitive to the detrimental effect of anthropic flow intermittency in dam-regulated Mediterranean rivers (Mor et al., 2018; Ruhí et al., 2016). Food-web analyses provide a more integrative measurement of the taxonomic composition and trophic interactions in river communities than the traditional structural metrics of community composition (Bascompte, 2009; Bruder, Frainger, Rota, & Primicerio, 2019) and combining the two approaches has the potential to significantly improve our understanding of anthropogenic flow intermittency (Chessman, 2015).

In this study, we quantified the effect of anthropogenic flow intermittency on benthic macroinvertebrate and food-web topology in pools and riffles. Food-web models have been widely applied to assess the impact of anthropogenic stressors on natural communities, with stressors typically reducing diversity and complexity indexes (e.g., Binzer, Guill, Rall, & Brose, 2016; McCann et al., 2017; O’Gorman, Fitch, & Crowe, 2012). We predict a significant reduction of the food-web topology and a concomitant simplification in the food-web complexity under intermittent conditions that are more challenging for benthic organisms. We also expect that a quantitative analysis of the community and food webs topology will allow us to discriminate between communities inhabiting pools and riffles in intermittent and perennial regimes. Finally, we also predict that food-web analysis is a sensitive tool because it provides a more integrative measurement of the taxonomic composition and trophic interactions (Bascompte, 2009). To achieve our objectives, (a) we surveyed two small tributaries (one perennial and one anthropogenic intermittent) in a Mediterranean stream once a month over 1 year, (b) we analysed how community composition, food-web topology and food-web complexity differed between pools and riffles, and under perennial and anthropogenic intermittent flow regimes; (c) we compared the degree of similarity in the community composition and food-web topology of the benthic communities inhabiting pools and riffles in both streams types, and finally (d), we measured the fluctuation in these similarity values over the year. Our results arise from a combination of a very fine taxonomic resolution and a well-resolved characterisation of trophic interactions based on direct gut content analyses. This study provides further insights into how benthic communities are structured in stream ecosystems and how they respond to disturbances such as flow intermittency.

2 | METHODS

2.1 | Study site

The samples were collected in 2 second-order tributaries of the Río Bermejo (Figure 1; Natural Park of Sierra de Huétor, Granada, Spain; 1,200 m a.s.l.; permanent: 37°16′49″N; 3°31′38″W; intermittent: 37°16′43″N; 3°31′29″W), a typical Mediterranean stream affected by irregular and intense rainfall, mostly in winter, whereas summer

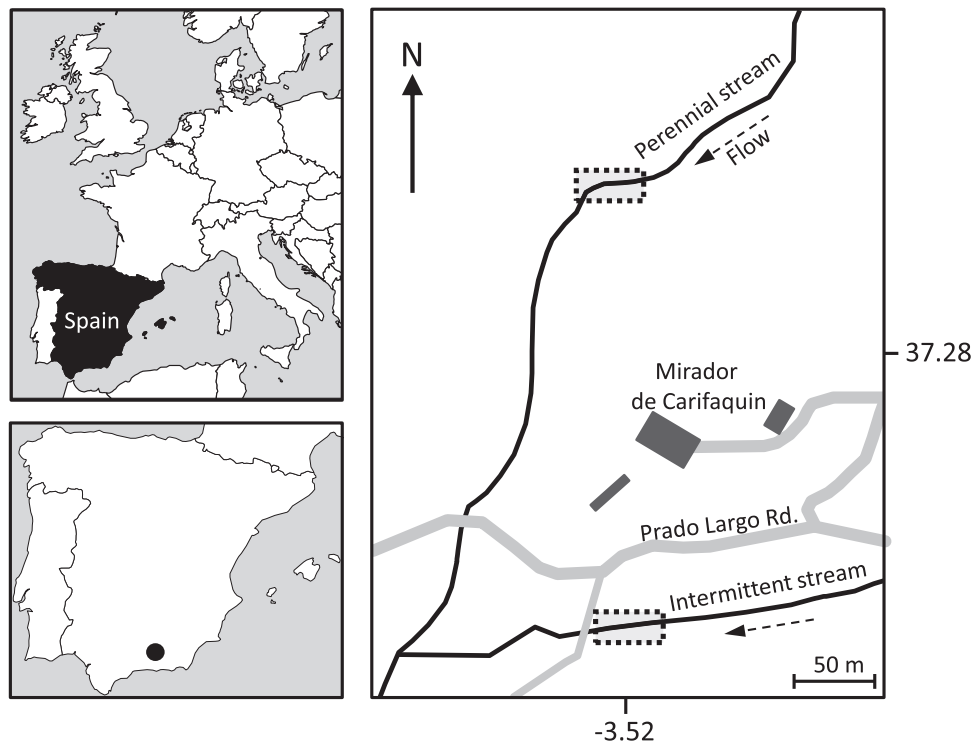


FIGURE 1 Location of the study site. The study reaches (grey areas with dotted lines) at the perennial and intermittent stream. Black lines represent the stream channels. Grey lines represent roads in the studied area. Latitude and longitude are shown on the bottom and right side

usually is very dry. After qualitative characterisation of the bed sediment across section transects, both tributaries showed similar sediment morphology (mainly cobbles and sand, and the presence of lime in pools). Also, both systems have similar riparian vegetation (dominance of *Cyperaceae*, *Salix* sp. and *Poaceae*). These systems were selected because even though they are near each other (~250 m), they present contrasting flow regimes. Although one has a naturally perennial flow regime, the other has an intermittent regime due to water abstraction for agricultural purposes. As a consequence of this anthropogenic pressure, the intermittent stream typically dries up completely during August and September (end of the dry season). However, the duration of the dry period might vary depending on annual conditions.

2.2 | Survey design and sample processing

Benthic macroinvertebrate samples were collected monthly over 12 months between October 2013 and September 2014. On each sample occasion, two riffle and two pool mesohabitats for each stream were identified as sampling sites along a 100 m reach. The same pools and riffles were sampled every month. Each month, instantaneous measurements of oxygen concentration, conductivity, and pH were taken to characterise the mesohabitats using a VWR symPHony multiparameter probe (VWR International Eurolab S.L., Barcelona, Spain; Figure 2 and Table S1). The flow (m^3/s) was quantified at each riffle and pool during every visit by measuring the width of the channel and the average depth of the section with a tape

measure, and the velocity of the water with a Global Water digital flowmeter (Global Water Instrumentation, Rancho Cordova, CA). Then, the community of macroinvertebrates inhabiting the streambed of each sampling site was collected quantitatively with a Surber sampler net (0.1 m^2 area and 250 mm mesh size; EFE & GB NETS; Cornwall, UK) over 3 min. On the basis of preliminary sampling activities, the narrowness of the channel (Figure 2 and Table S1) and length of the mesohabitats (0.5–4 m) in the sampling sites, two Surbers samples per treatment (each combination of factor levels: pool-intermittent, pool-perennial, riffle-intermittent, riffle-perennial; eight Surbers per date) were taken as representative sampling units. Samples were preserved in 70% ethanol for later processing in the laboratory. The efficiency of sampling size was later validated by comparing the observed and predicted macroinvertebrate richness based on Hills numbers (Figure S1).

In the laboratory, macroinvertebrates were identified to the lowest possible taxonomic level (Table S2) and counted. The taxonomic composition and relative abundance of each taxon were then used to calculate the Shannon–Wiener diversity index for each sampling site and date. The Shannon–Wiener diversity was calculated by setting a base sample size and using rarefaction and extrapolation based on Hill numbers (Chao et al., 2014; Hsieh, Ma, & Chao, 2014) using the R-package iNEXT (Hsieh et al., 2014; R Core Team, 2018).

Trophic information of individuals from all collected taxa, except for those identified as fluidophagous, was obtained by examination of the gut contents using the transparency method of Bello and Cabrera (1999). Following Peralta-Maraver, López-Rodríguez, and Tierno de

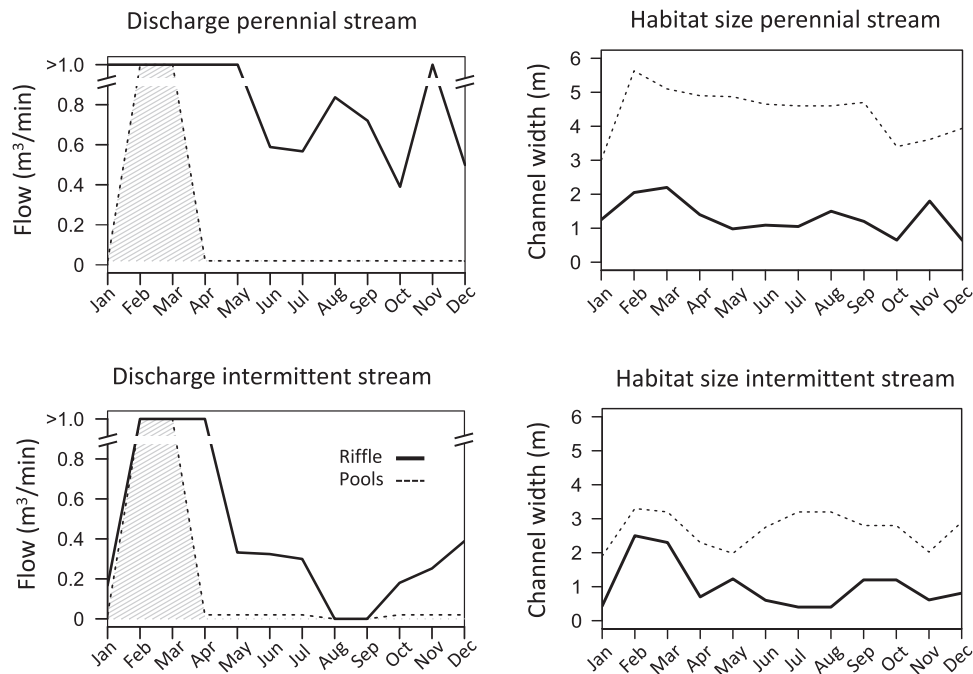


FIGURE 2 Average discharge measurements for pools and riffles at each site and habitat size, measured as the channel width in the sampled pools and riffles. Habitat size was measured as the channel width in the sampled pools and riffles

Figuroa (2017), gut contents of up to 30 individuals from the same taxon (node) and each sampling point and date were examined to account for possible changes in diet with time. Whole individuals were introduced into vials with Hertwig's liquid and heated in an oven at 65°C for a period of 6–24 hr (depending on the body size and hardness of the exoskeleton when present). This process rendered the animals transparent without affecting the gut contents. Subsequently, individuals were examined under a microscope. First, at $\times 40$ magnification to determine the total percentage of food content and second, at $\times 400$ magnification to determine the relative percentage of each type of food item—prey, fine particulate organic matter, diatoms, fungi, coarse particulate organic matter, pollen or unknown. Information from gut contents informed diet composition and the percentages of the various resources consumed by each taxon, giving a quantitative value for the links composing the actual food webs. The applied transparency method did not allow the identification of gut content in fluidophagous organisms. Their trophic information was added following Tachet, Richoux, Bournaud, and Usseglio-Polatera (2010), but they were not included in the food webs.

First, trophic information was used to build the food webs for different sampling sites throughout the study period. After Peralta-Maraver et al. (2017), trophic links between consumers and resources were constructed based on the proportion of ingested items, here referred to as dietary proportions (quantitative food webs). This methodology allowed the quantification of temporal dietary shifts of consumers due to ontogenetic changes. Second, the topology of the resultant food webs was captured by constructing binary matrices and matrices based on dietary proportions. Third, food-web

descriptors, including the number of nodes, number of links, links per node, connectance, and the proportion of omnivorous, cannibal, intermediate, top, and basal nodes, were also measured. Food webs were built and analysed using R-package Cheddar (Hudson, Reuman, & Emerson, 2015) to obtain the set of basic structure and food-web complexity indexes (Table S3).

2.3 | Statistical analysis

Nonmetric multidimensional scaling (NMDS) models were applied to compare the dissimilarities in community composition and food-web topology between mesohabitats (pool vs. riffle) and flow regime (intermittent vs. perennial regime) during the study period. Community composition and food-web topology were compiled monthly by treatment (mesohabitats \times flow regime; four treatments). Then, the quantitative Bray-Curtis similarity index was used to build the distance matrix between treatments during the study period. Relative abundances of taxa and consumption values of links were transformed using Wisconsin double standardization (Bray & Curtis, 1957) to improve detection by similarity index (Oksanen, 2015). Subsequently, the effect of mesohabitat and river regime on the community composition and the food-web topology was evaluated by fitting these factors to the ordinations. Food-web descriptors were also fitted to the ordination based on the food-web topology. The degree of association between variables fitted into the ordinations was assessed by comparing the model of pairwise interactions with 1,000 permutations of a given null model. Samples were nested by sampling date (strata = date in the *envfit* function, see below) during

the fitting routine to control for differences associated with temporal replication. In this manner, differences across treatments did not confound interpretation of variation during the year. Then, following Bogan, Boersma, and Lytle (2013), we applied indicator species analysis (Dufrêne & Legendre, 1997) to identify whether particular taxa were indicative of each treatment. Also, we adopted this analytical framework to identify the indicative trophic interactions of each treatment (indicator interaction analysis).

Finally, two-way analysis of variance (ANOVA) tests were fitted to assess differences in Shannon–Wiener diversity and food-web descriptors between mesohabitat and river regimes. The dependency structure of the residuals with the sampling date was incorporated in the previous ANOVA tests as a correcting factor. In this manner, we accounted for repeated measures (potential nondependence of residuals with sampling date in the ANOVA tests) and potential noise related to the temporal dynamics of the macroinvertebrate community. Underlying assumptions of normality and homoscedasticity in ANOVA tests were validated after Zuur, Ieno, Walker, Saveliev, and Smith (2009).

All statistical analyses were performed using the R software platform. NMDS ordinations and subsequent variable fitting were carried out using the functions *metaMDS* and *envfit* of the R package *Vegan* (Oksanen et al., 2013). Indicator species and interaction analyses were carried out using the function *multipatt* of the R-package *indicspecies* (de Cáceres, Jansen, & de Cáceres, 2015).

3 | RESULTS

A total of 14,748 macroinvertebrates belonging to 88 taxa were collected. From the gut content analysis (Table S2), 400 trophic interactions (links) were identified (data of the food-web descriptors are available in Supporting Information data set 1). All the sampled communities were dominated mainly by Ephemeroptera (35%), Diptera (32%) and Plecoptera (15%), with a relatively good representation of Oligochaeta (15%) and Coleoptera (3%) (Table S2) and a lower presence of Hemiptera and some noninsect orders. Food-web complexity indexes fluctuated notably over time. However, they showed the highest complexity from February to May in all sites (Figure S2), and a sharp decrease in complexity over summer. Diversity, the number of nodes and links decreased during the dry season under perennial flow conditions, whereas they collapsed drastically when surface water disappeared under intermittent conditions (Figure S2). However, recovery to pre-drought values was very rapid in both riffle and pool communities and some of the community descriptors reached even higher values than those before the drought (Figure S1).

3.1 | Community composition and food-web topology analysis

The NMDS ordination models based on community composition and food-web topology had a very high goodness of fit between the distances in the ordination and the data (linear R^2 and nonmetric fit

$R^2 > 0.7$ in both cases; Shepard plots of the ordination are available as Figure S2). Consequently, original dissimilarities in the community composition and food-web topology were well preserved in the two dimensions of the ordination. The NMDS ordination, based on community composition discriminated between mesohabitats (Factor 1) and flow regimes (Factor 2) along axis 1, drawing the four treatments as different group treatments (Figure 3a). Even though differences between previous factor levels were detected as significant after variable fitting into the ordination, differences between studied assemblages were better explained by mesohabitat than by flow regime (higher R^2). Differences in food-web topology between assemblages comparing pools and riffles were also stronger than those between different flow regimes, particularly when comparing communities of pools (no significant differences as 95% confidence interval around centroids of pools overlap; Figure 3b). In other words, the links identity, links arrangement, and their consumption value differed between mesohabitats more than between the perennial and anthropogenic flow regime.

Food-web descriptors showed a significant increase in complexity and size of the food webs in riffles under both intermittent and perennial regimes (mean value and standard deviation of food-web complexity metrics is available as Table S4). ANOVA tests comparing food-web complexity indexes and Shannon–Wiener diversity also showed significant differences between habitats and flow regimes for almost all the studied metrics (Figure 3c,d; Table S5). Food webs showed a marked trend of decline in size, complexity, and diversity within pools and under perennial flow. Food webs in pools were characterised by a higher proportion of basal nodes, a higher degree of cohesion (connectance), and a higher proportion of cannibal species in comparison with riffles (Figure 3c). Similarly, the proportion of basal nodes was also higher under perennial conditions, whereas the proportion of top predators did not differ significantly (Figure 3d).

3.2 | Indicator taxa and trophic interactions

Indicator taxa analysis identified several significant indicators that mainly differed between the four treatments ($A > 0.85$; Table 1). More diverse indicative taxa were recorded from riffles than from pools, both in the perennial and the intermittent stream. Indicator taxa of riffles under intermittent conditions were slightly more diverse than in perennial sites, including the typical taxa of temporary water systems (e.g., Tipulidae). Indicator trophic-interaction analysis also identified several unique feeding links for different treatments with the sole exception of pools under intermittent conditions (Table 2). Also, some indicative interactions included nonindicative taxa in riffles of perennial (*Ecdyonurus* sp., *Wormaldia* sp. and Stratiomyidae; Table 2) and intermittent flow sites (*Hydropsyche* sp., *Isoperla* sp., Prosimulini, *Polycentropus* sp.; Table 2). This result suggests distinctive diet preferences of common taxa depending on the flow regime. Moreover, the number of indicative trophic interactions, including those that included nonindicative taxa, was notably higher in riffles under intermittent conditions.

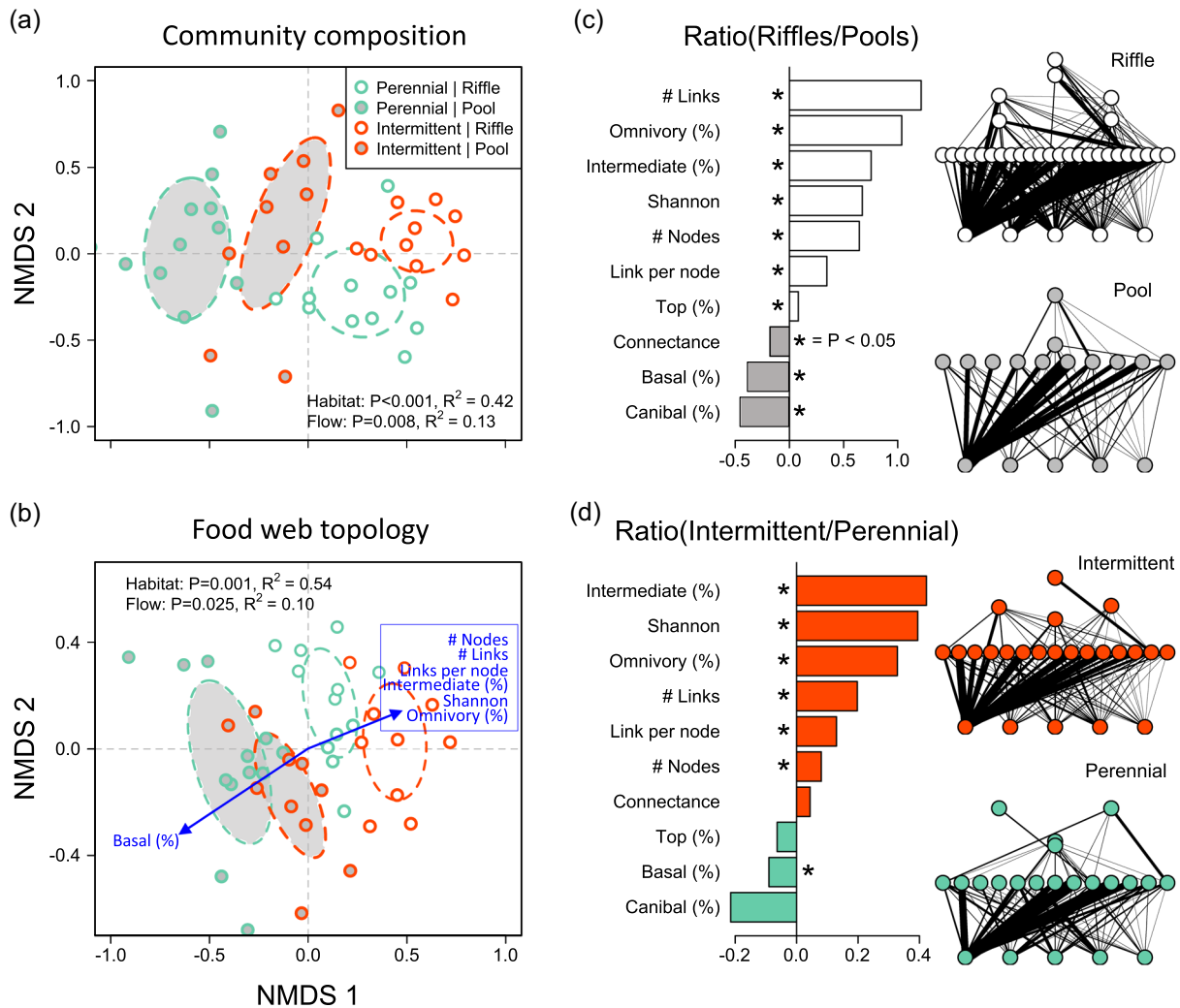


FIGURE 3 Nonmetric multidimensional scaling (NMDS) ordination models based on Bray-Curtis index comparing dissimilarities in the community composition (a, stress = 0.21) and the food-web topology (b), overlapped with those food-web descriptors (blue) that were significantly correlated ($p < .05$) with the ordination (b, stress = 0.53). Ellipses show the 95% confidence intervals on the location of centroids for each treatment. Differences in food-web descriptors and Shannon-Wiener diversity (Shannon) between pools and riffles (c) and flow regimes (d), expressed as the ratio between mean estimates for the factor levels (pools vs. riffles for mesohabitat factor; perennial vs. intermittent for flow regime factor). Asterisks denote significant differences based on the ANOVA tests. Food-web diagrams show model conditions for the different mesohabitats and flow regimes

3.3 | Similarity of communities inhabiting pools and riffles

During the year, the community composition and food-web topology of pools and riffles showed periods of great similarity (Bray-Curtis similarity index) followed by periods in which communities were very different (Figure 4). The Bray-Curtis similarity values comparing mesohabitats reached higher values between January and April, coinciding with a period of heavy rain (and concomitant increase in flow discharge; Figure 2). The range of similarity values fluctuated markedly during late autumn, winter, and spring seasons, whereas they tended to be smaller during summer

(dry season). Amplitudes were higher (higher sensitivity to variation) for community composition than for food-web topology, but the phase was reasonably consistent in both habitats (~3-months phase). However, the annual pattern of similarity between habitats differed notably when comparing flow regimes. Under intermittent conditions, the phase of the annual sequence advanced in time both for community composition and food-web topology (i.e., peak in similarity occurred earlier). This pattern was more pronounced when studying food-web topology (~2 months) than for community composition (~1 month). Consequently, the arrangement and consumption values of the trophic links showed high sensitivity to small variations in the community composition.

TABLE 1 Results from the indicator species analysis for each mesohabitat (pool and riffle) at perennial and intermittent flow conditions

Regime	Mesohabitat	Taxa	A	B	IV	p value
Perennial	Pool	<i>Cloeon</i> sp. (Ephemeroptera)	0.840	0.500	0.650	.005
		Corixidae (Hemiptera)	1.000	0.330	0.580	.021
	Riffle	<i>Austropotamobius pallipes</i> (Decapoda)	0.940	0.330	0.560	.014
		<i>Calopteryx</i> sp. (Odonata)	0.970	0.420	0.640	.004
		<i>Esolus</i> sp. (Larvae) (Coleoptera)	0.800	0.420	0.580	.008
		<i>Onychogomphus</i> sp. (Odonata)	0.890	0.580	0.721	.001
		<i>Protonemura</i> sp. (Plecoptera)	0.980	0.580	0.757	.001
		<i>Tinodes</i> sp. (Trichoptera)	0.940	0.750	0.840	.001
Intermittent	Pool	<i>Stictionectes</i> sp. (Adult) (Coleoptera)	0.820	0.500	0.640	.010
	Riffle	<i>Cordulegaster</i> sp. (Odonata)	0.890	0.400	0.597	.005
		<i>Eiseniella</i> sp. (Oligochaeta)	0.852	1.000	0.923	.001
		<i>Erpobdella</i> sp. (Hirudinea)	0.875	0.500	0.661	.003
		Hemerodromiinae (Diptera)	1.000	0.300	0.548	.023
		<i>Hemimelaena</i> sp. (Plecoptera)	1.000	0.500	0.700	.001
		<i>Holocentropus</i> sp. (Trichoptera)	0.758	0.500	0.616	.015
		<i>Rhyacophila</i> sp. (Trichoptera)	1.000	0.400	0.623	.004
		<i>Sericostoma</i> sp. (Trichoptera)	0.900	0.500	0.671	.004
		Tipulidae (Diptera)	0.750	0.500	0.612	.007

Note: The indicator value (IV), the indicator value components (A and B) and the associated statistical p value (p) are shown. Asterisks indicate significance of the IV (** $p < .0001$; ** $p < .001$; * $p < .05$). IV results from calculations of A and B (see de Cáceres et al., 2015). Component A (or *specificity*) represents the probability that the sampled site belongs to the target treatment group given the fact that the organisms have been found (A = 1: maximum restriction of taxa *i* to treatment *j*), whereas component B represents the probability of finding the organisms in the sites belonging to the treatment group (B = 1: taxa *i* is found in all sites with treatment *j*).

4 | DISCUSSION

Our study showed differences in the organization, trophic structure, and traits composition of benthic macroinvertebrates between mesohabitats and flow regimes. Our findings agree with the widely reported increase in diversity and food-web complexity of communities inhabiting riffles compared to pools (e.g., Brown & Brussock, 1991; Cheshire, Boyero, & Pearson, 2005). Contrary to our predictions and in contrast to previous studies (e.g., Bogan et al., 2013; Datry, Larned, Fritz, et al., 2014; Lu et al., 2016), we detected an increasing effect of anthropogenic flow intermittency on food-web complexity indexes and Shannon–Wiener diversity.

Most species inhabiting lotic environments are vulnerable to nonnatural drought and modifications of habitat due to flow intermittency may remove sensitive taxa with detrimental impacts on community food webs (see Ledger et al., 2013). Nevertheless, this pattern might not be evident when analysing basic structural network complexity descriptors. Experimental approaches assessing the effect of drought on food webs show that compensation occurs in connectance and link density when better-adapted taxa replace less tolerant taxa with K-selected traits (Ledger et al., 2013). Recovery after drought by benthic macroinvertebrates is generally rapid (Boulton, 2003), especially in Mediterranean streams where organisms are well adapted to survive natural drying (López-Rodríguez

et al., 2012). This swift recovery reflects the long evolutionary history of drought in these aquatic environments (Boulton, 2003) and the intermittency in the streams we studied seems to act more as an intermediate disturbance than an extreme event for the benthic community. Thus, the intermediate disturbance hypothesis (IDH) may be a plausible explanation of our results. The IDH predicts that intermediate levels of physical disturbances maximise biodiversity and complexity in natural communities, whereas extreme episodes shrink it drastically, leading to either extinction of many taxa or dominance of the best adapted (Connell, 1978; Grime, 1973; Horn, 1975). This hypothesis has been widely applied in lotic studies (e.g., Death & Winterbourn, 1995; López-Rodríguez et al., 2012; Ward & Stanford, 1983) and might explain why the diversity, number of nodes and food-web complexity are higher under intermittent conditions in our study. Intermittent conditions may also promote the appearance of more niches that can be exploited by the organisms (McIntyre & Lavorel, 1994). Results from our indicator taxa and trophic-interaction analysis also support this, particularly for riffles. First, a more diverse set of indicative taxa was detected under anthropogenic flow intermittency. Second, we observed that nonindicative taxa, common both under perennial and intermittent conditions, exploit new different trophic resources under intermittent conditions producing new interactions (larger trophic niche; e.g., *Hydropsyche* sp., Prosimulini) and resulting in new distinctive links.

TABLE 2 Results from the indicator interaction analysis for each mesohabitat (pool and riffle) at perennial and intermittent flow conditions (see Table 1 for details)

Regime	Mesohabitat	Consumer	Resource	A	B	IV	p value	
Perennial	Pool	<i>Cloeon</i> sp. (Ephemeroptera)	Pollen	0.687	0.583	0.633	.022	
		<i>Cloeon</i> sp.	FPOM	0.676	0.583	0.628	.016	
	Riffle	<i>Astropotamobius pallipes</i> (Decapoda)	FPOM	1.000	0.333	0.521	.024	
		<i>Astropotamobius pallipes</i>	Orthocladinae (Diptera)	1.000	0.333	0.577	.017	
		<i>Calopteryx</i> sp. (Odonata)	Orthocladinae	1.000	0.250	0.500	.043	
		<i>Ecdyonurus</i> sp. (Ephemeroptera)	CPOM	1.000	0.500	0.707	.002	
		<i>Esolus</i> sp. (Larve; Coleoptera)	FPOM	0.868	0.417	0.601	.010	
		<i>Esolus</i> sp. (Larve)	Fungi	0.832	0.417	0.589	.009	
		<i>Esolus</i> sp. (Larve)	Pollen	0.956	0.333	0.565	.019	
		<i>Esolus</i> sp. (Larve)	Diatoms	0.884	0.417	0.607	.003	
		<i>Onychogomphus</i> sp. (Odonata)	<i>Baetis</i> sp.	1.000	0.417	0.645	.001	
		<i>Onychogomphus</i> sp.	Chironomini (Diptera)	0.764	0.417	0.564	.011	
		<i>Onychogomphus</i> sp.	CPOM	1.000	0.250	0.500	.045	
		<i>Protonemura</i> sp. (Plecoptera)	FPOM	0.934	0.583	0.738	.001	
		<i>Protonemura</i> sp.	Fungi	0.884	0.583	0.718	.001	
		<i>Protonemura</i> sp.	CPOM	1.000	0.500	0.707	.001	
		<i>Stratiomyidae</i> sp. (Diptera)	Fungi	1.000	0.250	0.500	.049	
		<i>Tinodes</i> sp. (Trichoptera)	CPOM	0.863	0.750	0.805	.001	
		<i>Tinodes</i> sp.	Fungi	0.824	0.750	0.786	.001	
		<i>Tinodes</i> sp.	FPOM	0.806	0.750	0.777	.001	
		<i>Tinodes</i> sp.	Pollen	0.699	0.750	0.724	.001	
		<i>Wormaldia</i> sp. (Trichoptera)	<i>Wormaldia</i> sp.	1.000	0.250	0.500	.042	
	Intermittent	Pool	–	–	–	–	–	–
		Riffle	<i>Cardulogaster</i> sp. (Odonata)	Orthocladinae	0.860	0.400	0.587	.019
<i>Cordulegaster</i> sp.			FPOM	0.897	0.300	0.519	.038	
<i>Cordulegaster</i> sp.			CPOM	0.811	0.300	0.493	.044	
Hemerodromiinae (Diptera)			Diatoms	1.000	0.300	0.548	.022	
Hemerodromiinae			Fungi	1.000	0.300	0.548	.022	
Hemerodromiinae			FPOM	1.000	0.300	0.548	.022	
<i>Hemimelaena</i> sp. (Plecoptera)			CPOM	1.000	0.300	0.548	.017	
<i>Hemimelaena</i> sp.			Chironomini	1.000	0.300	0.548	.017	
<i>Hemimelaena</i> sp.			Orthocladinae	1.000	0.300	0.548	.022	
<i>Hemimelaena</i> sp.			FPOM	1.000	0.300	0.548	.017	
<i>Holocentropus</i> sp. (Trichoptera)			Tanypodiinae (Diptera)	0.708	0.400	0.532	.013	
<i>Hydropsyche</i> sp. (Trichoptera)			<i>Baetis</i> sp.	0.976	0.600	0.765	.001	
<i>Isoperla</i> sp. (Plecoptera)			FPOM	0.790	0.600	0.688	.002	
<i>Isoperla</i> sp.			Fungi	0.758	0.600	0.674	.002	
<i>Isoperla</i> sp.			CPOM	0.792	0.400	0.563	.025	
<i>Isoperla</i> sp.			Pollen	1.000	0.300	0.548	.020	
<i>Isoperla</i> sp.			<i>Leuctra</i> sp.	0.908	0.300	0.522	.036	
<i>Isoperla</i> sp.			Diamesinae (Diptera)	0.745	0.300	0.473	.044	
<i>Polycentropus</i> sp. (Trichoptera)			CPOM	1.000	0.300	0.548	.022	
Prosimulini (Diptera)			Orthocladinae	0.920	0.500	0.678	.003	
<i>Sericostoma</i> sp. (Trichoptera)			Pollen	1.000	0.500	0.707	.001	
<i>Sericostoma</i> sp.			CPOM	0.836	0.500	0.646	.002	
<i>Sericostoma</i> sp.			Fungi	0.807	0.400	0.568	.007	
Tipulidae (Diptera)			Orthocladinae	0.862	0.300	0.509	.025	
Tipulidae			Pollen	0.857	0.300	0.507	.029	

Abbreviations: CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter; IV, indicator value.

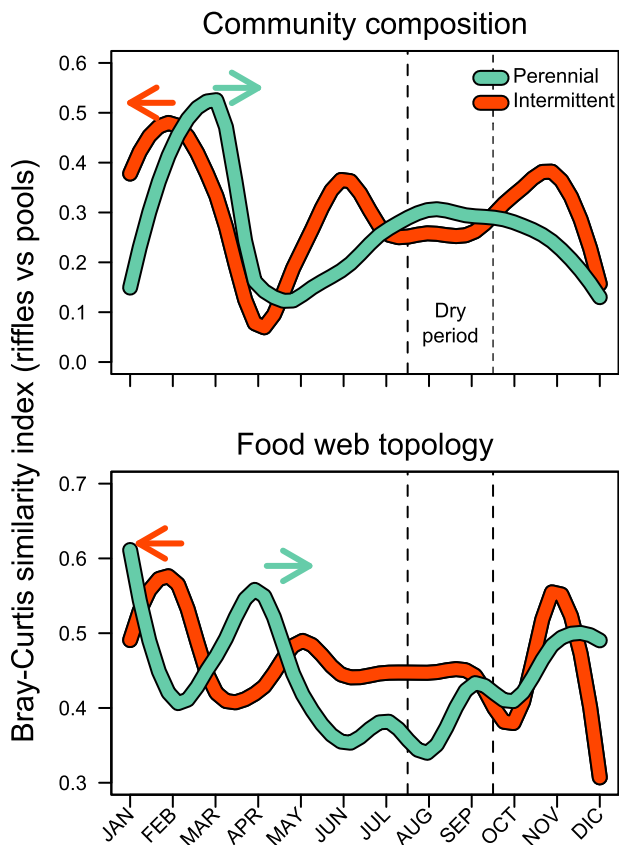


FIGURE 4 Bray-Curtis similarity index across the year for the community composition and food-web topology when comparing pools and riffles under different flow regimes. Arrows represent the direction of the mismatch for the annual dynamic of similarity values when comparing flow regimes

Applying similar analytical methods on community composition, previous studies have determined that the assemblages inhabiting pools and riffles are discrete biological communities (Cheshire et al., 2005; Herbst et al., 2018). However, this is the first time that the integrity (as a distinct assemblage of organisms) of these communities has been compared using food-web topology providing a more unified measurement. We also measured for the first time how the integrity of these communities (Bray-Curtis index) oscillates during the year. Delineating communities is a challenging task but critical to defining ecosystems (see Peralta-Maraver et al., 2018; Post, Doyle, Sabo, & Finlay, 2007; Smock, Gladden, Riekenberg, Smith, & Black, 1992). Here, we also evidenced the importance of the temporal scale when delineating communities, particularly when comparing mesohabitats such as pools and riffles. We report a higher similarity between communities inhabiting pools and riffles coinciding with high flow events, potentially a result of the homogenisation of the whole system. However, communities inhabiting different mesohabitats quickly regained their integrity when discharge declined. Nevertheless, as a result of anthropogenic flow intermittency, the phase of the sequential pattern of similarity between the

communities in the two mesohabitats advances in time. The same sequence of similarity/dissimilarity phases during the year takes place in a shorter period (10 months), possibly because species that colonise intermittent flow conditions tend to have short life cycles, fast growth and active dispersal stages (i.e., *Baetis* sp. or Chironomidae species in this system) that allow them to recolonise easily after drought (Williams, 2006).

In summary, the studied benthic communities showed high capacity of recovery, to the point that a low pulse of anthropogenic flow intermittency, here as an intermediate disturbance, even promoted the increase of diversity and complexity. However, particular caution must be taken when interpreting these trends. The perennial system showed a strong mismatch in the structural dynamics of the benthic communities inhabiting pools and riffles. Our findings demonstrate the high uncertainty regarding the response of communities to the future increase in water scarcity resulting from climate change and the associated intensification of water abstraction (Jackson et al., 2001; Larned et al., 2010). Mediterranean stream communities have a great adaptive resiliency to drought events (Boulton, 2003), and as reported here, many taxa might face anthropogenic-caused intermittent flow conditions. However, stream organisms from higher latitudes are mostly adapted to permanently flowing waters (Lake, 2003; Lytle & Poff, 2004) and projections of intermittent flow conditions associated with climate change predict detrimental impacts on these communities (Ledger et al., 2013). The IDH applied here suggests that diversity and complexity metrics, and by extension community stability (McCann, 2000), follow a hump-shaped pattern (convex-shaped effect) along the disturbance gradient (Townsend, Scarsbrook, & Dolédec, 1997). Consequently, if the stream community stage is near the top of this hump-shaped pattern, just a small increase in the dry period might overcome its recovery capacity and cause extinctions of several specialist taxa and pronounced collapses of the food webs. Thus, our results may contribute to stream management decisions regarding the permissible periods of water abstraction, especially during the dry season in Mediterranean areas.

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