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Effects of antecedent drying events on structure, composition and functional traits of invertebrate assemblages and leaf-litter breakdown in a former perennial river of Central Apennines (Aterno River, Abruzzo, Central Italy)

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Abstract

Because of global change and increasing anthropogenic pressures, non-perennial rivers and streams are predicted to drastically increase in the European-Mediterranean region. Some river basins already subject to reduced levels of available superficial flow may present a further reduction, with a significant increase in intermittence phenomena and complete drought of former perennial rivers. In this context, a sound knowledge of the ecological effects of increasing drying events on these watercourses may help to better predict impacts of the altered flow regime on structure and functions of freshwater ecosystems. In this paper, we assessed the long-term response of invertebrate assemblages and ecosystems processes to antecedent drying events (drying memory) in a Central Apennine river (Italy). We demonstrated that compared to the perennial reach, the 7-km downstream intermittent site, after more than 1 year from a complete superficial flow resumption, still conserved the 'memory' of past disturbance with marked differences in structure, composition and functional traits of assemblages which, in turn, negatively influenced the leaf-litter breakdown process. Despite total abundance and taxa richness were on average higher at the intermittent site, antecedent droughts determined a decline of shredders and scrapers and an increase of collectors. In addition, some more sensible, semivoltine and rheophile taxa were replaced by generalist, multivoltine and more resistant taxa. Our findings confirm and extend the 'drying memory' hypothesis and suggest that irregular drying events in former perennial Apennine rivers may have dramatic long-term effects on both structure and functions of lotic ecosystems.

KEYWORDS

alpha diversity, Apennine rivers, beta diversity, drying memory, functional traits, irregular droughts, leaf-litter breakdown, macroinvertebrate assemblages, Mediterranean

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1 | INTRODUCTION

Global climate changes and human pressures (i.e., dams, water abstraction for agriculture use and eutrophication) are the main drivers of the worldwide qualitative and quantitative degradation of freshwater resources (Grill et al., 2019; Vörösmarty et al., 2000). Extreme weather events cause serious alterations in the hydrological regime at various spatial scales, involving both surface waterbodies (Woodward et al., 2016) and groundwater aquifers (Cuthbert et al., 2019; Taylor et al., 2013), with a drastic decrease in the discharge of watercourses in periods of drought alternating with periods of intense rainfall and flash-flood events (Beniston et al., 2007; Di Baldassarre et al., 2017). Non-perennial rivers and streams now represent more than 50% of the global river network (Datry, Larned, et al., 2014; Skoulikidis et al., 2017), but these numbers are predicted to drastically increase in some climatic and geographic regions (Acuña et al., 2014; Arnell, 1999; Döll & Schmied, 2012). For example, in the coming decades, a decrease in the discharge of rivers and streams in the European-Mediterranean region is expected (Milly et al., 2005; Skoulikidis et al., 2017); some river basins already subject to reduced levels of available superficial flow may present a further reduction of 10% by 2030, with a significant increase in the intermittence phenomena and complete drought of former perennial rivers (IPCC, 2018). Under this scenario, an adequate knowledge of the ecological effects of increasing drying events would be essential to better understand future impacts of the altered flow regime on freshwater ecosystem structure, processes and services (Datry et al., 2018; Larned et al., 2010; Ledger et al., 2013). While a consolidated literature exists on the effects of seasonal droughts on non-perennial rivers (Datry et al., 2017; Lake, 2011 and references therein), little is known about the ecological impacts of dry events on rivers and streams becoming irregularly intermittent which are thus in a transitional phase from perennial to temporary watercourses (i.e., former perennial rivers). In addition, recent field and mesocosm experiments on streams/rivers which are experiencing flow regime modification gave contrasting results on the effects of antecedent droughts and on the recovery capacity of ecosystem structure and processes (Bruno et al., 2020; Dolédec et al., 2017; Doretto et al., 2018; Leigh et al., 2016; Leigh et al., 2019; Majdi et al., 2020; Pařil et al., 2019; Piano, Doretto, Falasco, Fenoglio, et al., 2019; Piano, Doretto, Mammola, et al., 2020; Pinna et al., 2016, Vander Vorste et al., 2016).

In the Mediterranean, the Central Apennine represents a key geographic area where the combined effects of climate change and increasing water demand on hydrology and flow regime of perennial watercourses are expected to be more intense (Skoulikidis et al., 2017). For this reason, we started a long-term study on one of the most important (in terms of total length and discharge volumes) perennial watercourse of Central Apennine. In the last decades however, some reaches of the river were subjected to an irregular recurrence of complete summer drought (Pinna et al., 2016; Vignini, 2009). For our field experiments, we selected two nearby sites of the river characterized by a different hydrological regime (perennial vs. intermittent), but during the period of observation, both sites

showed similar flow conditions, and no seasonal drought was recorded at the intermittent site. This condition allowed us to assess possible ecological impacts of antecedent droughts on irregularly intermittent streams and rivers and to test the so-called 'drying memory' (Datry et al., 2011).

Based on recent research on Alpine rivers and streams (Piano, Doretto, Falasco, Fenoglio, et al., 2019; Piano, Doretto, Mammola, et al., 2020) and results of a previous study conducted on a 40-km downstream reach of the same river (Pinna et al., 2016), we hypothesized that antecedent drought conditions may extend their influence also after the return of the natural flow regime. In this context, we predicted that former droughts at the irregularly intermittent site would affect structure, composition and functional traits of invertebrate assemblages with possible negative repercussions on the process of leaf-litter breakdown.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The field experiment started on January 2018 and was conducted in a second-order reach of the Aterno River (Abruzzo, Central Italy), one of the main Italian watercourses (total length = 152 km; catchment area = 3190 km²; mean discharge at the mouth = 57 m³ s⁻¹) discharging into the Adriatic Sea south of the Po River (Figure 1). In this reach, located about 15-km distance from spring source, we selected two sampling sites: the upstream permanent site (P_s) (coordinate 42°26'42.78"N; 13°16'25.29"E; altitude 718 m asl) never experienced seasonal flow cessation, while the 7-km irregularly intermittent downstream site (I_s) (coordinate 42°23'27.82"N; 13°18'58.01"E; altitude 657 m asl) showed an irregular pattern of seasonal intermittency with extended period of complete drought (from August to November) in the years 2006, 2007, 2011 and 2017 (Di Sabatino, pers. obs.). However, except for the different hydrological regime, the

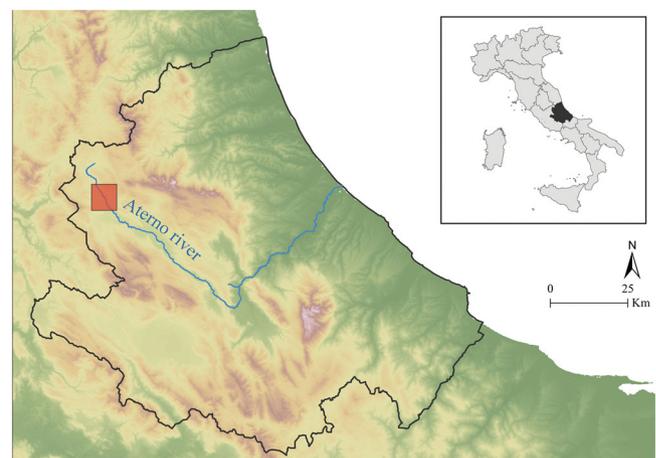


FIGURE 1 Map showing the localization of the study area on the upper course of the Aterno River

two sites are characterized by very similar hydromorphological and abiotic attributes. No substantial between-site differences were found in geological substratum composition (10% cobbles, 50% pebbles, 30% sand and 10% silt), riparian zone vegetation/extension (mainly *Populus nigra* and *Salix alba*) and water physicochemical parameters. As described above, during the 1-year period of observation, both sites showed similar flow conditions; therefore, our experimental design (Figure 2) allowed us to ascertain if the II_S site still conserved the 'memory' of antecedent drying events.

2.2 | Sampling protocol and laboratory procedures

The survey was conducted from January 2018 to February 2019, with a sampling frequency of about 40 days, for a total of seven sampling dates. To guarantee the full comparability of data, at P_S and II_S sites, abiotic and biological parameters were recorded on the same sampling day by the same operators.

Structure and composition of benthic invertebrate assemblages and leaf-litter breakdown were assessed by using the LN method (Di Sabatino et al., 2016). Two PVC nets of 0.1 × 0.1 m (0.01 m²) were filled with a single layer of air-dried and pre-weighed *P. nigra* leaves (Figure S1). The foliar material was collected along the riparian zone of the study area in the period of abscission (October to November 2017) and was then left in a dry and ventilated room to complete the dehydration process. Each sampling unit consisted of four overlying LN with a total area colonizable by invertebrates equal to 0.08 m² (0.01 m² × 4 × 2); see Di Sabatino et al. (2016, 2018) and Cristiano et al. (2019) for details on construction procedures. At each sampling occasion in both sites, six assembled LN were randomly placed at the stream bottom and fixed to the substrate with boulders and pebbles. In total, 84 LN (6 replicates × 2 sites × 7 sampling dates) were deployed. After about 40 days of immersion, LN were carefully

retrieved, labelled and transported to the laboratory in a cooled box. In laboratory, LN were opened, and the remaining leaf material was first carefully cleaned to remove inorganic substances and macroinvertebrates and successively stored in a thermostatic oven at 60°C for 72 h. The remaining leaf mass was weighed by using an analytical balance (±0.01 g), and the dry mass loss of poplar leaves was evaluated as difference between initial and remaining dry weight and expressed as percentage of dry mass loss.

The colonizing invertebrates were stored in alcohol at 70° and subsequently sorted and identified at the lowest possible taxonomic level (genus and species) using a stereomicroscope (Leica M165C).

The taxa collected were grouped into Functional Feeding Groups (FFG) (Tachet et al., 2010) and were also classified according to their biological traits following a fuzzy coding procedure (Chevenet et al., 1994). Affinity scores (0–5) in relation to 9 biological traits and 46 different modalities (Table 1) were assigned to each taxon following Tachet et al. (2010) and Di Sabatino et al. (2014). For each sample, traits modalities were weighed by taxa relative abundance and then normalized and transformed to proportions.

At each sampling occasion in both sites, some hydraulic (river width and depth, current velocity, and discharge) and physicochemical (water temperature, pH, dissolved oxygen and conductivity) parameters were measured along an orthogonal transect with a magnetic flow probe (FP-01) and a multiparameter probe (Hach Lange HQ40D Multi), respectively.

2.3 | Data analysis

Differences in hydrological (depth, current velocity and discharge) and physicochemical (temperature, dissolved oxygen, pH and conductivity) parameters recorded at P_S and II_S sites were analysed using Student *t*-tests. Of the 84 LN initially placed, 22 were lost mostly because of

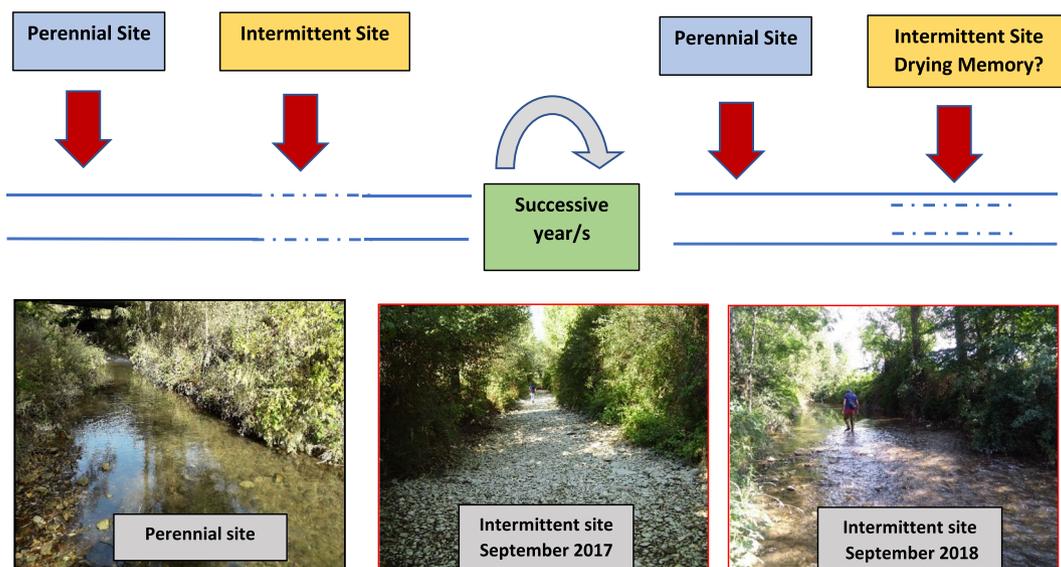


FIGURE 2 Schematic representation of the experimental design and photos showing the characteristics of the two sampling sites

TABLE 1 List and abbreviations of traits and trait modalities used in functional diversity analysis

Traits	Modalities
1. Maximum potential size	S1 < 0.25 cm S2 0.25–0.5 cm S3 0.5–1 cm S4 1–2 cm S5 2–4 cm S6 4–8 cm S7 > 8 cm
2. Life cycle duration	LC1 < =1 year LC2 > 1 year
3. Reproductive cycles	RC1 < 1 per year RC2 1 per year RC3 > 1 per year
4. Aquatic stages	AS1 Egg AS2 Larva AS3 Pupa AS4 Adult
5. Reproduction	Rep1 Ovoviviparity Rep2 Isolated eggs, free Rep3 Isolated eggs, cemented Rep4 Clutches, cemented or fixed Rep5 Clutches, free Rep6 Clutches in vegetation Rep7 Clutches, terrestrial Rep8 Asexual reproduction
6. Dissemination	D1 Aquatic passive D2 Aquatic active D3 Aerial passive D4 Aerial active
7. Resistance form	Resi1 Eggs, statoblasts Resi2 Cocoons Resi3 Housing against desiccation Resi4 Diapause or dormancy Resi5 None
8. Respiration	Resp1 Tegument Resp2 Gill Resp3 Plastron Resp4 Spiracle (aerial) Resp5 Hydrostatic vesicle (aerial)
9. Locomotion and substrate relation	L1 Flier L2 Surface swimmer L3 Full water swimmer L4 Crawler L5 Burrower (epibenthic) L6 Interstitial (endobenthic) L7 Temporary attached L8 Permanently attached

vandalism and extreme high flow conditions. From the recovered material, 23 LN were randomly chosen for each study site to have a balanced dataset ($n_{PS} = n_{IIS} = 23$). Between-site differences in structure and functional organization of invertebrate assemblages was assessed by applying Student *t*-test on values of taxa richness, total density ($\log(x + 1)$ transformed), richness of Ephemeroptera Plecoptera and Trichoptera (EPT) taxa, Simpson diversity index (1-D) and arcsin transformed percentages of shredders, collector-gatherers, collector-filterers, scrapers and predators.

Differences in the composition of invertebrate assemblages colonizing LN were evaluated by applying permutational multivariate analysis of variance (PERMANOVA) on the Bray Curtis dissimilarity matrix of square root transformed densities. Sample distances were also ordered and graphically represented by the nonMetric Multi-Dimensional Scaling (nMDS) method.

Temporal variation in beta diversity between the intermittent and permanent site was assessed by computing differences of randomly selected pair of samples, considering both presence-absence (Jaccard index) and abundance data (Bray-Curtis index). The incidence-based beta diversity index was also partitioned into the richness (nestedness) and replacement (turnover) components following Carvalho et al. (2012). The resemblance traits-by-samples matrix (Euclidean distance) was analysed with PERMANOVA to assess multivariate differences in traits composition of assemblages at both sites. Among-samples distance in traits composition was also graphically represented along the first two nMDS axes. The SIMPER routine in Primer was applied to detect the traits more responsible of the observed difference. Between-site difference in leaf-litter breakdown was assessed by applying Student *t*-test on the arcsin transformed percentages of dry mass loss of poplar leaves.

For all dependent variables, normality and homogeneity of variance assumptions were verified with Anderson-Darling and Levene tests, respectively. Statistical analyses were performed using XLSTAT 2016.02.27444 and PRIMER v6.1.16 & PERMANOVA + v1.0.6. The significance of statistical tests was set at $p = 0.05$.

3 | RESULTS

3.1 | Hydrological and physicochemical parameters

Flow discharge values confirm that the Aterno River has a typical temperate-apennine regime, with minimum flow in summer and maximum in winter-spring seasons (Figure 3).

These values did not differ significantly between the two investigated sites (P_S mean = 0.71 ± 0.57 SD $m^3 s^{-1}$; $IIS = 0.70 \pm 0.59$ $m^3 s^{-1}$; $t = 0.02$, $p = 0.983$). No significant between-site differences were also found for mean stream depth ($P_S = 0.15 \pm 0.06$ m; $IIS = 0.12 \pm 0.06$ m; $t = 0.90$, $p = 0.374$) and current velocity ($P_S = 0.38 \pm 0.20$ $m s^{-1}$; $IIS = 0.41 \pm 0.23$ $m s^{-1}$; $t = 0.36$, $p = 0.722$).

Permanent and intermittent sites showed similar values of water temperature ($P_S = 11.0 \pm 4.6^\circ C$; $IIS = 12.1 \pm 5.5^\circ C$; $t = -0.51$,

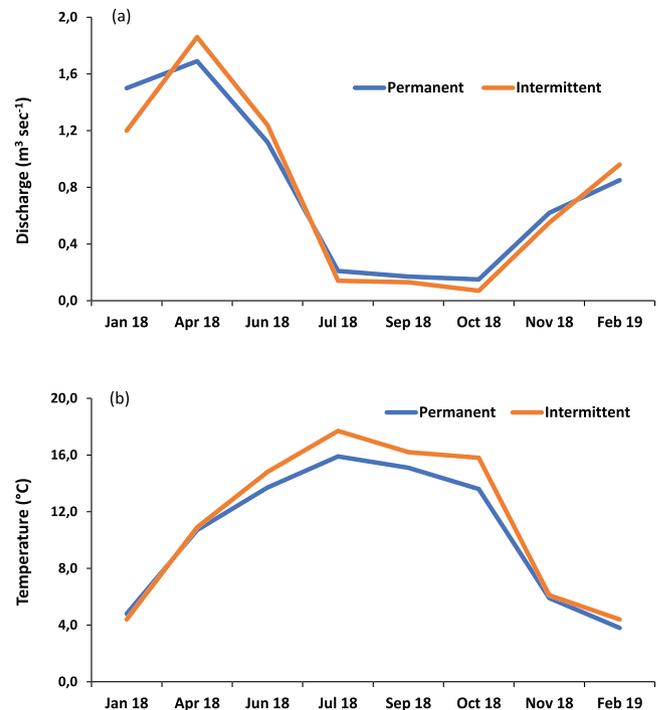


FIGURE 3 Discharge (a) and temperature (b) variations at the permanent and intermittent site of the Aterno River during the 1-year period of observation

$p = 0.616$), although slightly higher values were recorded at the intermittent site during summer low-flow condition (Figure 3). No significant differences were also found for pH ($P_S = 8.17 \pm 0.37$; $IIS = 8.29 \pm 0.34$; $t = -0.79$; $p = 0.437$), oxygen concentration ($P_S = 10.49 \pm 1.15$ $mg L^{-1}$; $IIS = 10.53 \pm 1.86$ $mg L^{-1}$; $t = 0.062$; $p = 0.95$) and conductivity ($P_S = 301 \pm 18$ $\mu S cm^{-1}$; $IIS = 300 \pm 17$ $\mu S cm^{-1}$; $t = 0.02$; $p = 0.981$) (Table 2).

3.2 | Invertebrate assemblages

A total of 44,478 individuals and 49 taxa were collected and identified (34,500 individuals and 45 taxa at IIS and 8112 individuals and 37 taxa at P_S). The two sites shared 33 taxa, while 4 and 11 taxa were exclusively found at P_S and IIS , respectively (Table S1). On average, taxa richness was significantly higher at the IIS site ($P_S = 17.3 \pm 3.6$ SD taxa; $IIS = 20.3 \pm 3.2$ taxa; $t = -3.04$, $p = 0.004$). Differences in invertebrate density were more accentuated and considerably lower at P_S site ($P_S = 4409 \pm 2770$ ind. m^{-2} ; $IIS = 18,750 \pm 11,469$ ind. m^{-2} ; $t = -7.08$, $p < 0.0001$). However, assemblages at the permanent site hosted a higher number of EPT taxa ($P_S = 7.1 \pm 1.4$ EPT taxa; $IIS = 4.9 \pm 1.3$ EPT taxa; $t = 5.43$; $p < 0.0001$) with higher values of Simpson diversity ($P_S = 0.68 \pm 0.10$; $IIS = 0.55 \pm 0.17$ 1-D; $t = 3.24$, $p = 0.002$) (Figure 4).

At the permanent site, Chironomidae dominated the assemblages (50%), followed by Gammaridae (16%) Plecoptera (10%), Trichoptera (7%) and Ephemeroptera (5.5%). The intermittent site was

TABLE 2 Physicochemical and hydrological parameters recorded at the permanent (P_S) and intermittent (I_S) site of the Aterno River during the 1-year period of observation

Parameter	Jan 2018		Apr 2018		Jun 2018		Jul 2018		Sep 2018		Oct 2018		Nov 2018		Feb 2019	
	P _S	I _S														
Temperature (°C)	4.8	4.4	10.7	10.9	13.7	14.8	15.9	17.7	15.1	16.2	13.6	15.8	5.9	6.1	3.8	4.4
pH	7.36	7.93	8.06	8.5	8.33	8.55	8.84	8.6	8.47	8.26	8.36	8.14	8.01	8.57	7.97	7.89
Conductivity (µS cm ⁻¹)	314	315	292	293	300	298	289	287	279	287	288	309	335	335	312	300
O ₂ (mg L ⁻¹)	11.73	11.58	10.2	10.4	9.32	9.34	9.39	9.45	9.82	10.28	9.84	7.11	11.62	11.42	12.48	12.27
O ₂ (% sat)	99	96	99	100.8	97.7	99.4	100.6	105	105	116	102.4	77.4	100.1	98	100.5	100
Discharge (m ³ s ⁻¹)	1.51	1.22	1.69	1.86	1.12	1.24	0.21	0.14	0.17	0.13	0.15	0.07	0.62	0.55	0.85	0.96
Depth (m)	0.23	0.18	0.26	0.22	0.19	0.16	0.1	0.09	0.07	0.05	0.11	0.08	0.16	0.13	0.16	0.17
Current velocity (m s ⁻¹)	0.68	0.65	0.65	0.8	0.58	0.66	0.17	0.24	0.18	0.15	0.14	0.07	0.41	0.36	0.45	0.49
Width (m)	7.0	7.2	6.5	7.4	6.6	7.8	6.4	7.5	6.4	7.7	5.5	7.0	6.5	7.5	6.8	7.8

Note: Depth and current velocity are mean values measured along the orthogonal transect.

characterized by a higher proportion of Chironomidae (69%) and a remarkable higher abundance of ostracods (9%), while Plecoptera and Trichoptera were less abundant (<4%). The composition of assemblages at P_S and I_S sites differed significantly (PERMANOVA, pseudo- $F_{1-45} = 35.07$; p (perm) = 0.0001), and the nMDS ordination pattern indicates a clear segregation between samples from the permanent and intermittent river reach (Figure 5). These differences were mainly due to the higher abundance of Chironomidae, the ephemeropteran *Caenis martae* and Ostracoda at the intermittent site along with a drastic reduction in the abundance of *Gammarus elivirae*, *Ecdyonurus venosus*, *Leuctra hyppopus*, and hydroptichid Trichoptera.

The two sites showed similar values of alpha diversity during the first 5–8 months after flow resumption (from April 2018 to July 2018) but, successively (from September 2018 to February 2019), assemblage richness was higher at the intermittent site (Figure 6a). Between-site beta diversity on presence-absence and abundance data showed a common pattern of temporal variation with the highest values recorded in October 2018, after about 11 months from flow resumption (Figure 6b). During the whole study period, the replacement component of beta diversity between the intermittent and permanent site was relatively more important than the nestedness component (Figure 6c). Moreover, it is interesting to note that the dissimilarity between the two assemblages increased as superficial flow decreased and reached its peak during the period of the lowest discharge (Figure 3a) when also alpha diversity at both sites attained the lowest values (Figure 6a,b).

3.3 | Functional traits and leaf-litter breakdown

The feeding traits of invertebrates sampled at both sites were mainly represented by shredders and collector-gatherers. However, shredders occurred with a notably higher percentage at the permanent site (P_S = 30.4 ± 15.0%; I_S = 5.5 ± 6.1%; $t = 8.058$, $p < 0.0001$) while collectors-gatherers were proportionally more abundant at the intermittent site (P_S = 54.3 ± 11.7%; I_S = 87.1 ± 8.0%; $t = -11.004$, $p < 0.0001$). Significant between-site differences were also found for the percentages of scrapers (P_S = 6.6 ± 4.6%; I_S = 1.4 ± 2.2%; $t = 6.142$, $p < 0.0001$) and collector-filterers (P_S = 4.8 ± 7.3%; I_S = 0.7 ± 0.9%; $t = 4.59$, $p < 0.0001$) while predators occurred with similar proportions (P_S = 3.7 ± 2.5%; I_S = 4.7 ± 3.0%; $t = -1.19$, $p = 0.240$) (Figure 7a).

Results of functional traits analysis revealed significant overall difference between assemblages sampled at the permanent and intermittent site (PERMANOVA, pseudo- $F_{1-45} = 20.26$; p (perm) = 0.001). nMDS and SIMPER analyses showed that I_S assemblages were mainly characterized by higher proportions of traits conferring resistance and resilience to drought as for example short life cycle, multivoltinism, presence of resistance forms (cocoons and diapause), tegument respiration, adaptation to the interstitial and aerial passive dispersal (Figure 8). By contrast, crawlers, semivoltine taxa with longer life cycle and gills respiration were more represented at P_S.

FIGURE 4 Taxa richness (a), log ($x + 1$) transformed abundance (b), EPT taxa richness (c) and Simpson diversity (d) of invertebrate assemblages from the permanent and intermittent site of the Aterno River during the 1-year period of observation. Bar values are mean \pm SE. Student t -tests indicated that all differences were statistically significant

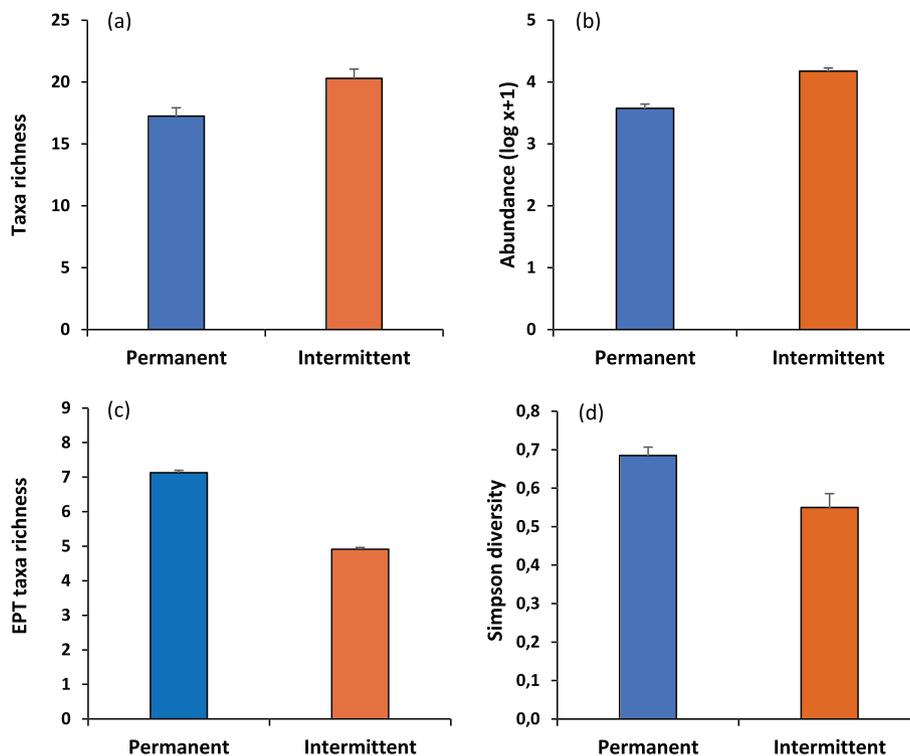
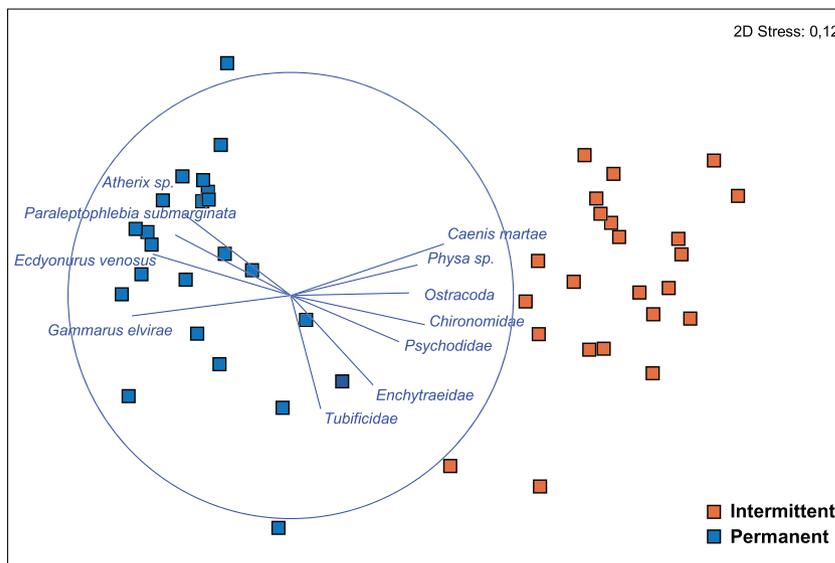


FIGURE 5 Ordination of between-samples dissimilarity in assemblage composition (Bray Curtis index on square root transformed abundance) along the first two nMDS axes. Vectors of taxa with Pearson's correlation > 0.5 are superimposed to the graph. Samples of the permanent and intermittent site are indicated with different colours



Differences in taxonomic and functional diversity of communities in the investigated stream reaches also influenced the leaf-litter breakdown process (Figure 7b). In fact, the mean percentage of dry mass loss of *P. nigra* leaves was significantly higher at the permanent site ($P_5 = 74.4 \pm 12.2\%$; $II_5 = 62.6 \pm 12.6\%$; $t = 3.17$, $p = 0.003$).

4 | DISCUSSION

During the period of investigation, the two sites on the Aterno River were characterized by very similar hydrological and environmental

conditions, and no substantial differences were found for all abiotic parameters investigated. However, the biological attributes of assemblages at P_5 and II_5 varied significantly. According to our predictions, in less than 7-km distance, we found a considerable shift in community structure and composition. Insect taxa, mainly Plecoptera, Trichoptera and Ephemeroptera (Heptageniidae and Leptophlebiidae) and crustacean gammarids, were more represented at the upstream permanent site while Chironomidae, Ephemeroptera (*Caenis martae*), oligochaetes and Ostracoda were more abundant at the intermittent site. A drastic reduction of EPT taxa and a considerable increase of chironomid abundance was already reported in intermittent alpine

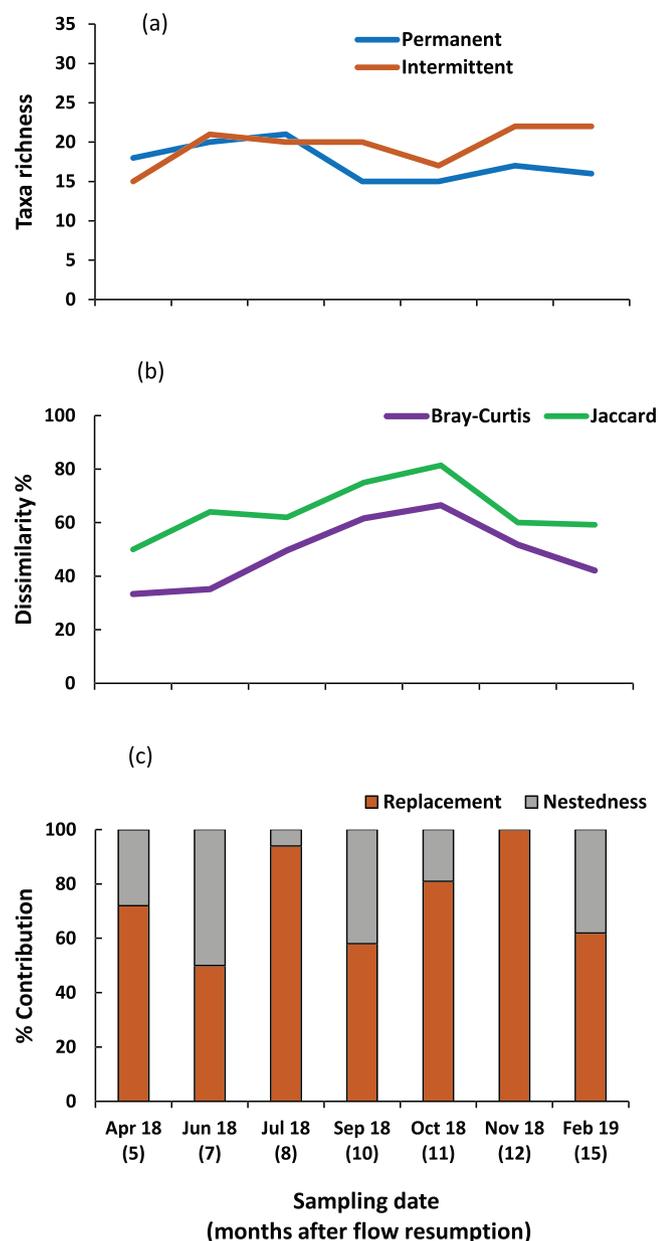


FIGURE 6 Variations in alpha diversity (a), beta diversity (b) and replacement/nestedness components of beta diversity (c) at the permanent and intermittent site of the Aterno River during the 1-year period of observation

stream reaches after more than 6 months from flow resumption (Piano, Doretto, Falasco, Fenoglio, et al., 2019) and in Mediterranean rivers after 4 weeks from the return of the superficial flow at the intermittent sites (Sánchez-Montoya et al., 2018). At II_5 , the almost total substitution of *Gammarus elvirae* with ostracod microcrustaceans was remarkable. In fact, Ostracoda are considered good dispersers with resistance/resilience traits well adapted to colonize temporary ponds or intermittent streams (Dole-Olivier et al., 2000; White et al., 2018). Our data confirm that flow disturbance in rivers/streams may favour generalist and less specialized taxa with a consequent disappearance or decline of more sensible and less tolerant taxa (Leigh & Datry, 2017).

Compared to the permanent section of the river, the major occurrence of non-insect taxa at the downstream intermittent site determined an increase in taxa richness with considerable higher values of total abundance and this contrasts with results of previous studies that have demonstrated a sensible decline in richness and abundance of assemblages in intermittent stream reaches (Datry et al., 2011; Datry, Learned, & Tockner, 2014; Leigh & Datry, 2017; Piano, Doretto, Falasco, Fenoglio, et al., 2019; Piano, Doretto, Mammola, et al., 2020; Soria et al., 2017). However, our results are not so surprisingly because some authors have already emphasized that the higher spatial and temporal heterogeneity of non-perennial sections of watercourses may create new niche opportunities for resistant/resilient taxa with an increase in richness and abundance of whole assemblages (Acuña et al., 2005; Aspin et al., 2018; Bonada et al., 2007; Stubbington et al., 2017). On the other hand, we should emphasize that this condition in the Aterno River is counterbalanced by the loss of more sensible and less tolerant insect taxa (mainly EPT) which seem more strictly linked to the permanent section of the watercourse.

Dissimilarity in community composition between P_5 and II_5 (beta diversity) was remarkable throughout the whole period of investigation and followed a clear temporal trend with the highest values recorded during the low-flow condition (after more than 10 months from the antecedent drying events) when also alpha diversity of both sites started to diverge with higher values recorded at the intermittent site.

We tentatively also demonstrated that most of the compositional difference was essentially due to taxa replacement rather than community nestedness. That is, assemblages at the downstream intermittent site are not a filtered subset of those present in the upstream permanent reach. According to Aspin et al. (2018) and Leigh et al. (2019), it seems that the replacement component of beta diversity would have a major importance in structuring freshwater assemblages at the site subjected to irregular seasonal drying. This evidence contrasts the general assumption to which intermittency and flow related disturbance in streams may select taxa from the undisturbed upstream community (Datry, Learned, & Tockner, 2014; Larned et al., 2010; Leigh et al., 2016; Piano, Doretto, Mammola, et al., 2020; Sánchez-Montoya et al., 2018) but see also Datry et al. (2016). Therefore, we can reasonably suppose that antecedent drying events at the intermittent section of the Aterno River may favour the colonization (aerial dispersal) of taxa with more resistant/resilient traits from downstream or nearby sources. In this case, upstream drift and vertical migration from hyporheic refugia will have a marginal role to ensure community persistence at the intermittent site. However, our considerations on the importance of replacement/nestedness components of beta diversity should be taken with caution because of the reduced dataset used in the analysis.

In parallel with structural and compositional changes, we also found a considerable shift in the functional traits of permanent and intermittent-reach assemblages. According with results of other studies (Belmar et al., 2019; Bogan et al., 2015; Bonada et al., 2007), a higher proportion of traits conferring resilience/resistance to

FIGURE 7 Feeding traits composition (a) and percentage of dry mass loss of black poplar (b) at the permanent and intermittent site of the Aterno River during the 1-year period of investigation. Bar values are mean \pm SE. Student *t*-tests indicated that all differences except the percentage of predators were statistically significant

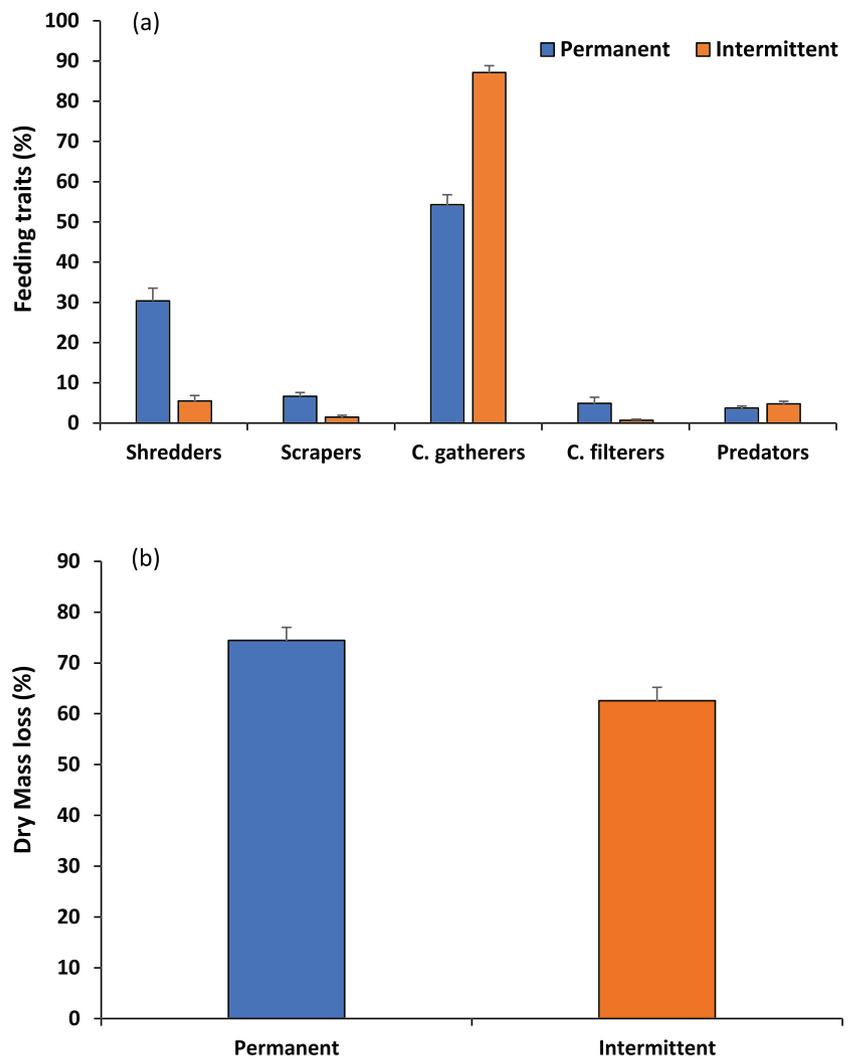
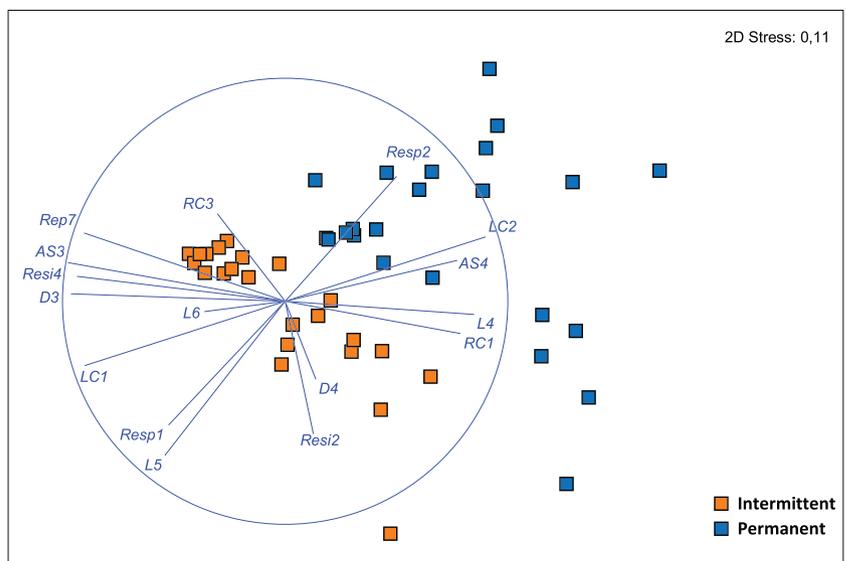


FIGURE 8 Ordination of between-samples dissimilarity in functional traits of assemblages (Euclidean distance on abundance weighed and arcsin transformed trait proportions) along the first two nMDS axes. Vectors of traits contributing most to between-site differences (SIMPER analysis) are superimposed to the graph (trait modality abbreviations are as in Table 1). Samples from permanent and intermittent site are indicated with different colours



desiccation was recorded at the downstream irregularly intermittent site where multivoltine taxa with short life cycle, aerial dispersal and diapause or cocoons as desiccation adaptations were more abundant

or exclusive. Considering the feeding traits, we also demonstrated that at the intermittent site, the decline in shredders and scrapers was compensated by an increase of collector-gatherers. Similar results

were obtained by Piano et al. (Piano, Doretto, Falasco, Fenoglio, et al., 2019; Piano, Doretto, Falasco, Gruppuso, et al., 2019) in Alpine streams and Datry et al. (2011) in French Mediterranean rivers. In addition, Piano, Doretto, Falasco, et al. (2020) demonstrated that in Alpine streams, recurrent seasonal droughts significantly altered CPOM availability, reduced shredder biodiversity and induced a shift in the ecological niche of some shredder species with consistent bottom-up effect on the whole stream functionality. Although we did not directly assess the quantity of CPOM at P₅ and II₅, we can reasonably assume that during the period of investigation a similar input of foliar material characterized both sites. Therefore, the lower rate of detritus breakdown at II₅ was mainly due to a significant decline of shredder richness and abundance, more than to differences in CPOM availability (Martínez et al., 2015; Monroy et al., 2016).

The amount of dry mass loss of poplar leaves at the permanent site was similar to that reported in a cold spring of the same river basin (Cristiano et al., 2019; Di Sabatino et al., 2020, 2021) but, as described above, after more than 1 year from the previous drying, leaf-litter breakdown was significantly lower at the intermittent site. A decline in the efficiency of the decomposition process after flow resumption was already documented in Mediterranean intermittent rivers (Datry et al., 2011), in Alpine streams (Gruppuso et al., 2021) and in calcareous streams under oceanic climate conditions (Martínez et al., 2015). In this context, it is interesting to note as in a previous study conducted on a downstream fourth-order reach of the Aterno River, Pinna et al. (2016) demonstrated that the structure and composition of macroinvertebrate assemblages still conserved the memory of past disturbance while ecosystem processes (leaf-litter breakdown) were almost unaffected. The authors also showed that in the middle reach of the Aterno River, shredder detritivores were poorly represented both in term of richness and relative abundance and that the decomposition process was mainly driven by microorganisms. Probably, the high resilience of microbial community determined the fast post-drought recovery of leaf-litter decomposition rate. This implies that the recovery capacity of structure and functions in irregularly intermittent streams may be related to the location or position of the drying reaches in the context of the whole river network (Crabot et al., 2020; Van Looy et al., 2019). Headwater reaches of river and stream ecosystems will be more sensitive to drying events than middle or lowland sections (Soria et al., 2017). Therefore, we can predict that future impacts of climate change and anthropogenic pressures may be more pronounced on the upper section of former perennial Apennine watercourses.

In summary, we documented that the consistent shift in community structure, composition and functional organization between P₅ and II₅ also persisted after more than 15 months from the resumption of the natural flow regime at the intermittent site. To our knowledge, this 'long-term memory' of drought, although supposed (Acuña et al., 2005; Boulton & Lake, 1992), was never documented. In fact, most of the previous studies on the ecological effects of antecedent drying events have been conducted on a considerably smaller (6–9 months) temporal scale (Datry et al., 2011; Piano, Doretto, Falasco, Fenoglio, et al., 2019; Pinna et al., 2016). Furthermore, our

results contrast with the outputs of similar research in different geographical areas. For example, a high resilience and a rapid recovery of structure and processes after drying have been documented for lotic communities in large, braided rivers (Fowler, 2004; Vander Vorste et al., 2016), and this was mainly attributed to the presence of traits well adapted to cope with the natural high disturbance of these watercourses. Similarly, Dolédec et al. (2017) found that taxonomic and functional diversity of assemblages in natural intermittent rivers of the Mediterranean region may recover quickly after flow resumption. No memory of antecedent drying events and high resilience has also been documented for stream communities in humid continental climate of Central Europe (Pařil et al., 2019). In a large-scale study, Leigh et al. (2016) did not find significant differences between perennial and post-drying intermittent river reach communities and assumed that the persistence of communities was mainly explained by the presence of both resistant and resilient traits and by the dispersal from perennial sites. Most probably, the intensity (complete flow cessation and absence of residual pools), the duration (more than 4 months) and the unpredictability of past drying events negatively affected the recovery capacity of structural and functional attributes of the Aterno River communities. Therefore, we can assume that freshwater communities in former perennial Apennine watercourses are not particularly adapted to contrast the negative effects of irregular drying events. In fact, compared to the perennial section of the Aterno River, the 7-km downstream intermittent site, after more than 1 year from a complete recovery of the natural flow regime, still conserved the 'memory' of past disturbance with marked differences in structure, composition and functional traits of assemblages which, in turn, negatively influenced the leaf-litter breakdown.

5 | CONCLUSIONS

Our study confirms the importance of long-term research (Leigh et al., 2019) for a more realistic assessment and a better prediction of the effects of increasing intermittency on freshwater biota and ecosystem processes. Despite the small distance and very similar environmental conditions and flow regime, the two sites investigated on the Aterno River (perennial and irregularly intermittent) showed significant differences in structure, composition and functional traits of resident invertebrate communities with negative repercussion on the leaf-litter breakdown process.

Taxa richness and densities of assemblages were higher at the intermittent site, but the number and abundance of more sensible insect taxa were significantly higher at the site which never experienced complete flow cessation. The intensity, the duration and the unpredictability of antecedent drying episodes concurred to determine a low recovery capacity of community structure and functions. Compared to the upstream permanent site, differences in composition and functional traits of the intermittent-reach community seem mainly related to taxa replacement rather than nestedness.

Although limited to a single case-study, our findings confirm and extend the 'drying memory' hypothesis suggesting that irregular

drying events in former perennial Apennine rivers may have dramatic long-term effects on structure and functions of lotic ecosystems. Our research is still ongoing, and data collected in 2020, where a prolonged period of drought (from August to November) interested the intermittent site, will help to better understand the ecological effects of intermittency in streams and rivers of the Mediterranean region particularly exposed to the combined effects of global changes and anthropogenic pressures.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Table S1.

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