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RESEARCH ARTICLE

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How does water current velocity affect invertebrate community and leaf-litter breakdown in a physicochemically stable freshwater ecosystem? An experimental study in two nearby reaches (erosional vs. depositional) of the Vera Spring (Central Italy)

Giovanni Cristiano | **Antonio Di Sabatino**

Department of Life, Health and Environmental Sciences, University of L'Aquila, L'Aquila, Italy

Correspondence
Antonio Di Sabatino, Department of Life, Health and Environmental Sciences. University of L'Aquila, Via Vetoio, Coppito1, I-67100, L'Aquila, Italy.
Email: antonio.disabatino@univaq.it

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Abstract

The decomposition of allochthonous dead organic matter is a key process for the metabolism and functioning of stream and spring ecosystems. The litter breakdown process is influenced by several abiotic and biotic factors. Among abiotic parameters, the role of current velocity and physical abrasion was poorly investigated. Field studies gave contrasting results, mainly because of the covariation and the interaction of current velocity with other biotic/abiotic variables. For these reasons, we assessed leaf-litter breakdown and the structure of crenic assemblages in two nearby reaches (erosional vs. depositional) of a physicochemically stable rheocrene spring. The two zones investigated were characterized by similar environmental conditions, but water current velocity was about four times greater in the erosional reach. We found substantial differences in the structure and functional organization of crenic assemblages. Overall taxa richness and density were higher in the depositional reach, while diversity and abundance of Ephemeroptera, Plecoptera and Trichoptera were taller in the erosional zone. Shredders were more abundant in the erosional zone, and scrapers were more represented in the slow current sector of the spring. We also demonstrated that water flow may promote a faster decomposition of leaf detritus in the spring erosional reach mainly through indirect effects: higher richness and abundance of shredder detritivores. Our results indicate that water current velocity may have a key role in affecting both spring assemblage composition and ecosystem processes.

KEYWORDS
flow velocity, invertebrate community, litter decomposition, *Populus nigra*, spring ecosystems

1 | INTRODUCTION

Riparian organic detritus is the primary energy source in many low-order streams and forested springs. The decomposition of dead organic matter is therefore a key process for the metabolism and functioning of these ecosystems (Ferreira et al., 2020; Tank et al., 2010). The litter breakdown process occurs through four steps: leaching of soluble compounds, microbial colonization, conditioning and partial decomposition of foliar material and shredding fragmentation (Gessner et al., 1999; Graça et al., 2015). These steps may be influenced by the process of physical abrasion by water flow, can overlap over time and may be controlled by several external factors making this ecosystem process complex to interpret as a whole and in all the individual phases (Gessner et al., 1999). Previous studies have already documented as temperature, microorganism activity, nutrient concentration, leaf species characteristics and shredders diversity/abundance may significantly influence the rate of litter decomposition both at local and global scale (Boyero et al., 2016). Among abiotic parameters, the role of current velocity on litter breakdown was poorly investigated, and the first study on this argument was published about 20 years ago (Heard et al., 1999). Successively, field and mesocosm studies (Abril et al., 2015, 2021; Bastias et al., 2020; dos Santos Fonseca et al., 2013; Ferreira et al., 2006; Ferreira & Graça, 2006; Hoover et al., 2006; Lepori et al., 2005; Mora-Gómez et al., 2015) demonstrated that current velocity may affect coarse organic matter (CPOM) breakdown/decomposition both directly by influencing leaf-litter retention, transport and storage in the streambed and physical abrasive power on foliar texture and indirectly with significant effects on habitat/microhabitat diversity, microbial colonization/activity and richness/density of shredder invertebrates.

However, results of these studies were often equivocal. For example, Ferreira et al. (2006) did not find significant effects of current velocity on leaf-litter breakdown both on mesocosms and field experiments in streams. Similarly, Martins et al. (2015) and Imberger et al. (2008) demonstrated that current velocity had weak or no direct effects on leaf-litter breakdown in urban streams of Central Amazonia and Australia, respectively.

On the other hand, positive (direct and indirect) effects have been reported from field experiments by Mora-Gómez et al. (2015), Rezende et al. (2014) and Bastias et al. (2020). However, recent studies (Abril et al., 2021) demonstrated that the positive effect of current velocity on litter breakdown was only detectable at the late stage of foliar decomposition. In addition, Bruder et al. (2016) found that the higher decomposition rates in mesocosms with fast flow were mainly due to fungal activity more than to physical abrasion.

However, at least for that concerning field experiments, the results have been often confounded by the covariation and the interaction of current velocity with other biotic/abiotic variables as temperature, nutrient concentration, dissolved oxygen contents, community structure and dynamics. For these reasons, we conducted a field experiment in a stable spring ecosystem. We assessed leaf-litter breakdown and structure and composition of crenic assemblages in two nearby reaches of the Vera Spring with high (erosional) and low current velocity (depositional), respectively. We hypothesized that fast flow at the erosional site should increases habitat/microhabitat heterogeneity thus favouring the coexistence of more species. We also predicted that current speed may contribute to enhance the litter breakdown process both directly (physical abrasion) and indirectly (major occurrence of reophile shredder taxa).

2 | MATERIALS AND METHODS

2.1 | Study area

Vera Springs (L'Aquila, Abruzzo, Central Italy) are a complex of karst-limestone resurgences feed by the Gran Sasso basal aquifer. The spring area (natural reserve park) extends for about 30 ha and is characterized by a dense tree cover, mainly black poplar (*Populus nigra*), white willow (*Salix alba*) and red willow (*Salix purpurea*). We located our sampling sites at ‘Capo Tempera’ (coordinates 42°22′21.42″N, 13°27′30.51″E; altitude 664 m above sea level), a mid-sized rheocrene spring characterized by a mean annual discharge of about 0.18–0.2 $m^3\ s^{-1}$, low nutrient contents and seasonal constancy of the main physicochemical and hydrological parameters (Cristiano et al., 2019; Di Sabatino et al., 2018, 2020, 2021). After emergence, the spring water flows in a gently sloping terrain (0.016%) forming the main channel (width = 3.5 m) of the spring–springbrook system (Di Sabatino et al., 2021). However, part of the spring water flows laterally to the main channel in a flatter area. The Vera Spring system at ‘Capo Tempera’ is thus characterized by the presence of two nearby reaches (distanced by less than 10 m) with different characteristics (Figure 1). The erosional zone of the spring–springbrook channel shows high current velocity, turbulent flow and coarse substrata (stones, pebbles and gravels), while the lateral depositional area has low current velocity, laminar flow, finer substrata (silt, sands and organic particles) and a more abundant presence of periphyton, mimicking the characteristics of a rheolimnocrene spring type (Di Sabatino et al., 2003).

2.2 | Field and laboratory procedures

Structure and composition of benthic invertebrate communities and leaf-litter breakdown in the two reaches of Vera Spring were evaluated with the ‘leaf-nets’ (LN) method (Cristiano et al., 2019; Di Sabatino et al., 2016, 2018). Black poplar leaves were enclosed in two PVC nets (0.10 m * 0.15 m, mesh-size 0.01 m); four of these nets were overlapped and joined together representing a sampling area of 0.06 m^2. The leaf material was collected in the area surrounding the spring during the abscission period in autumn 2016 and subsequently dried in a well-ventilated laboratory room. The leaves enclosed in each LN were pre-weighed with an analytical balance (±0.01 g.) to determine the initial dry mass (g). The experiment was conducted from April 2017 to March 2018 for a total of four sampling dates. At

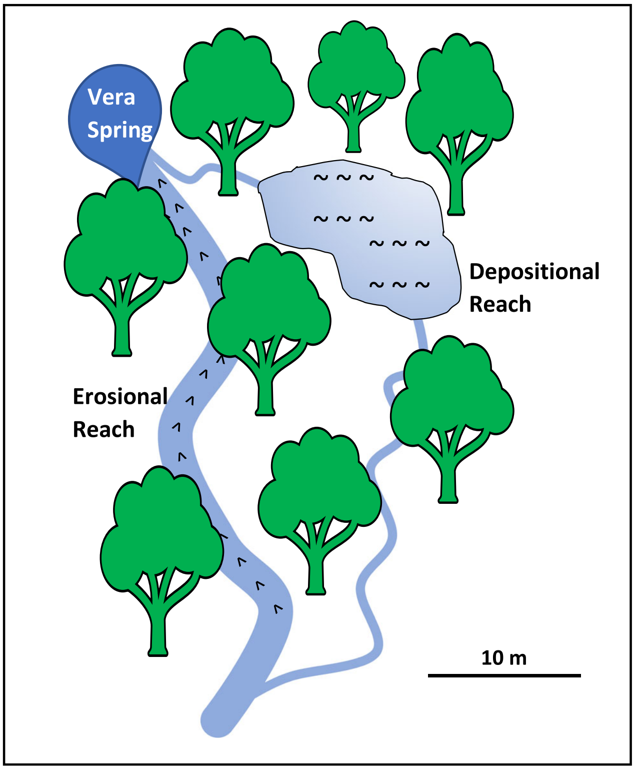

FIGURE 1 Schematic representation of the Vera Spring study area.

each sampling occasion, nine LN replicates were randomly deployed in the spring bed of both reaches (erosional [ERO] and depositional [DEP]) and anchored to the substratum with steel pegs. In total 72 LNs (2 reaches × 4 sampling occasions × 9 replicates) were used. After about 40 days of immersion, LN were carefully retrieved, enclosed in numbered plastic-bags and transported to the laboratory in a portable cooler. In the laboratory, LN were opened, and the remaining leaf material was rinsed with distilled water in order to remove any organisms and inorganic sediments. Successively, the leaves, after a first dehydration on absorbent paper, were placed in a thermostatic oven at 60°C for 72 h. Finally, the remaining leaf material was weighed to determine the final dry mass (g). The dry mass loss was expressed as percentage of the difference between initial and final dry mass of the incubated leaves.

The invertebrates collected were fixed in a 70% ethanol solution and subsequently identified to the lowest possible level of classification. Each taxon identified was also assigned to a specific functional feeding group (FFG) following Merritt and Cummins (1996) and Tachet et al. (2010). LN retrieved on April and June were assigned to the spring–summer (SS) season, while those recovered on September and December were assigned to the autumn–winter season (AW).

In both reaches, physicochemical and hydrological parameters were recorded during the deploying and the retrieving phase of LN. Water temperature, pH, dissolved oxygen and conductivity were measured in situ with a multi-parameter probe (Hach-Lange HD-40D). Water depth and current velocity were recorded with a FP-101 flow meter (accuracy ±0.01 m s^{-1}) along an orthogonal transect of 0.5-m cells length. The instantaneous discharge (m^3 s^{-1}) was calculated as the sum of single-cell discharges.

2.3 | Statistical analysis

Differences in abiotic parameters (conductivity, pH, dissolved oxygen, water temperature, water depth, current velocity and discharge) between the two sampling reaches were tested with Student *t*-tests. The structure of benthic invertebrate assemblages was assessed by applying two-way ANOVAs with taxa richness, total density (log $x + 1$ transformed), number of Ephemeroptera Plecoptera Trichoptera (EPT) taxa, density of EPT taxa, percentage of insect richness and percentage of Insect abundance as dependent variables and 'site' and 'season' as fixed factors. Differences in the proportional abundance of FFG's in both reaches were tested with Student *t*-tests after arcsine transformation of shredder, collector gatherer and predator percentages. Collector filterers were excluded from the analysis (percentages less than 1%). Permutational multivariate analysis of variance (PERMANOVA) was used to evaluate spatial (ERO vs. DEP) and temporal (SS vs. AW) differences in the composition (log $x + 1$ transformed densities) of crenic assemblages. Taxa occurring once and with a single individual were not included in the analysis. A single LN from the ERO site was also excluded because of incomplete colonization. The SIMPER procedure was applied to individuate the taxa most responsible of the observed differences. The percentage of dry mass loss of poplar leaves was assessed with a two-way ANOVA with 'site' and 'season' as fixed factors.

All statistical analyses were carried out using Addinsoft™ software XLSTAT 2014.1.09, PRIMER v6.1.16 and PERMANOVA+ v1.0.6. Parametric tests were conducted only after verification of normality (Anderson–Darling test) and variance homogeneity (Levene test) assumptions. The significance threshold was set at $p = 0.05$.

3 | RESULTS

3.1 | Physicochemical and hydrological parameters

Physicochemical variables did not differ significantly between the erosional and the depositional reach. Mean values of water temperature, conductivity and dissolved oxygen showed little variations and t-tests revealed no significant differences (Table 1). By contrast, the two zones were characterized by marked differences in the main hydrological parameters. Mean current velocity (ERO = 0.27 ± 0.02 m s^{-1}; DEP = 0.08 ± 0.01 m s^{-1}; $t = 23.173$; $p < 0.0001$) and discharge (ERO = 0.12 ± 0.01 m^3 s^{-1}; DEP = 0.09 ± 0.02 m^3 s^{-1}; $t = 3.889$; $p = 0.002$) were significantly higher in the erosional spring reach, while the depositional zone had higher values of mean channel depth (ERO = 0.15 ± 0.03 m; DEP = 0.27

± 0.01 m; $t = 12.257$; $p < 0.0001$). As expected, the spatial variability of flow velocity and water depth along the orthogonal transect of both reaches were considerable higher in the erosional channel of the spring (Figure 2).

TABLE 1 Mean values (+*SD*) of some physicochemical and hydraulic parameters recorded in the two investigated reaches of the Vera Spring.

Parameter	Erosional ($n = 8$)	Depositional ($n = 8$)
Temperature (°C)	8.11 (±0.31)	8.06 (±0.20)
pH	8.05 (±0.40)	7.77 (±0.31)
Conductivity (μS cm^{-1})	149.9 (±1.6)	150.7 (±1.1)
O_2 (mg L^{-1})	10.57 (±0.48)	10.21 (±0.31)
O_2 (% sat)	96.2 (±2.3)	93.9 (±3.3)
Mean depth (m)*	0.15 (±0.03)	0.27 (±0.01)
Mean current speed (m s^{-1})*	0.27 (±0.02)	0.08 (±0.01)
Discharge (m^3 s^{-1})*	0.12 (±0.01)	0.09 (±0.02)

*Significant differences after Student *t*-tests.

3.2 | Macroinvertebrates

During the whole period of investigation, we totally sampled 19,582 individuals belonging to 35 taxa: 30 taxa and 6590 organisms were collected in the erosional reach and 33 taxa and 12,992 in the depositional zone (Table S1). Twenty-eight taxa were common to both reaches, *Crunoecia irrorata* and *Atractides loricatus* were exclusive of the erosional zone while Limoniid Diptera, *Rhyacophila foliacea*, *Pisidium* sp., *Sperchon squamosus* and *Hygrobates fluviatilis* were sampled only in the depositional reach. The Vera Spring community was characterized by the presence of a high number of crenobionts (12 species) and was dominated by non-insect taxa, with three species (*Gammarus elvirae*, *Belgrandia minuscula* and *Schmidtea polycroa*) occurring in almost all samples and representing about 83% of the total individuals collected. The most abundant insect taxa were Chironomid Diptera (7%), the coleopteran *Elmis aenea* (1%) and the endemic Trichoptera *Drusus aprutiensis* (1%).

Results of ANOVAs (Table 2) indicated that richness and density of assemblages were significantly higher in the DEP zone while EPT richness, EPT density, insect taxa (%) and insect density (%) were higher in the ERO site (Figure 3). No substantial seasonal variations were detected for the above metrics except for the total density of

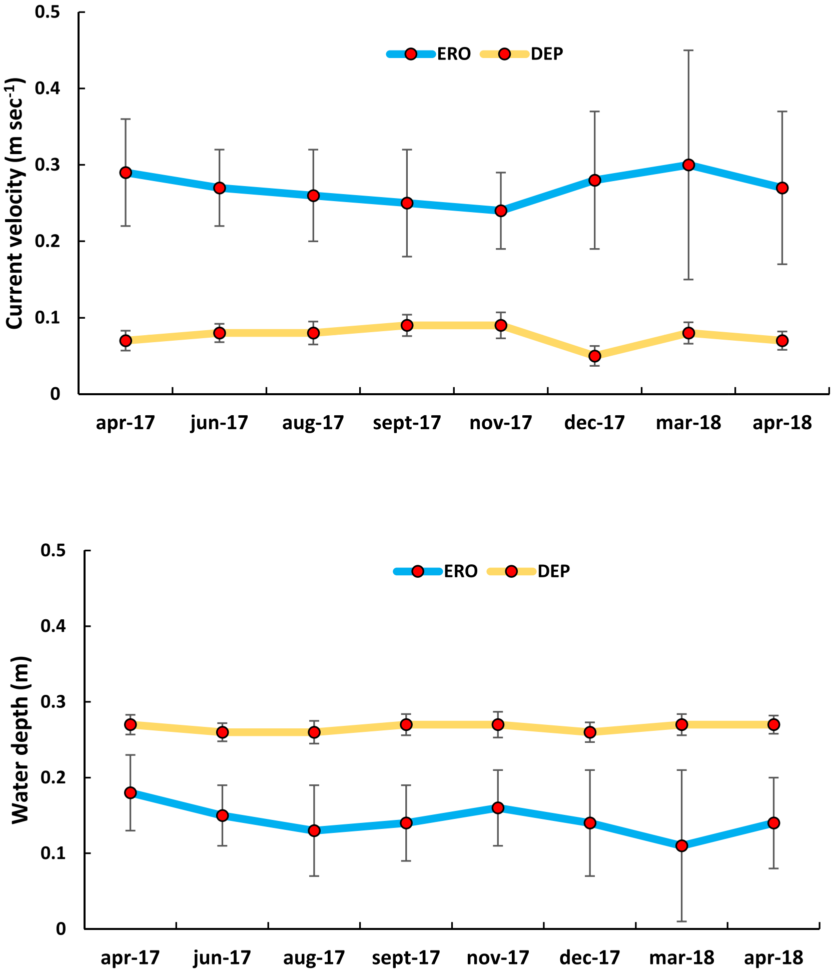

FIGURE 2 Current velocity and water depth (mean ± *SD*) measured along the orthogonal transect of the erosional and depositional reach of the Vera Spring during the whole period of observation.

TABLE 2 Results of ANOVAs testing spatial and seasonal differences on the structure of Vera Spring assemblages.

Source of variation		SS	MS	F	p
Richness					
Site	1	56.89	56.89	6.74	**0.012**
Season	1	12.50	12.50	1.48	0.228
Site * season	1	1.39	1.39	0.16	0.686
Residuals	68	574.33	8.45		
Total	71	645.11			
Density					
Site	1	2.44	2.44	40.94	**<0.0001**
Season	1	0.26	0.26	4.43	**0.039**
Site * season	1	0.001	0.001	0.009	0.925
Residuals	68	4.05	0.06		
Total	71	6.76			
EPT richness					
Site	1	8.68	8.68	5.23	**<0.0001**
Season	1	1.68	1.68	1.01	0.318
Site * season	1	0.68	0.68	0.41	0.524
Residuals	68	112.88	1.66		
Total	71	123.87			
EPT density					
Site	1	102503.86	102503.86	7.897	**<0.0001**
Season	1	7812.50	7812.50	0.602	0.441
Site * season	1	2040.89	2040.89	0.157	0.693
Residuals	68	882608.02	12979.53		
Total	71	994965.28			
Insect richness (%)					
Site	1	4345.51	4345.51	60.86	**<0.0001**
Season	1	337.54	337.54	4.73	**0.033**
Site * season	1	87.65	87.65	1.23	0.272
Residuals	68	4855.45	71.40		
Total	71	9626.20			
Insect density (%)					
Site	1	1193.40	1193.40	9.48	**0.003**
Season	1	691.60	691.60	5.70	**0.020**
Site*season	1	46.60	46.60	0.38	0.537
Residuals	68	8224.96	121.25		
Total	71	10,176.56			

Note: Factors are 'site' (erosional vs. depositional), 'season' (spring–summer vs. autumn–winter) and their interaction. Significant *p* values are in bold.

assemblages and insect richness/density, significantly higher in the spring–summer period at both reaches (no significant interactions).

Although a high number of taxa was shared between the ERO and DEP site, the composition of assemblages in the two zones differed significantly (PERMANOVA, pseudo-$F_{1,70} = 19.00$, p [perm] $= 0.001$) and the nonmetric multidimensional scaling ordination pattern clearly shows a net separation between ERO and DEP samples (Figure 4). Results of SIMPER analysis demonstrated that the observed differences were mainly due to the higher abundance of *D. aprutiensis*, *Leuctra fusca*, *Protonemura ausonia*, *Isoperla saccai*, *Atractides pennatus* and *Sperchon thienemanni* in the erosional zone. Conversely, *Lebertia stigmatifera*, *B. minuscula*, Lumbriculidae, Copepoda, Ostracoda, *Ancylus fluviatilis*, *Plectrocnemia conspersa* and *H. fluviatilis* were more represented in the depositional reach. The composition of assemblages was rather homogeneous through time, and no seasonal differences were detected for the DEP site (PERMANOVA, pseudo-$F_{1,35} = 1.25$, p [perm] $= 0.283$), while it was marginally significant for the ERO site (PERMANOVA,

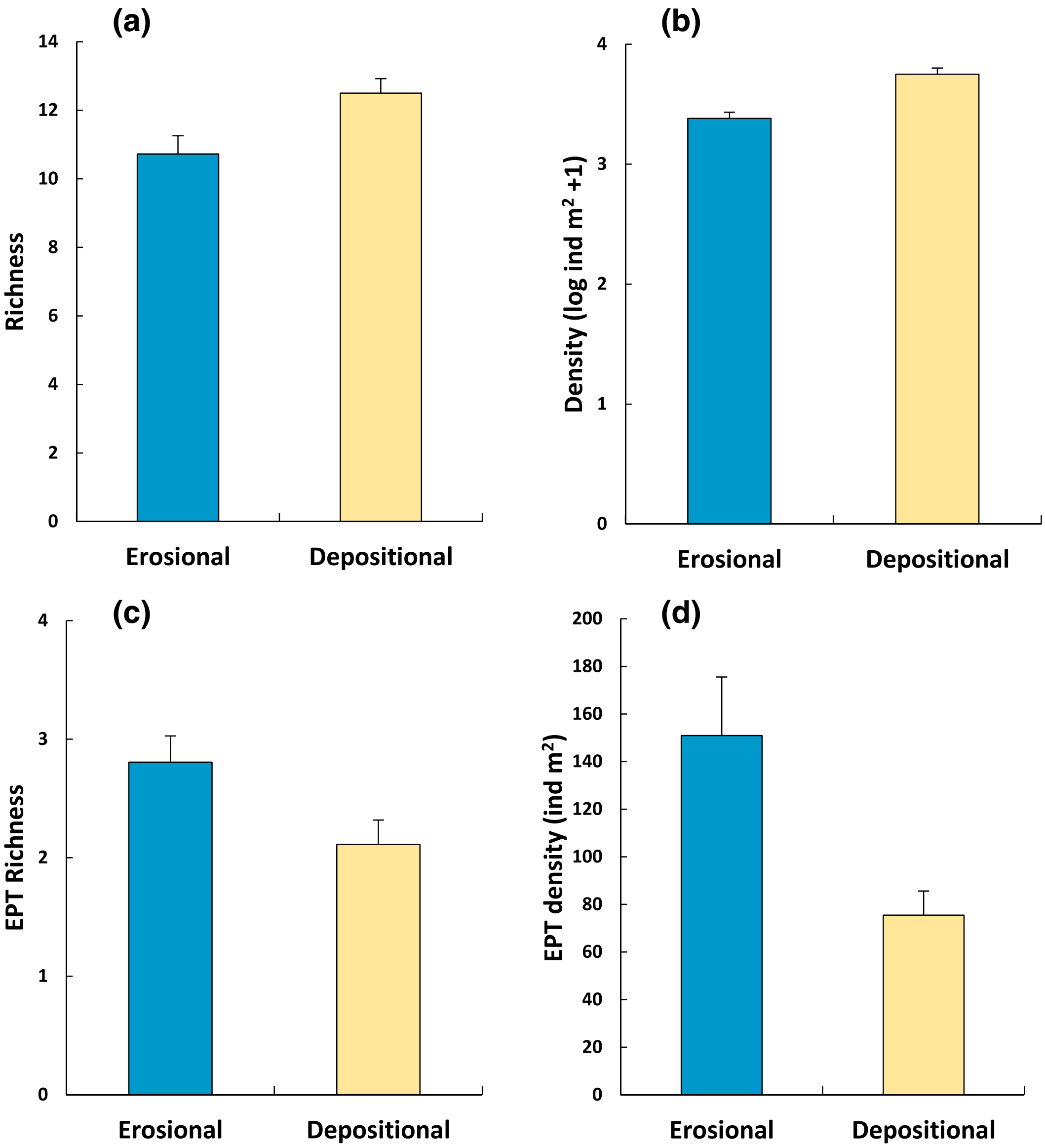

FIGURE 3 Mean values (+SE) of taxa richness (a), total density (b), Ephemeroptera Plecoptera Trichoptera (EPT) richness (c) and EPT density (d) of crenic assemblages in the erosional and depositional reach of the Vera Spring. Results of *t*-tests showed that all differences were significant (*p* value <0.05).

pseudo-$F_{1,34} = 2.32$, p [perm] $= 0.045$). Crenobiont and crenophil species occurred with almost similar richness in both reaches but with densities slightly higher at the DEP site.

3.3 | Functional organization of assemblages and leaf-litter breakdown

Shredder organisms were significantly more abundant in the erosional reach (ERO 35 ± 25%; DEP 8 ± 5%; $t = 6.486$; $p < 0.0001$), while the percentage of scrapers was higher in the depositional site (ERO 40 ± 29%; DEP 67 ± 18%; $t = 4.854$; $p < 0.0001$). No substantial between-reach differences were detected for the relative abundance of collector-gatherers and predators (Figure 5a). Results of litter breakdown experiment showed that, on average, after 40 days of immersion, the dry mass loss of poplar leaves was significantly higher at the erosional reach (ERO 68 ± 10%; DEP 51 ± 8%) with no significant seasonal differences and no relevant site × season interactions (Figure 5b; Table S2).

4 | DISCUSSION

The two sampled reaches of Vera Spring showed identical abiotic characteristics except for current velocity (higher in the erosional site) and channel depth (higher in the depositional site). The depositional site was characterized by rather constant and homogenous spatial conditions of substrate and microhabitats diversification,

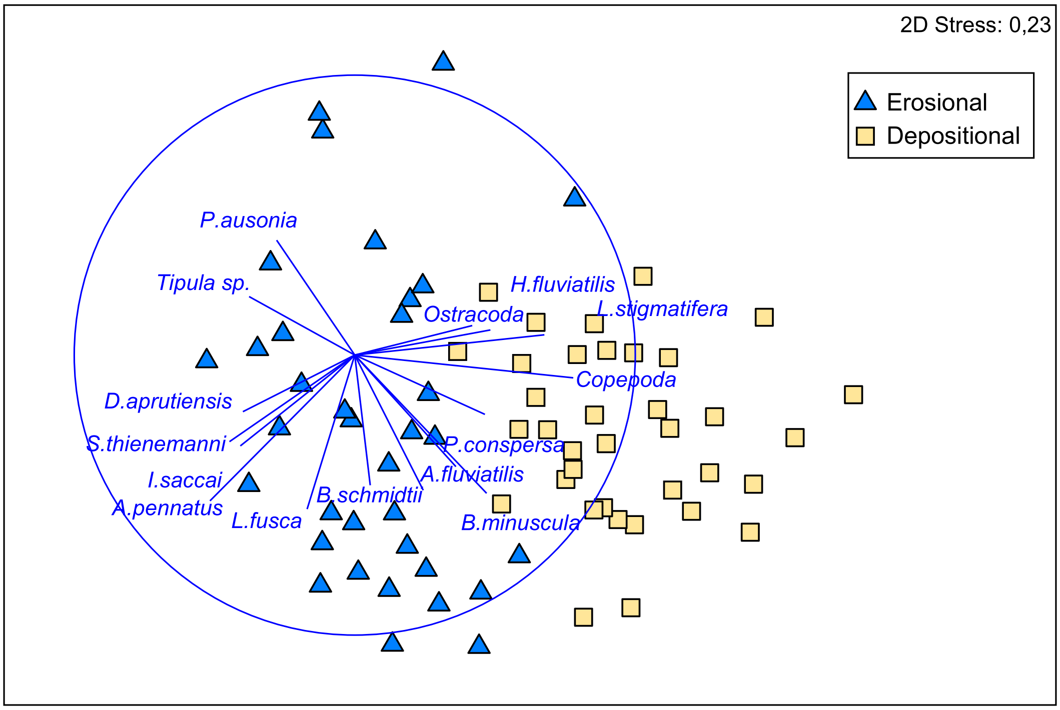

FIGURE 4 Nonmetric multidimensional scaling ordination pattern of between-sample compositional differences (Bray–Curtis distance on square root transformed densities) of crenic assemblages in the erosional and depositional reach of the Vera Spring. Vectors of taxa with Pearson's correlation coefficient >0.4 were superimposed to the graph.

while depth and flow velocity at the erosional site were more variable both in space and time.

As already demonstrated for rheocrene limestone springs (Glazier, 1991, 2014), the invertebrate community of both reaches of Vera Spring was dominated by non-insect taxa, with insects occurring with lower abundance but higher richness. Richness and density of crenic assemblages were similar to those recorded in similar springs (Bottazzi et al., 2011); therefore, we can confirm the efficiency of LN in sampling spring invertebrates (Cristiano et al., 2019; Di Sabatino et al., 2018). In fact, compared to results of a previous study conducted in the same spring but with a modified surber sampler (Di Sabatino et al., 2021) and considering the different sampling efforts, the less-invasive LN method gives comparable results in term of richness, density, composition and ecological specialization of spring communities.

Contrary to our expectations, taxa richness and density of crenic assemblages were higher in the depositional reach, but in the erosional zone we found a higher diversity and abundance of EPT taxa. In fact, most EPT taxa living in cold rheocrene springs have preference for fast flowing waters (Maiolini et al., 2011; von Fumetti et al., 2006). Similarly, Blöcher et al. (2020) demonstrated that in microcosm experiments with slow (0.0 m s^{-1}), medium (0.14 m s^{-1}) and fast (0.26 m s^{-1}) current velocity treatments, richness of assemblages was higher at slow flow while total abundance increased at high current velocity. In this context, EPT richness was almost unaffected by current velocity, but EPT abundance was higher at fast flows. Conversely, Elbrecht et al. (2016) found that richness and total abundance of invertebrate community was mostly unaffected by slow (0.02 m s^{-1}) or high (0.12 m s^{-1}) current velocity treatments, but both richness and abundance of EPT taxa decreased significantly in microcosms with slow current. Strong negative effects of flow reduction (from 0.15 to 0.05 m s^{-1}) on invertebrate richness and abundance were reported by Matthaei et al. (2010) in manipulated channels of New Zealand agricultural streams, with EPT taxa significantly reduced in slow flow channel treatments. Accordingly, Dewson et al. (2007) demonstrated a significant decrease of invertebrate richness in low current sectors of streams because of the concomitant reduction of habitat/microhabitat diversity. Therefore, we can assume that the overall higher diversity and total abundance of invertebrates we observed in the slow flowing sector of the spring may be due to changes in energetic inputs and spring-reach metabolism (see below) more than to differences in environmental parameters or microhabitats availability and heterogeneity.

The invertebrate community of the two investigated reaches also differed in composition and these differences were mainly due to the major occurrence of less specialized taxa (Copepoda, Ostracoda, Lumbriculidae, *A. fluviatilis*) at the depositional site and to a spatial segregation of crenobionts in response to lotic/lentic spring flow conditions. Water mites confirm their high specialization to spring habitats (Di Sabatino et al., 2003, 2004; Gerecke et al., 2018) with 6 crenobiont species totally collected. These species showed a different spatial distribution with *A. pennatus*, *A. loricatus* and *S. thienemanni* almost exclusively sampled in the erosional site, while *L. stigmatifera* and *S. squamosus* seem to prefer the low-current section of the Vera Spring. A similar spatial pattern was also found for other crenobionts:

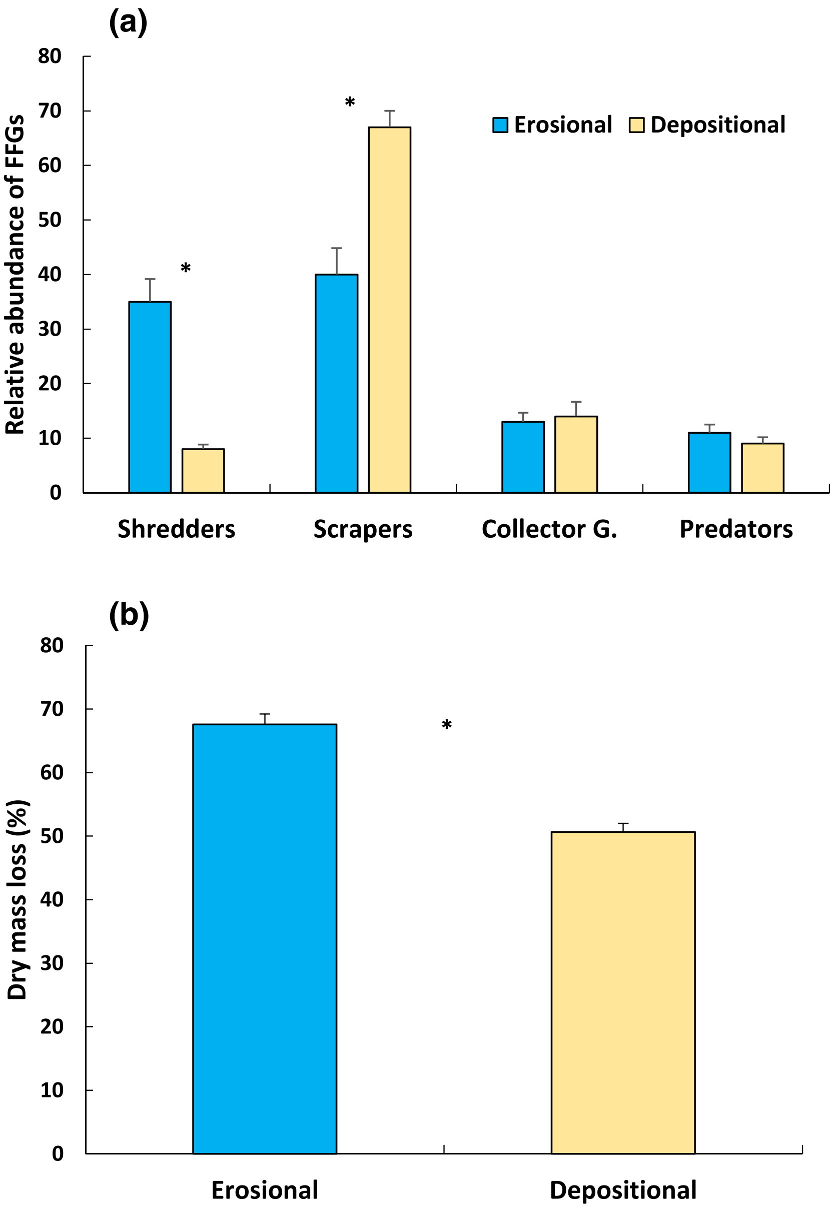

FIGURE 5 Mean (+SE) of feeding traits relative abundance (a) and percentage of dry mass loss of black poplar leaves (b) in the erosional and depositional reach of the Vera Spring. Dry mass loss was calculated after about 40 days of leaf-nets immersion. Asterisks indicate significant differences after Student *t*-tests (feeding traits) and ANOVA (dry mass loss). Results of ANOVA were reported in Table S2.

C. irrorata, *D. aprutiensis* and *I. saccai* exhibited preference for the erosional zone while *P. conspersa* and *B. minuscula* were more represented in the low current sector of the spring. Therefore, as already demonstrated for low-order streams (Allan & Castillo, 2007; Dewson et al., 2007), current velocity may have a fundamental role in shaping spring communities, more than other physicochemical variables (von Fumetti et al., 2006).

The differential distribution of taxa in the two sites also determined a diverse functional organization of assemblages. The erosional reach was characterized by a higher percentage of rheophile shredders (*L. fusca*, *P. ausonia*, *D. aprutiensis*, *Sericostoma italicum*, *Tipula* sp. and *G. elvirae*) while limnophile scrapers dominated in the depositional site (*B. minuscula* and *Bythinella schmidtii*), indirectly suggesting a more abundant presence of periphyton in the slow current sector of the spring, as in fact we observed during the whole sampling period.

We also found that compared to the slow current sector of the spring (mean current velocity 0.08 m s^{-1}), the mass loss of poplar leaves was significantly higher at the erosional site (mean current velocity 0.27 m s^{-1}) and was not influenced by the sampling season. This contrasts with results of field studies in streams where no effects of current velocity (up to 1.2 m s^{-1}) on leaf-litter breakdown was demonstrated (Ferreira et al., 2006; Ferreira & Graça, 2006). Conversely, recent mesocosm and field experiments (Bastias et al., 2020; Bruder et al., 2016) clearly documented the negative effects of reduced flow velocity (from 0.32 to 0.01 m s^{-1}) on leaf-litter decomposition. A significant increase of leaf-litter mass loss in artificial channels with flow velocity treatments from 0.00 to 0.10 m s^{-1} was also documented by dos Santos Fonseca et al. (2013). Our study confirms that water velocity along the erosional channel of the Vera Spring positively affect the rate of leaf-litter breakdown with both direct (physical abrasion) and indirect effects (abundance of shredder detritivores). As in other field studies, we cannot distinguish the relative contribution of each single component, but according to Bruder et al. (2016) and Ferreira et al. (2006), it seems that the direct effect of physical abrasion is marginal. We can also exclude that leaf-litter decomposition between the two investigated reaches was influenced by dissolved oxygen concentrations (Bruder et al., 2016) and differences in other physicochemical parameters. Therefore, as already documented for streams (Ferreira et al., 2006; Mora-Gómez et al., 2015), we think that between-reach differences in the mass loss of poplar leaves was mainly explained by the indirect positive effects of current velocity on shredder richness and abundance. However, despite the scarce presence of shredders and about near-zero current velocity, in the depositional reach, almost 50% of the dry mass of incubated leaves was lost. This confirms the importance of microbial decomposition of foliar detritus in cold water springs (Di Sabatino et al., 2021) and seems in contrast with the assumption that reduced flow velocity may favour the deposition of inorganic particles on submerged leaves with negative effects on microorganism colonization and activity (Bruder et al., 2016). In any case, the presence of two distinct zones in Vera Spring characterized by high and low water current velocity contributed to increase the structural and functional complexity of the system with positive effects on the overall spring biodiversity.

5 | CONCLUSIONS

Our findings suggest that current velocity is an important factor shaping freshwater communities and ecosystem processes also in coldwater springs. Although we have not directly assessed between-reach differences in food sources and energetic input, we can suppose that the depositional zone of Vera Spring may act as a retention structure where CPOM is metabolized slowly with only a little fraction of FPOM exported downstream. This condition, coupled with the major energetic input from autotrophy, could have positively affected the richness and abundance of assemblages, but with a major occurrence of less rheophile and generalist taxa. On the other hand, higher flow (physical abrasion) and shredders activity (fragmentation) at the erosional zone may have contributed to a faster decomposition of leaf-detritus with an abundant source of FPOM for downstream springbrook/first-order stream communities. These conditions might explain the observed spatial differences in spring community structure and functions. However, further studies are needed to confirm our assumptions.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Antonio Di Sabatino https://orcid.org/0000-0001-9871-907X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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