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Temporal Changes in Freshwater Invertebrate Communities During the Drying Phase of a Newly Intermittent River in Central Italy

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Abstract: The transition from a perennial to an intermittent regime in newly intermittent rivers (nIRs) negatively affects both taxonomic and functional diversity, with significant repercussions on freshwater ecosystem processes and services. However, to better understand how changes in the natural flow regime may influence the structure and functioning of freshwater ecosystems, it is fundamental to assess variations in abiotic and biotic parameters throughout the hydrological phases characterizing nIRs. For these reasons, we evaluated the temporal changes in community structure and composition during the drying phase of a Central Apennines stream (Italy) over two consecutive drought years. We demonstrated that the different hydrological regime of the pre-drought phase profoundly affected the structure and composition of freshwater communities. The reduced discharge during the low-flow conditions of 2024 led to a transition from insect- to non-insect-dominated communities, with small-sized, lentic-adapted and generalist taxa replacing rheophile and more sensitive insect taxa. We also found marked interannual differences in temporal beta diversity. However, in both years, taxa richness did not exhibit a negative stepped response pattern during the sequence of channel contraction, flow cessation and pools formation. Consequently, we can assume that in newly intermittent Apennine rivers, the response of freshwater communities to drying is strictly dependent on the local and interannual variable hydrological context. This study emphasizes the need for further investigation to better understand the ecological impacts of increasing intermittence in formerly perennial streams and rivers.

Keywords: newly intermittent rivers; drying phase; macroinvertebrates; temporal β diversity; taxa richness; stepped response

Citation: Di Sabatino, A.; Rossi, F.; Ercolino, G. Temporal Changes in Freshwater Invertebrate Communities During the Drying Phase of a Newly Intermittent River in Central Italy. *Environments* **2024**, *11*, 295. https://doi.org/10.3390/environments11120295

Academic Editor: Chin H. Wu

Received: 26 November 2024
Revised: 16 December 2024
Accepted: 18 December 2024
Published: 20 December 2024

1. Introduction

Many formerly perennial rivers and streams are expected to become intermittent across global regions over the coming decades [1,2]. Factors such as climate change, water abstraction and alteration of land use are the main drivers of these changes [3]. The transition from perennial to intermittent regime in these newly intermittent rivers (nIRs) negatively affects both taxonomic and functional diversity [4,5], with significant impacts on the structure and functioning of freshwater ecosystems, as well as global carbon fluxes [6–10]. However, the ability to withstand the adverse conditions of stream intermittence (the presence of resistance and/or resilience traits) may contribute to mitigating the impacts of droughts in freshwater ecosystems [11–15]. In any case, to better understand how changes in the natural flow regime affect the structure and processes of freshwater ecosystems, it is fundamental to assess variations in abiotic and biotic parameters throughout the four hydrological phases characterizing nIRs [16,17]. Specifically, more research is needed on how these parameters may fluctuate during normal flow conditions (flowing phase), in the successive drying and dry periods and after flow resumption (rewetting) [12]. Throughout these different hydrological conditions, freshwater assemblages are continuously reshaped and reorganized, with populations undergoing contraction, expansion, extinction and recolonization, resulting in complex metacommunity dynamics [18–20]. Moreover, the duration, frequency and intensity of the drying/dry phase may substantially affect the response of freshwater invertebrates to drought [21] and may influence the post-drought recovery of communities and processes [16,22].

Compared to Alpine or Central European streams, Apennine watercourses are likely more affected by flow intermittence [23–27] and recent studies have demonstrated that freshwater communities in Apennine nIRs have a limited post-drought recovery capacity [7,28]. It seems that freshwater taxa in formerly perennial Apennine streams have not evolved specific resistance and resilient traits to cope with the negative effects of flow intermittence. However, there is currently no information on how communities in Apennine nIRs respond to extreme reductions in discharge and complete cessation of superficial flow. Indeed, the drying phase is the most critical for freshwater biota due to the drastic changes in hydraulic, physicochemical and environmental parameters [29,30]. Drying streams first experience a strong reduction in flow, causing channel contraction and the loss of lateral connectivity. As the flow decreases further, riffle habitats disappear and lentic residual pools develop, leading to the loss of longitudinal connectivity. Finally, the pools dry out completely, bringing the stream into the dry phase [31,32]. Freshwater communities respond to the adverse conditions of drying channels by altering their structure and composition. For example, taxa richness constantly decreases from the initial phase of drying until the complete desiccation of pools and more sensitive and rheophile taxa are replaced by more tolerant and slow-current adapted species [33,34]. It was also assumed that the temporal dynamic of these changes is not linear but stepped [11,29,34–36]. In other words, taxa gradually disappear when the increasing level of disturbance exceeds their tolerance threshold values [29]. Although this model has a robust theoretical basis, its general applicability has been rarely demonstrated [36,37]. In this study, we assessed temporal changes in community structure and composition during the drying phase (approximately two months) of a Central Apennines stream (Italy) over two consecutive drought years. Based on results of previous research, we hypothesized that community metrics, taxa richness in particular, would have a negative and stepped response during the drying phase. We also predicted that overall compositional changes in communities from the flowing phase until complete superficial flow cessation would be substantial and subjected to few interannual differences.

2. Materials and Methods

2.1. Study Area and Data Collection

The Aterno River is one of the most important watercourses of Central and Southern Apennines (Italy), flowing for approximately 150 km before discharging into the Adriatic Sea. Over the past 10 years, the upper reach of the river (about 15 s from the spring source) has experienced irregular phenomena of seasonal intermittence. However, in the last five years, summer droughts have occurred regularly [7,38], with a long dry phase (from July–August to November–December). We located our sampling site at the midpoint of the 8 km intermittent reach (coordinates 42°23′27′′ N; 13°18′58′′ E; altitude 657 m asl). In this area, the watercourse is a second-order stream with a mean discharge of 0.8 m^3 s^{-1}. The channel is approximately 7 m wide and is surrounded by a small extension of natural riparian vegetation with poplar and willow trees. The substrate is mainly composed of pebbles, cobbles and sand, with patches of leaf litter accumulation (Figures 1 and 2). In spring 2024, the stream bed was covered by a dense growth of filamentous green algae (Figure 2). More details on the study area can be found in Di Sabatino et al. [7,38]. In this stream-reach, we assessed temporal variations in community structure and composition during the drying phase over two consecutive years (2023 and 2024). Benthic invertebrates were sampled using a Surber net (0.06 m^2; 200 µm mesh size) and three random samples were collected at each sampling date for a total of 24 biological samples (one site × three Surber × four sampling dates × two years). Macroinvertebrates were transported to the laboratory. Then, they were sorted and identified to the lowest taxonomic level. Additional samples were collected about one week after the complete desiccation of pools in both years. One liter of sediments (from 0 to 10 cm depth) was collected, rewetted in the lab with tap water and subsequently examined under a stereomicroscope to check for the presence of invertebrate taxa.

Figure 1. Photos showing the characteristics of the Aterno River during the 2023 drying phase. Photo credit: Antonio Di Sabatino.

Figure 2. Photos showing the characteristics of the Aterno River during the 2024 drying phase. Compared to 2023, note the lower discharge and the extensive growth of filamentous green algae in spring. Photo credit: Antonio Di Sabatino.

Some hydraulic (channel width, mean depth, flow velocity, instantaneous discharge) and physicochemical parameters (pH, temperature, dissolved oxygen, conductivity) were recorded at each sampling date using a digital flow meter (FP 101, Global Water, Gold River, CA, USA) and a multiparameter probe (Hach HQ 4300, Hach-Lange srl, Milano, Italy).

2.2. Data Analysis

We used inferential and descriptive statistics to assess variation in the structure and composition of freshwater communities during the approximately two-month drying period in both years. Interannual differences in the overall taxonomic structure of community (total richness, total abundance, Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa richness, insect and non-insect relative abundance) were tested using non-parametric Mann–Whitney U-tests. The temporal dynamics of mean values of taxa richness, EPT richness and abundance were also graphically represented to determine whether a stepped response occurred. Between-year differences in overall community composition (three cumulated Surber samples) were assessed using Permutational Analysis of Variance (PERMANOVA) and graphically represented by applying non-metric multidimensional scaling (nMDS) on the Bray–Curtis dissimilarity matrix of log x + 1 transformed abundances. Similarity percentage (SIMPER) analysis was applied to detect the taxa most responsible for between-year dissimilarity. The additional samples from dry sediments were not included in these latter analyses. 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. Physicochemical and Hydrological Parameters

During the two-month drying period of the Aterno River, variations in physicochemical parameters were similar in both years (Table 1). Temperature increased from late spring to early summer; dissolved oxygen was always near 100% saturation, except for higher values during extreme low-flow conditions and filamentous green algal blooms in residual pools. Conductivity values in 2024 were generally higher than those recorded in 2023 but did not show an evident increase during channel contraction or in residual pools. Between-year differences in hydrological parameters were more accentuated (Table 1).

Table 1. Values of some physicochemical and hydrological parameters recorded during the drying phase (about two months) of the Aterno River in the years 2023 and 2024.

Year	2023				2024			
Date	**30-May**	**28-June**	**20-July**	**1-August ***	**17-April**	**31-May**	**20-June**	**28-June ****
Temperature (°C)	10.2	15.8	18.8	23.7	11.9	16.4	20.2	21.6
pH	7.8	8.07	8.04	8.02	8.71	8.42	8.33	8.25
Conductivity (µS cm^{-1})	290	299	305	299	390	450	520	515
O_2 (mg L^{-1})	9.91	9.09	8.31	9.17	13.86	8.89	9.05	10.48
O_2 (% sat)	98.1	99.6	98.6	117.0	140.1	93.7	107.0	127.0
Mean depth (cm)	25	10	6	5	15	13	5.9	3.5
Channel width (m)	7.9	7.7	6.7	4	7.2	5.4	4	3
Current velocity (m s^{-1})	0.68	0.4	0.17	0.12	0.31	0.26	0.09	0
Discharge (m^3 s^{-1})	1.53	0.51	0.12	0.037	0.34	0.29	0.035	0

* = presence of connected pools; ** = presence of disconnected pools.

Compared to 2023, the reduced amount of rainfall during the first months of 2024 resulted in lower discharges in late spring and an earlier start of the drying period. Indeed, in 2023, flow recession started after the end of June, followed by a period of low flow with the presence of connected or disconnected residual pools which persisted until the first days of August; the stream channel dried up completely on 9 August. In 2024, the drying period began earlier (31 May) and, approximately one month later, the intermittent river reach was characterized by complete flow cessation, with disconnected residual pools desiccating completely on 5 July. A progressive reduction in current velocity, mean depth and channel width were observed during the drying phase of both years, but these variations were more accentuated in 2024.

3.2. Macroinvertebrates

During the two years of investigation, 21,255 individuals belonging to 42 invertebrate taxa were collected and identified (Table S1). In the drying phase of 2023, the whole community was composed of 9124 individuals and 34 taxa, while 12,131 individuals and 36 taxa were collected and identified in 2024. Twenty-eight taxa were present in both years, six taxa (*Valvata* sp., *Paraleptophlebia submarginata*, *Rhyacophila rougemonti*, *Hydropsyche* sp., Hydroptilidae, *Calopterix* sp.) were exclusively sampled in 2023, and eight taxa (*Helobdella stagnalis*, *Physa* sp., *Ancylus fluviatilis*, *Pisidium casertanum*, Limnephilidae, *Dityscus circumflexus*, *Atherix* sp., Anthomyiidae) occurred only in 2024. *Simulium variegatum*, Chironomidae, *Baetis rhodani*, Oligochaeta and Ostracoda were the most abundantly collected and occurred almost in all samples (Table S1).

Taxa richness and total abundance of the freshwater community were higher in 2024, but these differences were not significant for abundance (Mann–Whitney test U = 92.5, $p = 0.248$) and marginally non-significant for taxa richness (Mann–Whitney test U = 105.0, $p = 0.059$). However, EPT richness (Mann–Whitney test U = 27.00 $p = 0.008$) and the relative abundance of insect taxa (Mann–Whitney test U = 0.00, $p < 0.0001$) were significantly lower in 2024 (Figure 3).

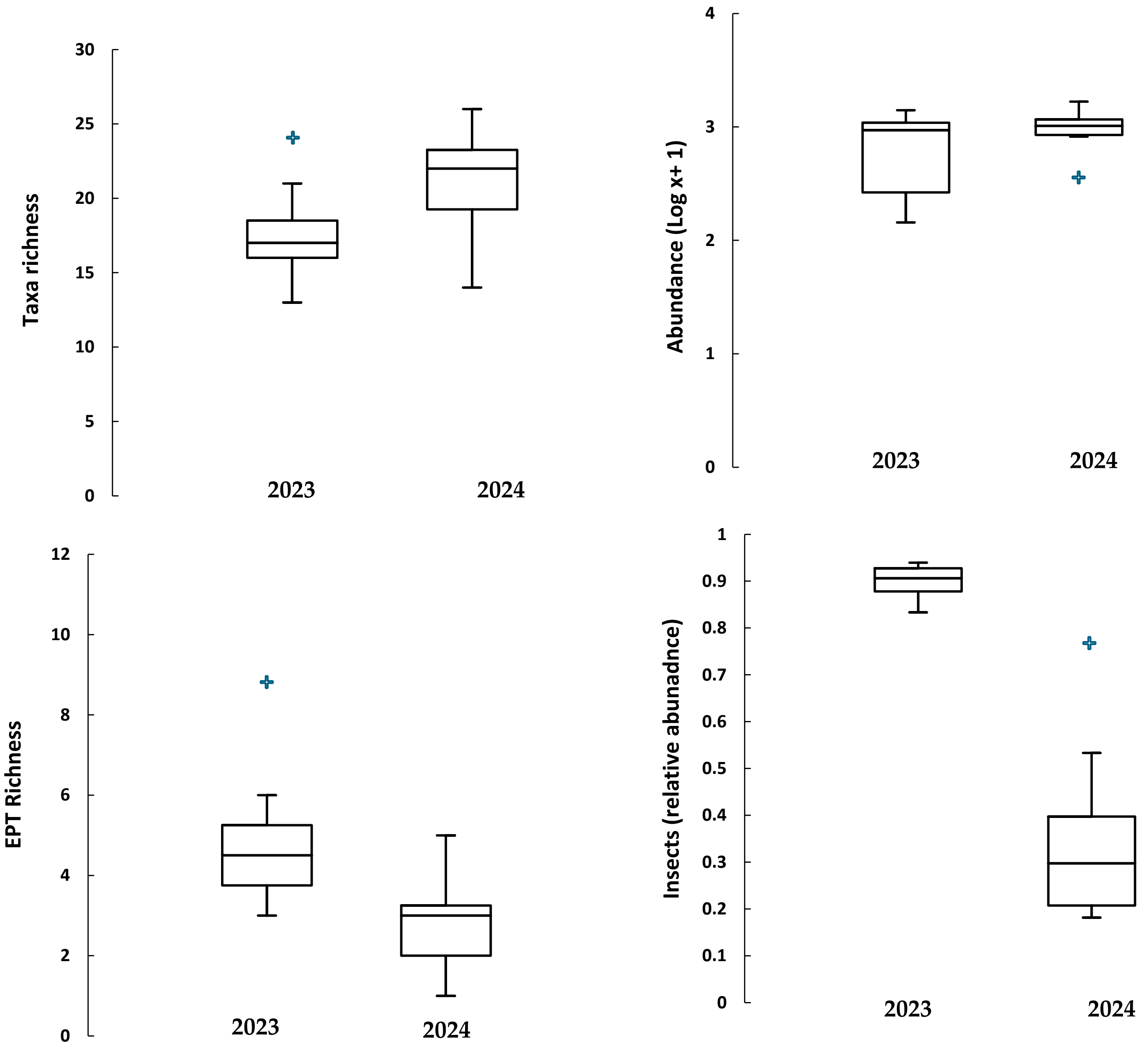

Figure 3. Boxplots of differences in some community metrics during the drying phase of the Aterno River in two consecutive years. Between-year differences were significant only for EPT richness and insect relative abundance. Outliers are indicated with a + symbol.

In 2023, taxa richness increased from May to July, despite a substantial reduction in flow discharge (Figure 4). Successively, richness decreased in connected residual pools and only a few taxa were sampled in the dry riverbed. Similarly, in 2024, richness increased from April to June and peaked during extreme low-flow conditions. Interestingly, a high number of taxa persisted in residual pools after superficial flow cessation (Figure 4).

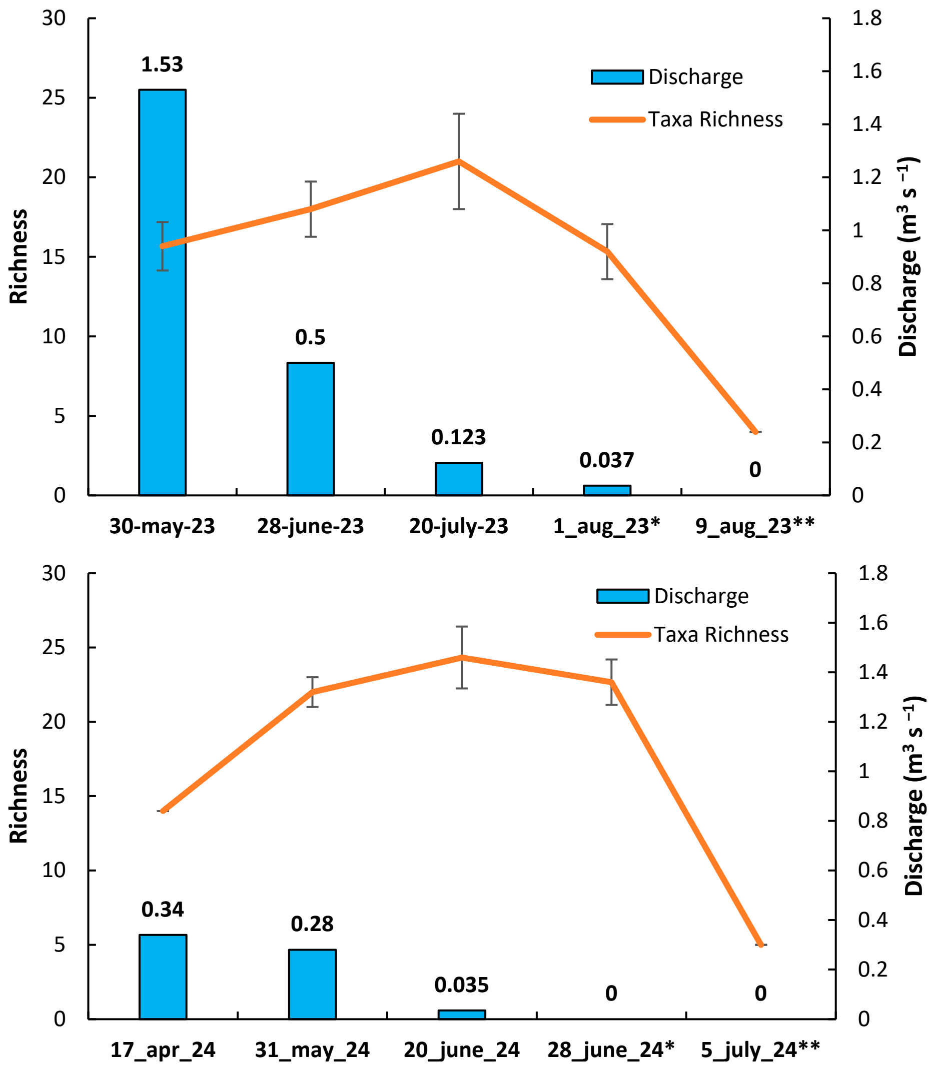

Figure 4. Temporal dynamics of taxa richness (mean ± sd) during the two-month drying period of the Aterno River in the years 2023 (graph **above**) and 2024 (graph **below**). * = presence of connected (2023) or disconnected (2024) residual pools: ** = dry streambed.

The total abundance of the invertebrate community was quite stable during the period of discharge reduction, from May to July 2023, and sharply declined in extreme low flow conditions (Figure 5). Only a few individuals were still present in the dry riverbed on 9 August. In the drying period of 2024, the total abundance of the community followed a different temporal pattern (Figure 5): abundance constantly increased from April to June, with the highest values recorded during low-flow conditions and in residual stagnant pools with no flowing water.

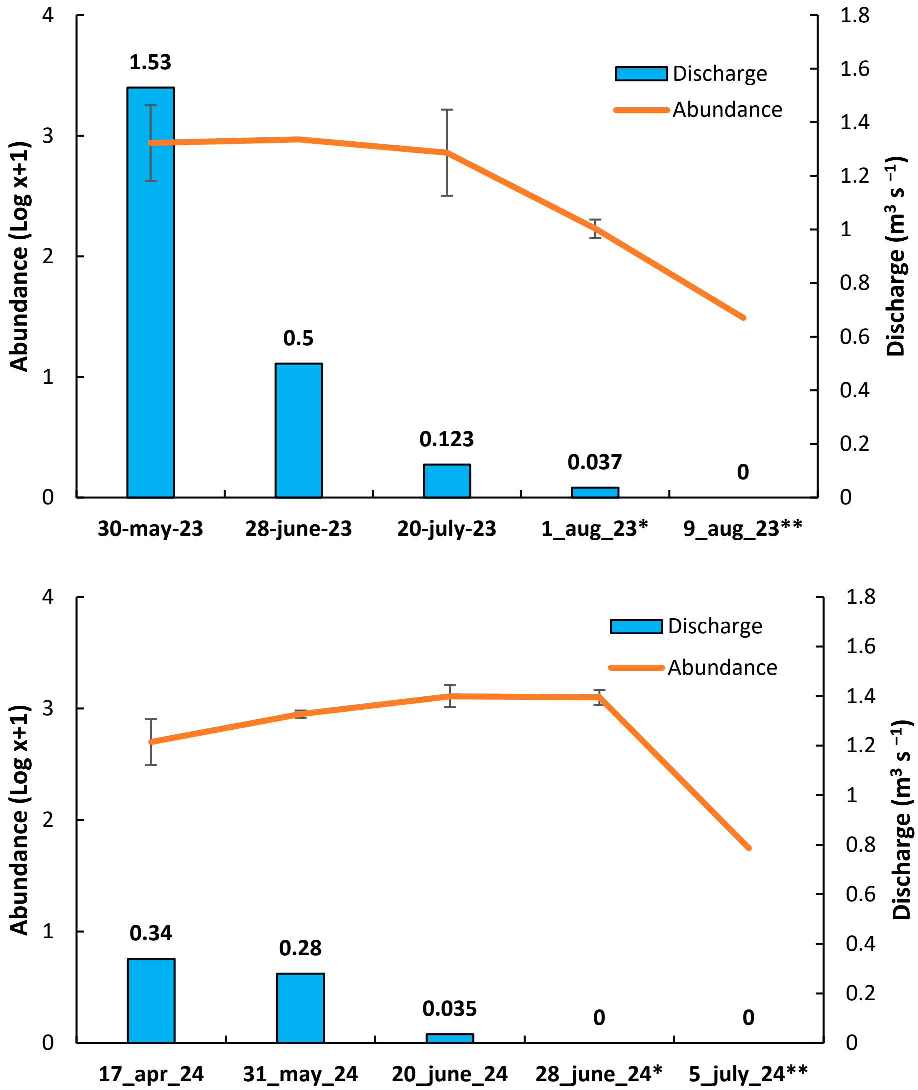

Figure 5. Temporal dynamics of community abundance (mean ± sd) during the two-month drying period of the Aterno River in the years 2023 (graph **above**) and 2024 (graph **below**). * = presence of connected (2023) or disconnected (2024) residual pools: ** = dry streambed.

The more sensitive EPT taxa occurred with low richness and abundance in both years. However, as explained above, in 2023, they were, on average, more diversified than 2024. In both years, EPT richness peaked during low-flow conditions and successively declined in residual pools with extremely low or null current velocity (Figure 6). Interestingly, sparse populations of some more sensitive EPT taxa (*Leuctra hyppopus*, *Rhithrogena semicolorata* and *Ecdyonurus venosus*) persisted during the final phase of the drying period in both years (Table S1). However, as expected, no EPT taxa were found in the dry riverbed approximately one week after the pools' desiccation.

The overall composition of assemblages during the drying period of 2023 and 2024 was significantly different (PERMANOVA, PseudoF = 5.76; $p = 0.035$) and showed a different temporal pattern of variation (Figure 7).

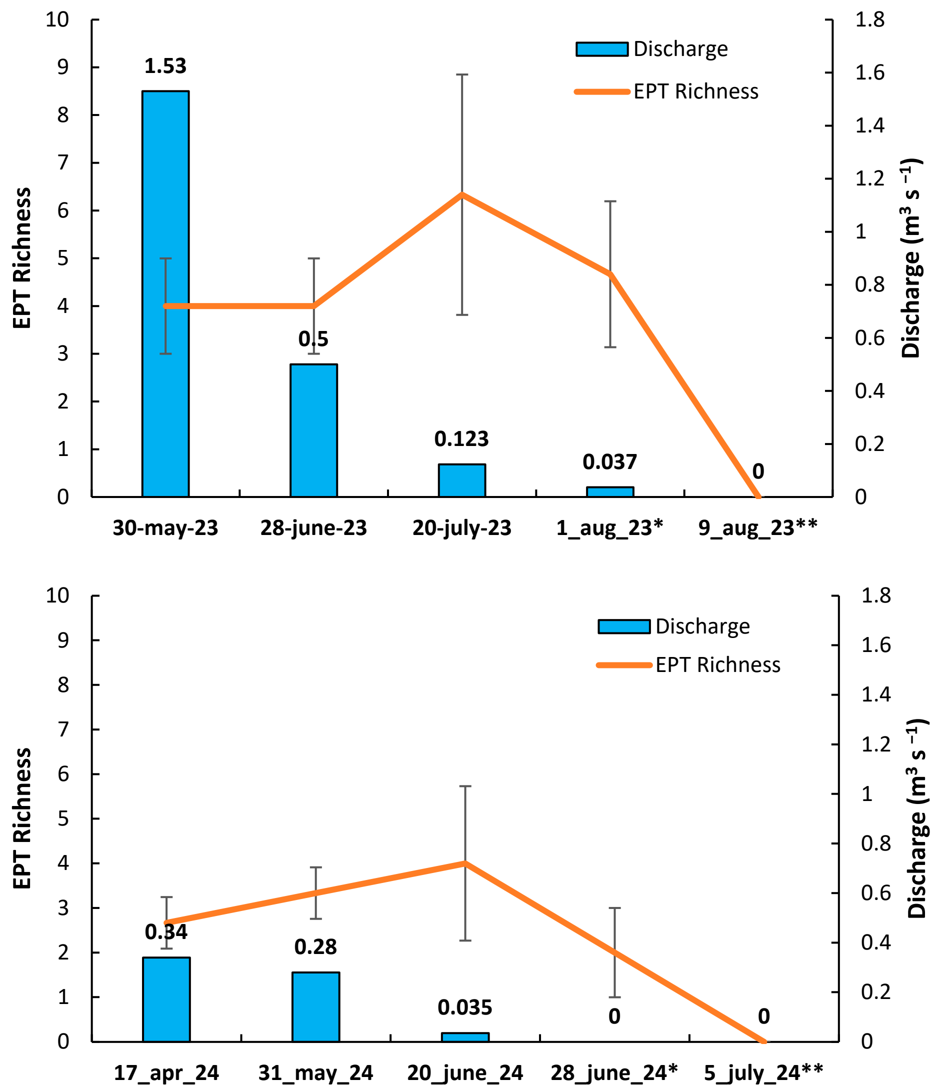

Figure 6. Temporal dynamics of Ephemeroptera, Plecoptera and Trichoptera (EPT) richness (mean ± sd) during the two-month drying period of the Aterno River in the years 2023 (graph **above**) and 2024 (graph **below**). * = presence of connected (2023) or disconnected (2024) residual pools: ** = dry streambed.

The taxa most responsible for these differences were *Baetis rhodani* and *Simulium variegatum*, which dominated the assemblages during the drying phase of 2023, while *Hydra* sp., oligochaetes, microcrustaceans and gastropods were more diversified and had remarkably higher abundances in 2024 (Figure 8).

In 2023, the composition of assemblages changed slightly during the early drying period (from May to July), but differences were more pronounced after the drastic reduction in stream discharge between 30 May and 28 June. The main compositional shift was observed in the assemblages sampled in residual pools in August. By contrast, in the following year, the main compositional differences were observed in the community sampled at the start of the drying period. Successively, during low-flow conditions and in disconnected residual pools, the composition of assemblages did not vary significantly. It should be noted that despite the marked annual differences in late-spring flow conditions, the communities at the initial phase of drying showed a more similar composition.

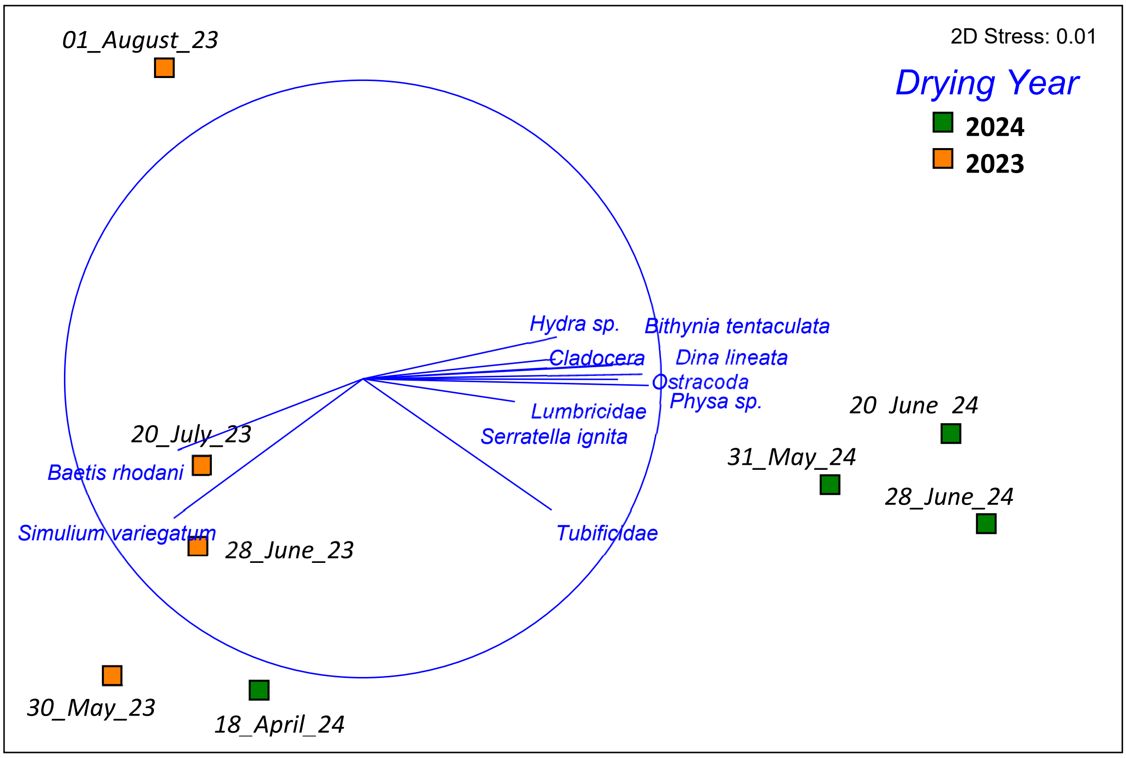

Figure 7. nMDS ordination pattern on differences in community composition (Bray–Curtis distance on log transformed abundance of three cumulated Surber samples) during the two-month drying period of the Aterno River in the years 2023 and 2024. Vectors of taxa contributing most to between-year dissimilarity (SIMPER Analysis) were superimposed to the graph.

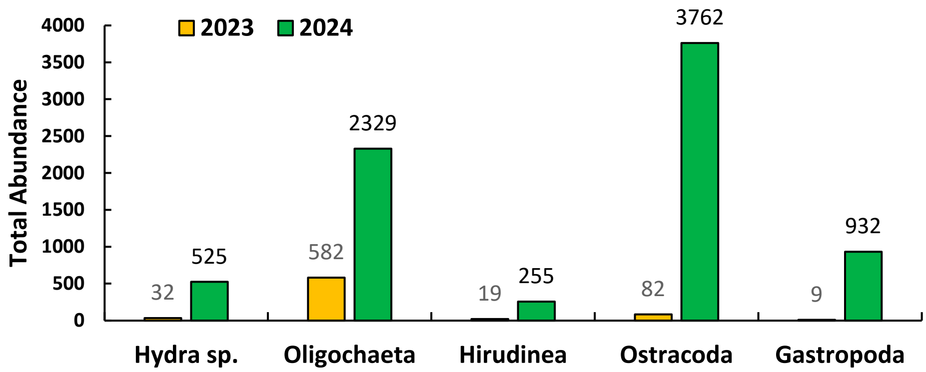

Figure 8. Interannual differences in the occurrence of the most abundant non-insect taxa during the two-month drying period of the Aterno River.

4. Discussion

We demonstrated that variations in the structure and composition of freshwater communities during the drying phase of a newly intermittent river in Central Italy were profoundly affected by the hydrological regime of the watercourse. In 2023, the intermittent stream reach was characterized by high flow in late spring, followed by a substantial but gradual decrease in flow discharge and formation of partly connected remnant pools in early August. In contrast, in the following year, the reduced precipitations resulted in a lower stream discharge in spring and an earlier start of the drying phase with the formation of residual pools and complete flow cessation in June. Overall taxa richness and total abundance of assemblages were higher during the low-flow conditions of 2024. However, the diversity of more sensitive and rheophile EPT taxa was significantly lower.

This implies that the reduced flow conditions in 2024 limited the presence of rheophile and more sensitive taxa while favoring the colonization of lentic-adapted and more generalist invertebrates, resulting in richer and more abundant communities [37]. In addition, the diverse hydrological regime also affected some functional characteristics of the assemblages. In fact, compared to the previous year, the massive growth of periphyton and the numerical explosion of small prey (ostracods) in 2024 resulted in a remarkably higher abundance of some herbivores (gastropods) and predators (*Hydra* sp.).

In any case, in both years, the communities experienced the same negative and adverse effects of stream drying: loss of lateral and longitudinal connectivity, shift from lotic to lentic conditions, contraction and/or loss of suitable microhabitats and an increase in water temperature [39]. However, we did not observe a decline in dissolved oxygen concentration and an increase in conductivity values. Instead, in 2024, the extensive growth of periphyton and filamentous green algae led to a substantial increase in photosynthetic activity, and stream water in low-flow conditions or in stagnant pools was often supersaturated during daytime, even if we cannot exclude a sharp decrease at night [17].

Contrary to our hypothesis, during the increasing disturbance caused by the progressive drying of the stream, community metrics like total richness, total abundance and EPT richness, though subjected to marked interannual differences (see above), did not show a clear negative response. Instead, these metrics generally increased, with values exceeding those recorded during the antecedent flowing phase. No effects of the progressive channel drying on taxa richness have been observed in mesocosm [36] and field manipulative experiments [37]. Furthermore, it has been previously demonstrated that, in some cases, the fragmentation and disconnection of microhabitats during the drying phase of nIRs may have apparent positive effects on the abundance and richness of freshwater assemblages [40,41]. That is, a higher environmental heterogeneity caused by the shift from lotic to lentic conditions may create new opportunities for the colonization of lentic taxa that can coexist with resident benthic species, thus leading to higher taxa richness. Therefore, in contrast to what generally reported in the literature [11,29,34–36], we did not find evidence for a negative stepped response of community metrics during the drying phase. Richness and abundance did not decrease following reductions in current velocity, flow discharge and channel width. Significant negative effects were evident only in the last period of the drying phase, when the increasing desiccation of residual pools may have led to extreme environmental conditions, not tolerable for most taxa [36,37,42]. However, we also observed that after flow cessation, sparse populations of more sensitive plecopterans (*Leuctra hyppopus*) and heptageniid ephemeropterans (*Rhithrogena semicolorata*) were able to persist in small patches of stagnant water accumulation. It is probable that these species may partially counteract the adverse effects of stream drying, suggesting that in some circumstances, isolated pools in stream drying reaches may act as a refuge for lotic taxa [41].

Despite the relative temporal stability in taxa richness and abundance, freshwater communities exhibited substantial compositional changes, but this finding only partially confirms our second prediction. That is, the composition of communities varied considerably during the drying period, but these changes were subjected to marked interannual differences. In 2023, the insect dominated community was progressively reorganized during the drying phase, with the main compositional changes observed at the end of the drying period in residual pools, and this evidence aligns with the widely observed pattern of temporal beta diversity variation during the drying phase [34,43]. By contrast, in the successive year, the non-insect-dominated community (mainly meiofaunal groups) showed only little variation during the sequence of channel contraction, flow reduction and pool formation (low turnover). These small-sized, lentic-adapted and more generalist taxa are more prone to counteracting the adverse conditions of stream drying [44]. Therefore, the richness, abundance and composition of communities did not vary significantly following channel contraction, flow cessation and pool formation. Consequently, we can assume that in newly intermittent Apennine rivers, the response of freshwater communities to drying is strictly dependent on the local and interannual variable hydrological context.

5. Conclusions

To our knowledge, this is the first field study that systematically analyzed the response of freshwater communities to stream drying. We demonstrated that the different hydrological regime of the Aterno River in two consecutive drought years substantially affected the response of freshwater communities to drying. A lower discharge and the early set-up of drying in 2024 determined substantial differences in freshwater community structure, composition and functional organization. However, in both years, the richness and total abundance of assemblages did not decline during flow recession and channel contraction; rather, they tended to increase. An abrupt negative change was only observed during the last period of the drying phase in desiccating residual pools. Therefore, no signals of a stepped response were evident in both years. We cannot exclude that interannual hydrological differences during the drying, but also the rewetting phase of nIRs, would have profound effects on the post-drought recovery capacity of freshwater communities. Finally, our findings suggest that outcomes on the response of freshwater invertebrates to drying conditions are still difficult to generalize. Therefore, further studies are necessary for a clearer and more precise understanding of the ecological impacts of the increasing intermittence in formerly perennial streams and rivers.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/environments11120295/s1: Table S1: List and abundance of invertebrate taxa sampled during the two-month drying period of the Aterno River in the years 2023 and 2024.

Author Contributions: Conceptualization, A.D.S. and F.R.; methodology, A.D.S. and F.R.; validation, A.D.S., F.R. and G.E.; formal analysis, A.D.S. and F.R.; investigation, G.E., F.R. and A.D.S.; resources, A.D.S.; data curation, A.D.S. and F.R.; writing—original draft preparation, A.D.S., F.R. and G.E.; writing—review and editing, A.D.S., F.R. and G.E.; supervision A.D.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: The data presented in this study are included in the article/Supplementary Materials. Further inquiries can be directed to the corresponding author.

Acknowledgments: We wish to thank Patrizia Vignini (L'Aquila) for her valuable support during the field and lab work. We also thank the anonymous reviewers for their useful comments and suggestions.

Conflicts of Interest: The authors declare no conflicts of interest.

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