Received: 14 March 2019 | Revised: 3 June 2020 | Accepted: 5 June 2020

DOI: 10.1111/fwb.13587

ORIGINAL ARTICLE

Freshwater Biology WILEY

Duration and frequency of non-flow periods affect the abundance and diversity of stream meiofauna

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Funding information
SPACESTREAM project, Grant/Award Number: CGL2017-88640-C2-1-R

Abstract

1. Intermittent streams (IS) comprise a large proportion of the drainage network in many parts of the world. The non-flow period of IS are known to impact stream biota because aquatic habitats dry out. However, less well understood are the relative effects of the temporal component of these drying events including their duration and frequency.
2. Here, we characterised effects of temporal component of drying events on abundant and species-rich meiofauna. The effects were assessed in 22 streams in the north-eastern Iberian Peninsula. The duration and frequency of non-flow events was characterized over a period of 250 days prior to sampling the sediment-dwelling meiofauna in riffle zones that completely dried out.
3. Overall, meiofauna abundances were amongst the highest ever reported for streambeds. Most meiofaunal taxa correlated positively with the frequency of drying events and correlated positively with the length of dry periods recorded shortly before sampling, suggesting that the community was able to recover quickly. Tardigrades were the only group to correlate positively with the longest dry periods, suggesting that they had the best resilience capabilities in streams that had experienced the longest droughts.
4. On average, nematodes made up half of the meiofauna. We identified a total of 113 different nematode species. The nematode community was more taxonomically diverse in IS, with a smaller proportion of bacterivores and a higher proportion of fungivore species such as *Filenchus vulgaris*. Thereby resembling the trophic structure commonly observed in soil ecosystems.
5. Our results show that most meiofauna were positively influenced by drying disturbance, that is being able to quickly recover after them. This suggests outstanding resilience capabilities, and points out meiofaunal organisms as key players for *kick-starting* stream food webs and functions once flow returns.

KEYWORDS
community structure, ephemeral streams, functional diversity, meiobenthos, species distribution

1 | INTRODUCTION

Flow regime is defined as the temporal variability of stream or river discharge, which can be characterised by flow quantity, timing, and variability (Poff et al., 1997). Hydrological events include floods as well as drought periods and govern the geomorphology, water quality, and ecology of the river system. Under flowing conditions, the river basin is connected, and matter, energy and organisms are transported throughout the river network (Pringle, 2003). However, hydrological connectivity is affected when water ceases to flow, and implications extend to physical, chemical, and biological processes. Intermittent streams (IS) experience flow intermittency at any given segment and period, and account for more than 50% of the total length of the global river network (Raymond et al., 2013). The proportion of IS increases due to climate change and anthropogenic hydrological alterations (Döll & Müller Schmied, 2012; Döll et al., 2018; Pekel, Cottam, Gorelick, & Belward, 2016; Sabater et al., 2018; Sabater, Timoner, Borrego, & Acuña, 2016). Under dry conditions, water stress, direct effects of solar radiation, and high streambed temperatures progressively affect aquatic organisms (Lake, 2000). Consequently, the transition from flow to non-flow conditions may be viewed as a *ramp disturbance* with disturbance strength increasing steadily through time (Lake, 2000).

The non-flow period affects the abundance, species richness, and functional structure of streambed communities (e.g. Wood, Gunn, Smith, & Abas-Kutty, 2005; Schriever et al., 2015; Soria, Leigh, Datry, Bini, & Bonada, 2017; White et al., 2018; Bruno et al., 2019). Drying-associated decrease and fragmentation of aquatic habitats may lead to increased biotic interactions (predation, competition) and colonisation by a diverse terrestrial flora and fauna (e.g. Sandercok, Hooke, & Mant, 2007; Steward et al., 2011; Sánchez-Montoya, Moleón, Sánchez-Zapata, & Tockner, 2016; Corti & Datry, 2016). Thus, the occurrence of non-flow periods may act as a strong selection force for desiccation-sensitive and rheophilic taxa (Datry, 2012; Graeber, Pusch, Lorenz, & Brauns, 2013; Poff & Ward, 1990). Conversely, taxa possessing desiccation-tolerance traits or able to avoid dry conditions by seeking refuges may show better resilience capabilities (Clinton, Grimm, & Fisher, 1996; Durkota, Wood, Johns, Thompson, & Flower, 2019; Stanley, Buschmann, Boulton, Grimm, & Fisher, 1994). As an example, some resistant benthic macro-invertebrate species are able to diapause their eggs (Bogan, Boersma, & Lytle, 2013), or even show anhydrobiotic capabilities such as the chironomid *Polypedilum vanderplanki* Hint. (Cornette & Kikawada, 2011). Other species may show greater dispersal capabilities to cope with drying (Bonada, Dolédec, & Statzner, 2007). Aquatic macro-invertebrates use the hyporheic zone as a subsurface refuge under dry conditions (Durkota et al., 2019; Rosario & Resh, 2000).

Tiny invertebrates of the meiofauna have short life cycles, and can easily seek refuge in wet subsurface sediment (e.g. Clinton et al., 1996), and where appropriate, they may show the most outstanding desiccation-tolerance of the metazoa. For example, nematodes, rotifers, and tardigrades show developmental dormancy, diapause, formation of dauer larvae, anhydrobiosis, and even cryptobiosis (Rebecchi, Boschetti, & Nelson, 2020). Anhydrobiotic stages come along with increased dispersal capabilities and tolerance against temperature extremes and ionising radiations (well-evidenced in the tardigrades; Nelson & Marley, 2000). With those advantages, meiofaunal organisms may quickly colonise and help restore ecosystem functions in IS after flow returns (Gaudes, Artigas, & Muñoz, 2010).

Amongst the meiofauna, free-living nematodes form species-rich assemblages, numerically dominant in sediments (e.g. Traunspurger, 2000; Beier & Traunspurger, 2003a; Traunspurger, Höss, Witthöft-Mühlmann, Wessels, & Güde, 2012). Their diverse life-history and feeding traits link to ecosystem productivity, microbial trophic channels, and disturbance regime (Majdi et al., 2011; Traunspurger, Reiff, Krashevska, Majdi, & Scheu, 2017; Traunspurger, Wilden, & Majdi, 2020). Moreover, nematodes are abundant both in streambeds and in adjacent soils, although the structure of species assemblages seems to be distinct in aquatic versus terrestrial biotopes. In streams, nematode communities are dominated by bacterivorous species and include algal-feeding species (Beier & Traunspurger, 2003a,b; Hodda, 2006; Traunspurger, 2002; Traunspurger, Threis, & Majdi, 2015). Soil nematode communities have a higher proportion of suction-feeders with a stylet allowing them to feed on a variety of prey including plant roots, protozoans, other metazoans, or fungi (Hohberg, 2003; Traunspurger et al., 2017; Yeates et al., 1993). Stream-dwelling nematodes respond to a variety of environmental drivers: sediment granulometry (Beier & Traunspurger, 2003a,b; Traunspurger, 2002), availability of dissolved and particulate resources (Majdi, Boiché, Traunspurger, & Lecerf, 2015; Majdi, Threis, & Traunspurger, 2017; Majdi et al., 2011; Traunspurger et al., 2015), spatial patterning at different scales (Gansfort & Traunspurger, 2019; Gansfort, Traunspurger, Threis, & Majdi, 2018; Ptatscheck, Gansfort, Majdi, & Traunspurger, 2020). Flow events such as floods may cause profound effects on stream-dwelling nematodes (Majdi et al., 2011), yet we have a very limited knowledge of nematode responses to flow intermittency. In particular, the relevance of frequency and duration of dry phases as potential drivers of nematode community structure.

Here, we examined the response of meiofaunal communities to flow intermittency in 22 Mediterranean streams. Streams ranged from permanent to intermittent, the later spanning a variety of duration and frequencies of dry periods. Because many meiofaunal organisms have short life cycles and are tolerant to desiccation, we predicted that: (1) minor or no differences in abundances may be observed between IS

and permanent streams (PS). However, we expected (2) a structuring effect of flow intermittency on meiofaunal communities in IS; higher frequencies of dry periods may have a beneficial effect on the diversity and the abundance of desiccation-tolerant taxa, whereas prolonged dry phases would only benefit the most tolerant taxa such as the tardigrades. (3) More species of nematode fungal-feeders and omnivores would occur in IS, while PS would show less diverse communities mostly made up of bacterivores and algivores.

2 | METHODS

2.1 | Study sites

We studied 22 Mediterranean streams from five different basins scattered across the NE Iberian Peninsula (Figure 1). The sampling sites encompassed a broad range of hydrological characteristics and land-uses. Altitude, catchment area, mean precipitation, and land-uses were determined from GIS layers using Quantum GIS (2.14.22) with GRASS (7.2.2). All streams were situated at moderate elevations (81–920 m) and were mostly influenced by Mediterranean climate. Annual precipitation ranged from 428 to 1,093 mm, rainfall mostly occurring during autumn-winter. Forests were the dominant land-use, followed by shrub/grass-lands and agricultural fields (Table S1). All stream sites showed substantial riparian canopy cover (mean: 64.6%) and a low degree of physical human impact (Table S1). Streams ranged from orders 2 to 5, and were either PS (continuous flow conditions) or IS (at least one drying event) (Table S1). The IS showed different durations and frequencies of their non-flow periods (Table S2). All samples (see below) were collected in November and December 2016 in both PS and IS, when all streams were flowing.

2.2 | Characterisation of the hydrological regime

Streambed temperatures were monitored every hour in 17 streams with temperature data-loggers (Minilig-II-T, VEMCO), while in the remaining five streams water levels were monitored every hour with level-loggers (Solinst levelloger, Edge, Model 3,001). All sensors were deployed in each stream at the bottom of riffle areas and measurements were performed over a period of 250 days before the sampling—meiofauna sampling was performed at the same reach on which the sensors were located. Air temperature was obtained from field loggers previously installed in the riparian zone or from nearby meteorological stations (Servei Meteorològic de Catalunya). The daily hydrological status in each of the sites was estimated comparing streambed and air temperatures, and the method was calibrated using water-level sensors (full procedure detailed in Colls, Timoner, Font, Sabater, & Acuña, 2019; results listed in Table S1). The daily hydrological status at the riffle was used to estimate the temporal components of the non-flow period. Temporal components were typified by means of three hydrological descriptors: total duration of the dry period (DD, expressed in number of dry days), the frequency of the dry period (F, expressed as number of drying events) and the mean duration of the dry period as a measure of the mean number of consecutive dry days

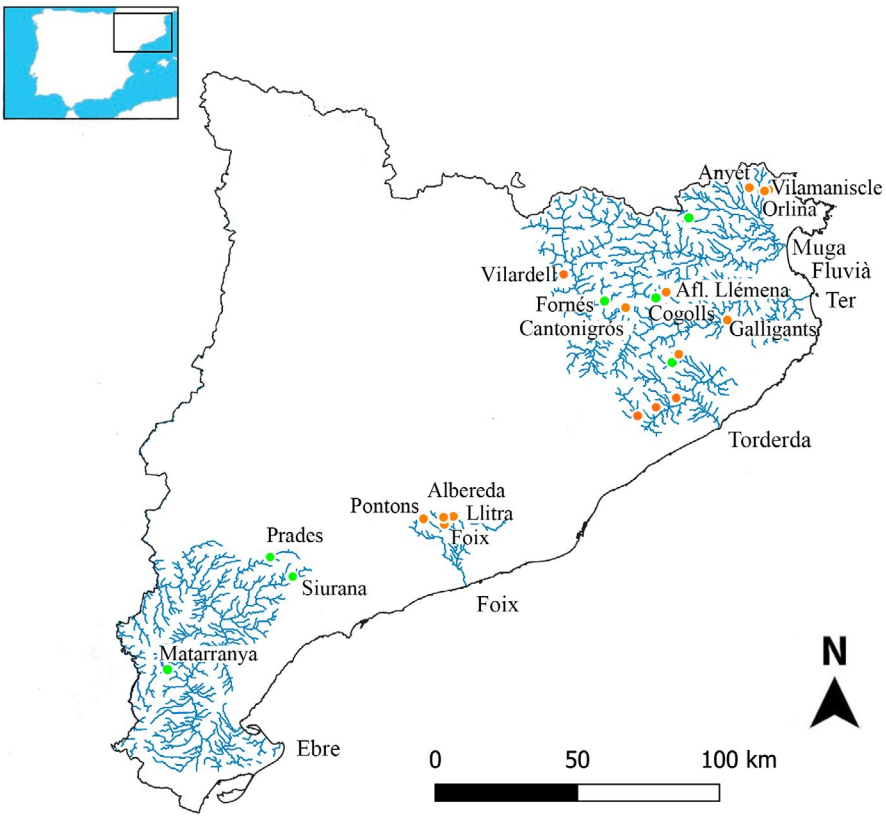

FIGURE 1 Distribution of stream sites across five river basins in the North-Eastern Iberian Peninsula. Green dots show the location of permanent stream sites, orange dots show the location of intermittent stream sites [Colour figure can be viewed at wileyonlinelibrary.com]

(MnD = DD/F). By contrast, the timing and length of flow resumption periods was calculated as the ratio between the total duration of flow resumption in flow days (FD), the frequency of flow events (FF), and mean number of consecutive flow days (MnF = FD/FF). The temporal components of the non-flow period provide information about the number of dry days, but its distribution may vary through time. We therefore determined the number of dry days for periods of 250, 150, 90, and 30 days before the sampling date. A positive correlation between one faunal descriptor and a component of the non-flow period occurring shortly before sampling would imply ability to recover quickly.

2.3 | Environmental assessment

Water temperature, conductivity, dissolved oxygen, and pH were measured at each site using hand-held probes (WTW multiline 3,310; YSI ProODO handled; YSI Inc.) (Table S2). Three water samples were collected per site, filtered through glass fibre filters (Whatman's GF/F) and frozen at −20°C until analysis. For each water sample, the concentration of DOC was measured on a Shimadzu TOC-V CSH analyser (Shimadzu Corp.), the concentration of nitrate was analysed by ion chromatography using a DIONEX C5000 (Dionex Corp.), and the concentration of ammonium was determined colorimetrically using an Alliance-AMS Smartchem 140 spectrophotometer (AMS). The granulometry of streambed was characterised in situ at each pre-defined transect following Wentworth's (1922) classification.

2.4 | Sediment collection, extraction, and assessment of invertebrate communities

At each stream site, three sediment samples were collected by pushing a plastic corer (2 cm diam.) into the streambed down to a depth of 5 cm. Samples were collected 25 m apart (i.e. 0, 25, and 50 m) in riffle areas within the reach, so each core was a replicated sub-sample in the stream site. Sampled sediment was immediately preserved in the field with a solution of 4% formaldehyde. When sampling, we took care to avoid pools so that the areas sampled for meiofauna reflected hydrological status as recorded by the deployed sensors. We also focused on soft-substrata habitats to reduce the variability of our bio-assessment protocol and because those habitats were very common throughout.

In the laboratory, the volume of sediment was measured, and invertebrates were extracted from the sediment using a density-centrifugation procedure using a solution of colloidal silica (Ludox TM-50®, specific gravity set at 1.14 g/cm^3) after Pfannkuche and Thiel (1988). The supernatant containing the invertebrates was rinsed over 20-μm meshes, and invertebrates were counted and assigned to coarse taxonomic groups under a stereomicroscope (×40 magnification). Faunal abundances were expressed as number of individuals per L (wet) sediment (ind./LSed). Note that faunal abundances may be expressed using a more commonly reported area unit, such as ind./10 cm^2, using a conversion factor of 0.05.

2.5 | Species identification of nematodes and feeding-type classification

Whenever possible, 50 nematode individuals were sorted (mean number of individuals per sample: 41.6, *SD*: ±14.7), and mounted on microscope slides following the protocol of Seinhorst (1959). A total of 2,624 nematode individuals were identified to species-level and assigned to feeding-type after the morphology of their buccal cavity following the classification of Traunspurger (1997). These were separated as (1) *deposit-feeders* (bacterivores), which showed small unarmed buccal cavities and were expected to feed mainly on prey in the bacterial-size range; (2) *epistrate-feeders* (algivores), which showed small teeth and were expected to feed on *armoured* microbial prey such as diatoms; (3) *chewers*, which showed large buccal cavities armed with robust teeth enabling them to engulf and break up the largest microbes as well as other meiofauna, they were further distinguished as mostly predacious on other invertebrates and protozoans (predators) or as omnivores; and (4) *suction-feeders*, showing hollow stylets to pierce the cuticle of a broad range of prey from fungal hyphae to larger metazoans and plant roots. Among suction-feeders a further distinction was also made between omnivorous species and species with delicate stylets mostly expected to feed on fungal hyphae and plant roots (hereafter referred to as fungivores), according to *a priori* knowledge about the diet and the ecological preferences of soil and freshwater nematode families and genera (Traunspurger, 1997; Yeates et al., 1993).

2.6 | Calculation of diversity indices

We calculated the index of trophic diversity (ITD) for nematodes after Heip, Vincx, and Vranken (1985). The ITD is defined as $\Sigma\theta^2$, with θ being the relative contribution of each of the five functional feeding-types (bacterivores, algivores, predators, omnivores, and fungivores) observed in one sample. ITD varies from highest feeding-type diversity: ITD = 0.2 (each feeding-type contributes 20%) to the lowest diversity: ITD = 1 (only one feeding-type is present). Diversity was estimated through species richness (S), Ln-based Shannon's diversity (H), Pielou's dominance (J), and Simpson's dominance (D).

2.7 | Data analysis

All data analyses were performed under R computational framework (R Development Core Team, 2018). The abundance of meiofaunal groups, as well as nematode ITD and diversity indices of intermittent versus permanent streams were compared using Wilcoxon's rank sum test (W, *wilcox.test* function in R), performed on untransformed data.

Pearson's coefficient correlation of the temporal components of flow and non-flow periods (i.e. DD, F, MnD, and MnF, calculated over periods of 250, 150, 90, and 30 days before sampling) in the IS was calculated versus faunal descriptors. Flow days and FF were not

TABLE 1 Mean abundance of meiofauna, and indices of taxonomic and functional diversity of nematodes in the sediment (Sed) of intermittent and permanent streams from north-eastern Iberian Peninsula.

	Intermittent streams	Permanent streams	Wilcoxon test
Faunal descriptors	**Mean ± *SE***	**Mean ± *SE***	***p*-value**
Meiofauna abundances (ind./LSed)			
Nematodes	28,423 ± 6,307	19,987 ± 3,149	0.97
Rotifers	15,638 ± 2,794	23,627 ± 5,962	0.31
Gastrotrichs	1,375 ± 323	893 ± 244	0.63
Harpacticoid copepods	436 ± 108	391 ± 111	0.69
Nauplii larvae	845 ± 197	444 ± 117	0.78
Ostracods	424 ± 85	625 ± 232	0.58
Oligochaetes	1,159 ± 200	1856 ± 363	0.02*
Chironomid larvae	569 ± 184	772 ± 263	0.40
Tardigrades	1,213 ± 248	1503 ± 319	0.04*
Ceratopogonidae larvae	641 ± 520	336 ± 113	0.03*
Other insect larvae	55 ± 14	148 ± 69	nd
Stonefly larvae	18 ± 9	5 ± 5	nd
Mites	59 ± 27	121 ± 94	nd
Mayfly larvae	100 ± 64	140 ± 61	nd
Gammarids	5 ± 3	0 ± 0	nd
Total meiofauna	50,959 ± 9,070	50,849 ± 9,033	0.53
Nematode diversity indices			
Cumulative number of species	108	58	nd
Species richness (per sample)	13.51 ± 0.69	11.65 ± 1.09	0.11
Simpson's dominance	0.18 ± 0.01	0.21 ± 0.03	0.42
Shannon's diversity	2.12 ± 0.06	1.95 ± 0.11	0.18
Pielou's evenness	0.84 ± 0.01	0.82 ± 0.03	0.69
Feeding-types contribution (%)			
Omnivores	21.06 ± 3.57	9.69 ± 3.06	0.03*
Predators	2.20 ± 0.69	3.98 ± 2.47	0.51
Bacterivores	57.20 ± 3.87	76.75 ± 5.10	0.003**
Algivores	9.45 ± 1.67	7.32 ± 2.10	0.40
Fungivores	10.09 ± 2.11	2.26 ± 1.06	0.005**
Index of trophic diversity	0.57 ± 0.02	0.70 ± 0.05	0.04*

Abbreviation: nd, not determined.

Significance-level : $p < 0.05$ (*), $p < 0.01$ (**).

tested because they strongly covaried with DD and F. Abundance data were $\log_{10}(x + 1)$-transformed to meet normality (controlled using Shapiro–Wilk test). Since multiple comparisons of data can inflate type I error rate, the *p*-values were adjusted using the Holm–Bonferroni sequential correction procedure (Field, Miles, & Field, 2013). The correlation matrix was summarised through a correlation plot on which the *p*-adjusted values ≤ 0.05 were highlighted.

Because of unbalanced number of sites in IS (15 sites) and PS (seven sites) we compared nematode species richness using sample rarefaction (*specaccum* function in R) based on the analytical solution known as *Mao Tau*, with associated standard deviation (Colwell, Mao, & .Chang, 2004). Comparison was performed on equivalent, minimum sampling effort (i.e. seven sites sampled). We further estimated maximum species richness in IS and PS communities using the non-parametric Chao2 estimator (*ChaoSpecies* function in R) using incidence data to estimate the number of undetected species in a community (Eq. 11a, in Chao & Chiu, 2016).

Differences in the structure of nematode species and feeding-types in IS versus PS were assessed using permutational analysis of variance using Bray–Curtis distance matrices (PERMANOVA, 9,999 permutations, *adonis* function), based on $\log_{10}(x + 1)$-transformed abundance data. To avoid confounding among-site variation with among-core variation, we considered stream sites as independent samples. Therefore, the PERMANOVA was run using the 22 stream sites as samples, for which we averaged the values of the 3 core samples. Multivariate homogeneity of group dispersion was tested

using Anderson's PERMDISP2 procedure (*betadisper* function). This procedure performs a multivariate analogue of Levene's test for homogeneity of variances, which we checked in order to assess variability among treatments having small, unequal numbers of samples (in our case, seven PS versus 15 IS; Anderson, 2006). Homogeneity of group dispersion was met in our case (999 permutations; for species: $F_{1,20} = 153$, $p = 0.23$; for feeding-types: $F_{1,20} = 1.25$, $p = 0.28$). We further used non-metric multidimensional scaling based on Bray–Curtis similarity matrix to ordinate sites and species scores. We used multi-level pattern analysis (*multipatt* function, 9,999 permutations) to highlight meaningful associations of nematode species with hydrological status (De Cáceres & Legendre, 2009; De Cáceres, Legendre, & Moretti, 2010).

3 | RESULTS

3.1 | Comparing meiofauna in IS versus PS

Mean meiofauna abundance was 50,924 ind./LSed (representing 2,546 ind./10 cm^2), varying between a minimum value of 4,000 and a maximum of 322,800 ind./LSed (Table 1). Overall, meiofauna abundance did not differ in IS versus PS ($W = 473$, $p = 0.53$). Nematodes dominated, making up on average 55.8 and 39.3% of the meiofaunal community in IS and PS, respectively. Rotifers were the second most abundant group making up on average 30.7 and 46.5% of the meiofaunal community in IS and PS, respectively. Although absolute and relative abundances seemed different in IS and PS (Table 1), the large variances caused that neither nematodes nor rotifers showed significant differences in their abundances in IS versus PS ($W < 498$, $p > 0.31$). The abundances of gastrotrichs (across all sites average: 2.4%), chironomids (1.2%), harpacticoid copepods (0.8%), and their nauplii (1.4%) as well as ostracods (0.95%) were not significantly different. However, oligochaetes (2.7%), tardigrades (2.5% of meiofauna), and Ceratopogonidae larvae (1.1%) showed significantly different abundances (Table 1). Mites, gammarids, and larvae of stoneflies and mayflies were seldom found in the samples (altogether: <0.5% of invertebrates), thus patterns in their distribution were not tested.

3.2 | Correlations with the temporal components of the flow intermittency in IS

The total abundance of meiofaunal organisms was positively correlated with the frequency of drying events in IS (Figure 2), and was negatively correlated with the mean duration of flow resumption (MnF_{250} and MnF_{150}). In contrast, the mean duration of flow resumption over shorter periods (MnF_{90} and MnF_{30}) had a positive impact on abundances, although correlations were relatively weak (Figure S1). This was characteristic for nematodes, rotifers, gastrotrichs, and chironomid larvae (Figure 2). Tardigrades were the only meiofaunal taxa correlating positively with the total number of dry days recorded over the longest periods of time prior sampling (DD_{150} and DD_{250}). Harpacticoid copepods and their nauplii, ostracods, oligochaetes, and larvae of Ceratopogonidae showed weaker patterns and correlations.

3.3 | Univariate effects on the taxonomic and functional diversity of nematodes

We identified 2,624 nematode individuals from which a total of 113 nematode morphospecies were counted across all samples (Table 2). A total of 58 species were identified in PS, the three dominant

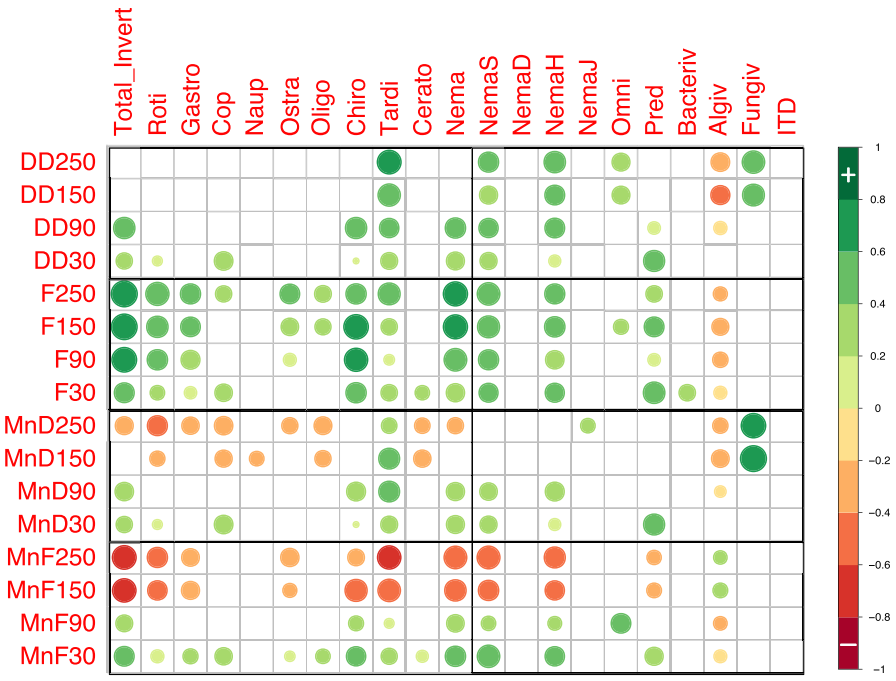

FIGURE 2 Correlation matrix between temporal components of non-flow/flow periods and faunal descriptors in the sediment of 15 intermittent streams. Circles show significant Pearson's correlation, the colour (or size) of circle shows the strength (value of Pearson's rho) and direction of the correlation (green: positive or red: negative). Predictors' abbreviations and values of correlations are detailed in Figure S1 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Mean abundance and relative contribution of species of free-living nematodes identified in the sediment (Sed) of intermittent and permanent streams from north-eastern Iberian Peninsula. Species were listed according to their feeding-types. Summaries of diversity indices and feeding-type distribution are given at the bottom of Table 1

		Permanent streams		Intermittent streams	
Nematode species	nMDS code	Contribution (%)	Abundance (ind./LSed)	Contribution (%)	Abundance (ind./LSed)
Bacterivores (Deposit-feeders)					
Acrobeloides spec	AcroSp	–	–	0.05	6.72
Acrobelophis minimus (Thorne, 1925)	AcroMini	0.24	17.46	–	–
Alaimus parvus Thorne, 1939	AlaiPar	0.31	8.33	0.38	40.40
Alaimus primitivus de Man, 1880	AlaiPrim	–	–	0.51	170.92
Anaplectus granulosus (Bastian, 1865)	PlecGra	–	–	0.48	44.36
Aphanolaimus aquaticus Daday, 1894	AphaAqua	0.10	26.39	0.23	99.89
Aphanolaimus attentus de Man, 1880	AphaAtt	–	–	0.05	12.91
Bastiania gracilis de Man, 1876	BasGra	–	–	0.10	19.50
Bursilla monhystera (Bütschli, 1873)	BurMon	0.20	55.99	2.19	135.81
Cephalobus persegnis Bastian, 1865	CephPer	2.08	104.25	2.18	379.75
Cylindrolaimus communis de Man, 1880	CylCom	0.10	12.24	0.15	145.80
Diploscapter coronatus (Cobb, 1893)	DipCor	0.10	26.39	0.24	6.43
Eucephalobus oxyuroides (de Man, 1876)	EucOxy	–	–	1.12	134.53
Eumonhystera andrassyi (Biró, 1969)	EumAnd	–	–	1.11	496.04
Eumonhystera barbata Andrássy, 1981	EumBar	2.57	475.21	3.24	1,112.13
Eumonhystera dispar (Bastian, 1865)	EumDis	3.77	716.81	3.08	1,466.08
Eumonhystera filiformis (Bastian, 1865)	EumFil	0.92	172.30	3.14	1,065.88
Eumonhystera gerlachi (Meyl, 1954)	EumGer	–	–	0.09	11.59
Eumonhystera longicaudatula (Gerlach & Riemann, 1973)	EumLon	1.45	162.31	0.74	219.89
Eumonhystera pseudobulbosa (Daday, 1896)	EumPse	6.27	1,008.23	3.05	1,350.49
Eumonhystera simplex (de Man, 1880)	EumSim	9.22	1,365.56	4.42	810.93
Eumonhystera vulgaris (de Man, 1880)	EumVul	11.63	2,350.91	11.65	3,374.54
Eumonhystera spec	EumSp	–	–	0.05	5.09
Euteratocephalus palustris (de Man, 1880)	EutPal	–	–	0.05	11.16
Goffartia cf heteroceri Hirschmann, 1952	GofHet	–	–	0.14	332.65
Heterocephalobus elongatus (de Man, 1880)	HetElon	–	–	0.05	22.48

(Continues)

TABLE 2 (Continued)

Nematode species	nMDS code	Permanent streams		Intermittent streams	
		Contribution (%)	Abundance (ind./LSed)	Contribution (%)	Abundance (ind./LSed)
Monhystera paludicola de Man, 1881	MonPal	–	–	0.29	82.58
Monhystrella macrura (de Man, 1880)	MonMac	0.30	71.76	0.19	96.81
Monhystrella paramacrura (Meyl, 1953)	MonPar	15.10	3,527.83	10.00	5,197.35
Panagrolaimus spec.	PanaSp	–	–	0.43	44.90
Panagrolaimus rigidus (Schneider, 1866)	PanaRig	–	–	0.42	39.89
Paramphidelus cf dolichurus (de Man, 1876)	ParamDol2	–	–	0.14	27.31
Plectus aquatilis Andrássy, 1985	PlecAqua	0.61	159.18	0.70	431.00
Plectus cirratus Bastian, 1865	PlecCir	–	–	0.05	16.37
Plectus opisthocirculus Andrássy, 1952	PlecOpi	2.35	371.49	1.46	362.76
Plectus parvus Bastina, 1865	PlecPar	0.61	208.06	0.76	193.28
Plectus spec	PlecSp	0.14	3.78	0.05	12.28
Rhabdolaimus aquaticus de Man, 1880	RhabAqua	10.66	3,546.20	0.16	23.40
Rhabdolaimus terrestris de Man, 1880	RhabTerr	3.17	1,057.22	0.76	335.96
Rhabditidae spec 1	RhabSp1	–	–	0.79	29.64
Rhabditidae spec 2	RhabSp2	–	–	0.24	39.68
Rhabditidae spec 3	RhabSp3	0.95	25.61	0.62	85.27
Rhabditidae spec 4	RhabSp4	–	–	0.05	35.50
Protorhabditis cf filiformis (Bütschli, 1873)	RhabFil	–	–	0.19	4.17
Species 2	Sp2	–	–	0.26	45.26
Species 3	Sp3	–	–	0.05	8.19
Teratocephalus spec	TeraSp	–	–	0.05	12.28
Theristus agilis (de Man, 1880)	TherAgi	–	–	0.05	3.43
Theristus vesentinae Andrássy, 1962	TherVes	–	–	0.05	12.28
Tylocephalus auriculatus (Bütschli, 1873)	TyloAuri	–	–	0.09	25.47
Udonchus tenuicaudatus Cobb, 1913	UdoTen	3.91	939.75	0.74	422.46
Algivores (Epistrate-feeders)					
Achromadora longicauda Schneider, 1937	AchroLongi	0.20	16.58	0.37	51.38
Achromadora micoletzkyi (Stefanski, 1915)	AchroMico	0.71	180.30	0.42	81.47
Achromadora ruricola (de Man, 1880)	AchorRuri	3.10	810.15	2.94	675.35
Achromadora terricola (de Man, 1880)	AchroTerri	–	–	0.23	101.41

(Continues)

TABLE 2 (Continued)

Nematode species	nMDS code	Permanent streams			Intermittent streams	
		Contribution (%)	Abundance (ind./LSed)		Contribution (%)	Abundance (ind./LSed)
Chromadorita leuckarti (de Man, 1876)	ChroLeu	1.35	31.67		–	–
Ethmolaimus pratensis de Man, 1880	EthPra	0.53	47.06		0.47	91.25
Prismatolaimus intermedius (Bütschli, 1873)	PrisInt	0.98	157.40		3.79	663.80
Prismatolaimus dolichurus de Man, 1880	PrisDol	0.24	30.18		0.21	8.08
Prismatolaimus spec	PrisSp	0.20	59.20	0.86		68.48
Prodesmodora loksai Andrássy, 1989	ProLok	–	–		0.14	37.93
Omnivores (Suction-feeders)						
Aporcelaimellus obtusicaudatus (Bastian, 1865)	AporObtu	0.10	26.39	1.79		440.62
Dorylaimus stagnalis Dujardin, 1845	DorSta	1.18	270.64		1.13	538.51
Eudorylaimus acuticauda de Man, 1880	DorAcu	–	–		0.09	39.56
Epidorylaimus agilis (de Man, 1880)	DorAgi	0.31	8.33		0.10	29.37
Eudorylaimus carteri (Bastian, 1865)	DorCar	0.20	30.73		0.18	97.74
Eudorylaimus centrocercus (de Man, 1880)	DorCen	–	–		0.19	3.88
Longidorus spec	LongSp	–	–		0.05	22.48
Mesodorylaimus bastiani (Bütschli, 1873)	DorBast	0.20	56.44		0.64	167.64
Mesodorylaimus spec	DorSp8	–	–		0.33	147.39
Paractinolaimus macrolaimus (de Man, 1880)	ParacMac	2.33	437.41	2.64		689.02
Prodorylaimium brigdammensis (de Man, 1876)	DorBrid	0.10	33.67	3.75		710.54
Thornia propinqua (Paesler, 1941)	ThorPro	0.22	58.53		0.19	66.75
Crassolabium ettersbergense (de Man, 1885)	ThorEtt	–	–		0.41	15.34
Tylencholaimellus affinis (Brakenhoff, 1914)	TyleAff	–	–		0.56	61.51
Tylencholaimus minimus de Man, 1876	TyleMin	–	–		0.23	96.72
Xiphinema diversicaudatum (Micoletzky, 1927)	XiDiv	–	–	0.09		6.86
Omnivores (Chewers)						
Diplogaster spec.	DipSp	–	–		0.17	4.65
Fictor fictor (Bastian, 1865)	FicFic	1.55	78.86		0.40	47.89
Mononchoides spec	MonoSp	–	–		0.05	110.88
Odontolaimus chlorurus de Man, 1880	OdoChlo	–	–		0.09	11.15
Tobrilus gracilis Bastian, 1865	TobGra	0.44	24.70		1.86	335.32

(Continues)

TABLE 2 (Continued)

Nematode species	nMDS code	Permanent streams			Intermittent streams	
		Contribution (%)	Abundance (ind./LSed)		Contribution (%)	Abundance (ind./LSed)
Semitobrilus pellucidus (Bastian, 1865)	TobPel	0.20	67.35		0.48	175.37
Epitobrilus stefanskii (Micoletzky, 1925)	TobStef	0.14	3.78		0.05	8.19
Tobrilus spec	TobSp	–	–		0.14	19.22
Tripyla glomerans Bastian, 1865	TryGlo	1.92	541.61		1.05	245.69
Trischistoma gracile Andrássy, 1985	TriGra	0.57	90.41		3.99	638.88
Trischistoma monohystera (de Man, 1880)	TriMon	0.24	16.03		0.29	34.20
Predators (Chewers)						
Ironus longicaudatus de Man, 1884	IroLon	–	–		0.05	2.85
Ironus tenuicaudatus de Man, 1876	IroTen	–	–		0.04	5.80
Mononchus aquaticus Coetzee, 1968	MonoAqua	3.54	217.81		–	–
Mononchus truncatus Bastian, 1865	MonoTru	0.30	44.26		1.72	676.59
Mononchus tunbridgensis Bastian, 1865	MonoTun	0.14	3.78		0.09	25.34
Mylonchulus sigmaturus Cobb, 1917	MylSig	–	–		0.05	8.19
Mylonchulus spec	MylSp	–	–		0.24	81.81
Fungivores (Suction-feeders)						
Aphelenchoides bicaudatus (Imamura, 1931)	ApheBic	–	–		0.52	42.99
Aphelenchoides fluviatilis Andrássy, 1960	ApheFluv	0.10	26.39		1.45	226.49
Aphelenchoides cf parietinus Bastian, 1865	AphePari	0.10	4.33	1.62		198.58
Aphelenchoides cf subparietinus Sanwal, 1961	ApheSub	0.60	26.00	–		–
Aphelenchus spec	ApheSp	0.48	34.92		0.14	36.84
Coslenchus costatus (de Man, 1921)	CosCos	0.30	82.84		0.06	5.25
Ditylenchus cf intermedius (de Man, 1880)	DipInt	0.14	3.78		0.31	29.68
Filenchus thornei (Andrássy, 1954)	FilThor	–	–		0.05	11.16
Filenchus vulgaris (Brzeski, 1963)	FilVul	0.44	26.13		4.53	1,257.24
Helicotylenchus pseudorobustus (Steiner, 1914)	HelPse	–	–	0.24		15.04
Hemicycliophora thornei Goodey, 1963	HemThor	–	–		0.09	25.82
Malenchus bryophilus (Steiner, 1914)	MalBryo	0.10	26.39		–	–
Paraphelenchus spec	ParapSp	–	–		0.05	17.75
Psilenchus aestuarius Andrássy, 1962	PsiAes	–	–		0.45	48.05
Tylenchorhynchus spec	TyleSp	–	–		0.05	2.85
Tylenchus davainei Bastian, 1865	TyleDav	–	–		0.46	40.40
Tylenchus spec	TyleBre	–	–		0.05	11.16
Unidentified	NotDet	–	–		0.30	44.84

nematode species were all bacterivores: *Monhystrella paramacrura* (15.1% of all individuals), followed by *Eumonhystera vulgaris* (11.6%) and *Rhabdolaimus aquaticus* (10.7%). Thirty-nine species showed a contribution <1% and could be considered as rare species (Table 2). In IS, a total of 108 species were identified. The top three species were two bacterivores: *Eumonhystera vulgaris* (11.6%) and *Monhystrella paramacrura* (10.0%), and one fungivore: *Filenchus vulgaris* (4.5%). In IS, 83 species showed a contribution < 1% and could be considered as rare (Table 2). Five species (including the algivore *Chromadorita leuckarti*) occurred only in PS. In contrast, 55 species were specific to IS (Table 2). In order to check if these differences were related to the unbalanced number of sites in IS versus PS, we compared species richness based on sample rarefaction, at equivalent sampling effort 81.6 and 58 species may be found in IS and PS, respectively (Figure 3). Estimating maximum species richness using Chao2 model gave 135.8 species (±12.5 *SD*) in IS, against 84.8 species (±13.4) in PS. This exercise confirmed the trend that nematode species richness was higher in IS in comparison to PS (see also clustering of species towards the right side of the biplot in Figure 4).

All feeding-types occurred in the samples, but ITD was significantly smaller in IS (W = 556, $p = 0.04$, Table 1) meaning that nematode assemblages showed a more even distribution of feeding-types. In contrast, bacterivores dominated in PS, accounting for 76.8% of the assemblage. Their dominance was lower in IS (57.2%; W = 629.5, $p = 0.003$) (Table 1, Figure 4b). The relative contribution of fungivores and omnivores were respectively four (W = 248, $p = 0.005$) and two times higher (W = 280, $p = 0.03$) in IS (Figure 4b). The contribution of algivores and predators was relatively low and did not differ significantly between PS and IS (Table 1).

Comparing IS only, nematode species richness (S) and diversity (H) correlated positively with all F and DD (including the number of dry days recorded over the longest periods of time prior sampling: DD_{150} and DD_{250} as observed in tardigrades), but conversely, nematode diversity correlated negatively with MnF_{250} and MnF_{150} (Figure 2). Although ITD did not correlate significantly with any hydrological descriptors in IS, the relative abundance of fungivores was positively correlated with the proxies for the longest periods of non-flow: DD_{250}, DD_{150}, MnD_{250} and MnD_{150}. Omnivore and predatory nematodes showed positive correlations with most DD and F proxies (Figure 2), while algivores had seemingly an inverse pattern being negatively correlated with any F and DD (except DD_{30}). The relative abundance of bacterivores only showed a weak positive correlation with F_{30} in IS.

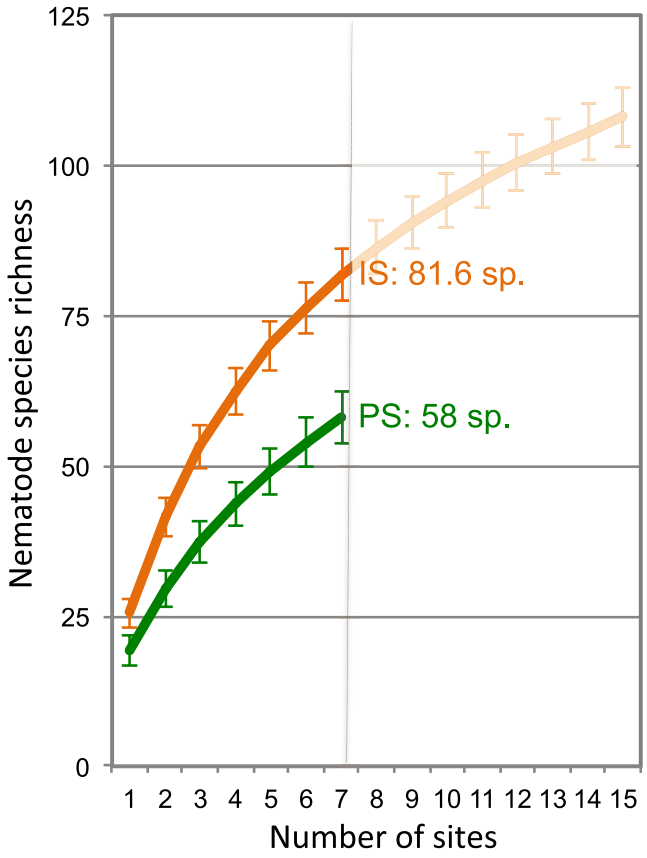

FIGURE 3 Sample-based rarefaction curves for nematode species richness measured in 15 intermittent streams (IS, orange line) and seven permanent streams (PS, green line) [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Effects on the structure of nematode communities

Overall, the hydrological status of streams (i.e. IS versus PS) significantly affected the species structure but not the feeding-types structure, although the latter effect could be considered marginally significant (Table 3). Out of 113 species, the multi-level pattern analysis only identified two species that could be significantly associated with the hydrological status of stream sites: The fungivore *Filenchus vulgaris* was significantly associated with IS (group-stat: 0.75, $p = 0.033$), while the bacterivore *Rhabdolaimus aquaticus* was associated with PS (group-stat: 0.61, $p = 0.037$; species highlighted in Figure 4a).

4 | DISCUSSION

4.1 | Abundance patterns in intermittent versus permanent streams

Overall, meiofauna was extremely abundant in the studied sites, abundance values being amongst the highest ever reported in streambeds, and about one order of magnitude higher than others reported (Beier & Traunspurger, 2003b; Gaudes et al., 2010; Majdi et al., 2017). This might be because riffles are generally well oxygenated and contain productive substrates supporting both epilithic and interstitial organisms. Still, our values were comparable with those observed in the sediment of a fourth-order stream (Palmer, 1990), or in epilithic biofilms coating the littoral of large rivers and lakes (e.g. Schroeder, Traunspurger, Pettersson, & Peters, 2012; Majdi et al., 2012). Nematodes and rotifers were numerically dominant and thrived in IS as well as in PS. Some relatively minor taxa were

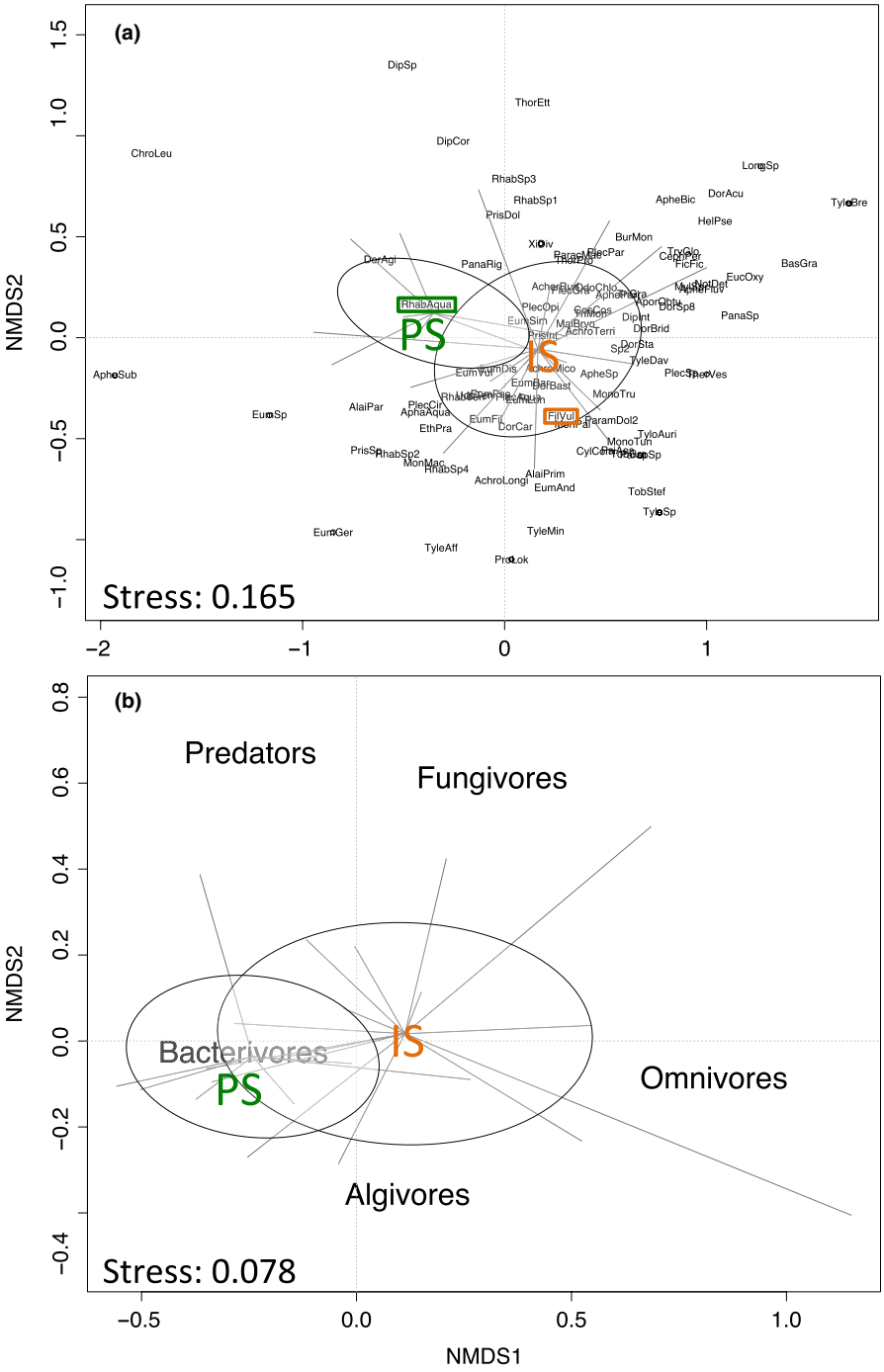

FIGURE 4 Structure of the nematode community in 22 Mediterranean streams as assessed through non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis similarity. (a) Distribution of species abundances (black text labels, abbreviations in Table 2). Two species (*Rhabdolaimus aquaticus* and *Filenchus vulgaris*) are framed as they are significantly associated with PS and IS, respectively (multi-level pattern analysis, see main text). (b) Composition of nematode feeding-types. *Spider webs* link each stream site to the centroid of its hydrological status (permanent, PS, or intermittent stream, IS); 95% confidence interval ellipses are also shown [Colour figure can be viewed at wileyonlinelibrary.com]

less abundant in PS or in IS, but altogether it did not affect total meiofaunal abundances. Overall, this confirms our first hypothesis that differences in total abundances between IS and PS would be small. A potential explanation of this pattern is the extremely high population turnover rates of the smallest meiofaunal organisms (i.e. rotifers and nematodes) complemented by their outstanding abilities to cope with desiccation (Rebecchi et al., 2020). This suggests that the important pool of resilient meiofauna dwelling in streambed sediments has the potential to quickly recolonise other epigean and highly productive habitats after flow returns (Gaudes et al., 2010). For example, bdelloid rotifers need only a few days to settle in recovering biofilms and are quite efficient as filter-feeders on suspended fine particles (Kathol, Fischer, & Weitere, 2011). Nematode grazers follow after rotifers, reaching higher densities after a few weeks of biofilm growth (Majdi et al., 2011, 2012; Peters, Wetzel, Traunspurger, & Rothhaupt, 2007). Evidence shows that meiofaunal organisms stimulate microbial-based processes such as denitrification and mineralisation of organic matter (Nascimento, Näslund, & Elmgren, 2012; Bonaglia et al. 2014), as well as primary production by micro-algal biofilms (Mathieu, Leflaive, Ten-Hage, de Wit, & Buffan-Dubau, 2007). Therefore, we may expect that nematodes and rotifers could *kick-start* intermittent stream ecosystems, allowing a quick re-establishment of trophic connections and benthic-pelagic exchanges in biofilms. As much as algae may provide an

TABLE 3 Permutational multivariate analysis of variance (PERMANOVA) table for nematode communities dwelling Mediterranean stream sites showing different hydrological status (HS: permanent or intermittent flow conditions)

Data tested	Source of variation	*df*	SS	Pseudo-*F*	*p*-value
Nematode species	HS	1	0.46	1.85	0.03*
	Residuals	20	5.01		
	Total	21	5.47		
Nematode feeding-types	HS	1	0.14	2.19	0.10
	Residuals	20	1.32		
	Total	21	1.47		

essential re-supply of high quality organic matter after flow returns (Ylla, Sanpera-Calbet, Muñoz, Romaní, & Sabater, 2011), meiofauna may have a hitherto unrecognised role in re-establishing several trophic links in temporary streams. This assumption would benefit from experimental manipulations (e.g. rewetting dry sediment cores as in Hay, Jenkins, & Kingsford, 2018) to carefully evaluate the role of meiofauna.

4.2 | Effects of frequency and duration of the non-flow period

In the field of intermittent stream ecology, most studies examine the effects of flow intermittency without accounting for its temporal dimensions: frequency and duration. Drying streambeds may represent a ramp disturbance for taxa able to find refuge in wet subsurface sediment (Lake, 2000). We hypothesised that frequent alternation of flow and non-flow would be beneficial to most meiofaunal taxa, while prolonged dry phase would impose much stronger constraints and only benefit the most desiccation-tolerant taxa (such as the tardigrades). We confirmed a non-uniform response of the different taxonomic groups to drying frequency. Nematodes reached high densities in the IS under a frequent cycle of drying/rewetting, probably because they show both short life cycles and relative tolerance to desiccation events (Rebecchi et al., 2020), but also presumably because they have a small vermiform body allowing them to migrate efficiently through interstices to seek refuge in the wet subsurface sediment. Interestingly, the abundance of nematodes showed a positive relationship with the duration of dry periods when considered shortly before sampling (DD_{30} and DD_{90}) suggesting that nematode populations are able to recover quickly after a few flowing days. Other groups, however, did not show those patterns: gastrotrichs, ostracods, oligochaetes, and Ceratopogonidae larvae showed weak correlations with the frequency of drying events and were not related to the number of dry days. Gastrotrichs have higher affinities with aquatic environments, and dry periods may be critical to them, since only resting eggs can assure the maintenance of populations (Nesteruk, 2017). However, it has been observed that gastrotrichs may show higher species richness following desiccation (Nesteruk, 2007). Ostracods are commonly found in intermittent ponds since many species have diapausing eggs, but the tolerance to dessication is not shared by all species (Castillo-Escrivà, Valls, Rochera, Camacho, & Mesquita-Joanes, 2016). Otermin, Basaguren, and Pozo (2002) noticed that the abundances of oligochaetes and ceratopogonids increased during the flowing phase in an IS.

The integrative descriptors of long non-flow and flow periods (namely MnD_{250}, MnD_{150}, MnF_{250}, and MnF_{150}) were negatively correlated with the abundances of most faunal groups. This result contrasts with the positive effect of alternate flow and non-flow periods. However, tardigrades were the exception to this rule, since they clearly benefitted from the longest dry periods. Tardigrades are exceptionally tolerant to the most extreme environmental conditions including total dehydration or intense ultraviolet radiation. These abilities help tardigrades to colonise a variety of limno-terrestrial environments that may totally dry out, such as lichens and mosses (Nelson & Marley, 2000; Rebecchi et al., 2020); their prevalence with respect to other meiofaunal invertebrates could be used as an indicator of streambed drying severity in IS.

4.3 | Diversity of nematodes in IS versus PS

Nematodes are powerful indicators of environment alterations (Wilson & Kakouli-Duarte, 2009), since they are ultra-diverse and play a central role in belowground stream and soil food webs (Hodda, 2006; Majdi & Traunspurger, 2015; Traunspurger, 2000, 2002; Yeates et al., 1993). We expected that the alternation of flow and non-flow periods would prevent competitive exclusion mechanisms and potentially provide more opportunities for typical soil nematode species to colonise streambeds (see potential rationales listed below). Our results confirmed this hypothesis: at equivalent sampling efforts, more nematode species occurred in IS in comparison to PS. Also Corti and Datry (2016) found a surprisingly high diversity of aquatic and terrestrial invertebrates in the dry riverbed of an intermittent stream, which they observed to be subsets of persistently flowing reaches and riparian areas. The higher nematode diversity of IS was positively correlated with the total duration and frequency of the non-flow period. These results also supported our third hypothesis that taxa diversity would react positively to an increasing frequency of drying events. The higher diversity of nematode species in IS might be explained by several causes:

- The Huston's (1979) dynamic-equilibrium model predicts that a balance would occur in frequently disturbed systems between the

rate of competition for niches and displacements. Such a balance should allow the coexistence of species that would otherwise go extinct at competitive equilibrium. Our results confirm that fluctuating environmental conditions (i.e. frequent alternation of flow and non-flow) prevent the prevalence of niche specialists. We could not determine, however, which was the disturbance threshold affecting the diversity of the nematode assemblage; this would need further studies.

- A higher abundance and diversity in IS could follow the hyporheic-refuge hypothesis (Palmer, Bely, & Berg, 1992; Williams & Hynes, 1974). This states that fauna from a variety of epigean stream habitats may seek refuge and accumulate in the sediment under hydrological constraints (Clinton et al., 1996). It is conceivable that a progressive hydric stress might force nematodes dwelling in various epigean stream habitats to accumulate and seek refuge in the sediment, as observed for macro-invertebrate communities during the first steps of the non-flow period (Acuña et al., 2005). Since nematodes may migrate more easily and may reach deeper locations in the sediment in comparison to most macro-invertebrates, this mechanism could be operative for them over longer periods than those for macro-invertebrates.
- Our results are in line with Corti and Datry's (2016) observations on the immigration of species from adjacent terrestrial soil ecosystems, here exemplified by the increased presence of nematode species from the family Tylenchidae (to which *Filenchus vulgaris* belongs) in IS, Tylenchidae being one of the most important taxonomic group of nematodes found in soil ecosystems (Andràssy, 1981).

Still, it is largely premature to propose some nematode species such as *Filenchus vulgaris* as potential indicator of the severity of dry phases in IS. Predicting which nematode species may wane or dominate in IS requires more specific knowledge of habitat preferences and life-history traits of the species, which is currently lacking. Moreover, the environmental plasticity of many nematode species (Hodda, 2006; Ptatscheck, Gansfort, & Traunspurger, 2018) further complicates potential predictions. Nevertheless, our results provide a first picture, and further research should take into account the hydrological background of IS as an important prerequisite to better understand community structure and species distribution patterns.

4.4 | Nematode feeding-types in IS versus PS

We predicted a larger share of stylet-bearing fungivores and omnivores in IS, since these feeding-types are more common in soil ecosystems (Yeates et al., 1993). As a contrast, we also predicted the higher abundance of bacterivores in PS, because these are known to be widespread and dominant in freshwater habitats (Beier & Traunspurger, 2003a,b; Hodda, 2006; Traunspurger, 2002; Traunspurger et al., 2015). Our results support those predictions. The lower ITD in IS supported that feeding-types of nematodes were more even in the systems experiencing an alternance of dry and wet phases, while in PS the trophic diversity was rather low, being strongly dominated by bacterivores. Moreover, as for tardigrades, the relative abundance of fungivores was positively correlated with the length of dry phases when considering the longest time periods before sampling (MnD_{150} & MnD_{250}; see Figure 2). The presence of fungivorous species such as *F. vulgaris* in IS might be indicative of basal trophic channels resembling those of soil ecosystems (Hohberg, 2003; Traunspurger et al., 2017; Yeates et al., 1993). However, the fact that fungivores did not correlate with the length of dry phases when measured shortly before sampling (i.e. MnD_{30}, MnD_{90}, DD_{30} and DD_{90}) suggests that these fungivorous species only thrived when the dry phase was long and continuous, otherwise they probably had lower chances to establish effectively.

5 | CONCLUSION

Meiofaunal organisms occurred ubiquitously in temporary streams, even in those having experienced the most severe dry conditions. The dynamics of flow, as it waxes and wanes, accounts for highly diverse communities in these systems. The changes occurring in the meiofauna community structure were indicative of extraordinary capabilities of resistance to desiccation associated with new niche opportunities occurring in dry streambeds. However, the role of meiofauna should not be viewed as restricted to flowing conditions, but also as part of the subsurface and hyporheic zone, or by interacting with the rhizosphere of pioneer xeric plants establishing in dry streams. Overall, the trophic versatility and ability to colonise stream habitats shown by meiofauna establish their key role in restoring aquatic food webs after flow returns.

ACKNOWLEDGEMENTS

This study was supported by the SPACESTREAM project (CGL2017-88640-C2-1-R) from the Spanish Ministry of Economy and Competitiveness and the Consolidated Research Group ICRA-ENV (2017 SGR 1124) from the Economy and Knowledge Department of the Catalan Government. ICRA is part of the CERCA programme. We deeply thank Jordi-René Mor, Rebeca Areas, Veronica Granados, and Giulia Gionchetta for their help in the field, Stefanie Gehner for the preparation of nematode specimen, Olivia Majdi for proof-reading, and Birgit Gansfort for helpful advice about statistical analyses.

CONFLICT OF INTERESTS

Authors have no conflict of interests to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Majdi N, Colls M, Weiss L, Acuña V, Sabater S, Traunspurger W. Duration and frequency of non-flow periods affect the abundance and diversity of stream meiofauna. *Freshwater Biology*. 2020;65:1906–1922. https://doi.org/10.1111/fwb.13587