



## Are functional freshwater Nematode traits a good tool for view an early succession on hard artificial substrate in a reservoir of Brazilian semiarid?

Traços funcionais dos Nematoda são uma boa ferramenta para visualizar uma sucessão ecológica em substratos artificiais em um reservatório do semiárido brasileiro?

Fábio Lucas de Oliveira Barros<sup>1,2\*</sup> , Sebastião Tilbert<sup>1</sup> , Taciana Kramer Pinto<sup>2</sup> ,  
Maria Cristina da Silva<sup>3</sup> , Francisco José Victor de Castro<sup>3</sup>  and Miodeli Nogueira Júnior<sup>1</sup> 

<sup>1</sup>Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba – UFPB, Cidade Universitária, CEP 58051-900, João Pessoa, PB, Brasil

<sup>2</sup>Laboratório de Ecologia Bentônica, Universidade Federal de Alagoas – UFAL, Campus Arapiraca, Av. Beira Rio, s/n, Centro Histórico, CEP 57200-000, Penedo, AL, Brasil

<sup>3</sup>Laboratório de Meiofauna, Centro de Educação e Saúde, Universidade Federal de Campina Grande – UFCG, Sítio Olho D'água da Bica, Zona Rural, CEP 58175-000, Cuité, PB, Brasil

\*e-mail: fabio.barrosnp@gmail.com

**Cite as:** Barros, F.L.O. et al. Are functional freshwater Nematode traits a good tool for view an early succession on hard artificial substrate in a reservoir of Brazilian semiarid? *Acta Limnologica Brasiliensia*, 2024, vol. 36, e30. <https://doi.org/10.1590/S2179-975X6723>

**Abstract: Aim:** The Brazilian tropical semiarid is a biome with small freshwater ecosystems, often intermittent, acting as a mosaic in constant transformation between dry and rainy seasons. Meiobenthic communities play crucial roles in these environments, and understanding their colonization and succession processes is essential to comprehend how these organisms' structure in a defaunated habitat. In addition to the traditional taxonomic approach, functional traits provide valuable insights into the dynamics of these processes. In this study, we tested the following hypotheses: i) although meiofauna consists of microscopic organisms with limited active dispersion, they quickly colonize new substrates, increasing in abundance, richness, and diversity; ii) functional traits of freshwater Nematoda are a good tool for view an early succession on hard artificial substrate in a lentic reservoir. **Methods:** We placed 27 ceramic plates in a reservoir in the Brazilian semiarid and randomly sampled three replicates each week over nine weeks. Weekly differences in community abundance, richness, and diversity were tested with one-way ANOVA and pairwise PERMANOVA. **Results:** Nematoda predominated in the first week, with Rotifera taking over from the second week of the experiment. No differences were observed in the Nematode taxonomic structure over the weeks. There was an increase in the functional complexity of the Nematoda community over time, as indicated by the maturity index and trophic structure. Colonizers/persistents emerged quickly in the first week. Deposit feeders dominated, but an increase in trophic diversity was observed with the growing presence of chewers over the weeks. **Conclusions:** This study highlights that the functional traits of Nematoda represent a robust tool for assessing ecological succession in freshwater lentic environments in the tropical semiarid.

**Keywords:** maturity index; trophic structure; Caatinga; meiobenthos.



**Resumo: Objetivo:** O semiárido tropical brasileiro é um bioma que possui pequenos ecossistemas de água doce, frequentemente intermitentes, que atuam como um mosaico em constante transformação entre as estações seca e chuvosa. As comunidades meiobentônicas desempenham papéis cruciais nesses ambientes, e compreender seus processos de colonização e sucessão é fundamental para entender como esses organismos se estruturam em um habitat defaunado. Além da abordagem taxonômica tradicional, os traços funcionais oferecem perspectivas valiosas sobre a dinâmica desses processos. Neste estudo, testamos as seguintes hipóteses: i) embora a meiofauna seja composta por organismos microscópicos com dispersão ativa limitada, eles colonizam rapidamente novos substratos, aumentando em abundância, riqueza e diversidade; ii) as características funcionais dos Nematoda de água doce são uma boa ferramenta para observar uma sucessão inicial em substrato artificial duro em um reservatório lântico. **Métodos:** Colocamos 27 placas de cerâmica em um reservatório no semiárido brasileiro e amostramos aleatoriamente três réplicas a cada semana, ao longo de nove semanas. As diferenças semanais na abundância, riqueza e diversidade da comunidade foram testadas com one-way ANOVA e pairwise PERMANOVA. **Resultados:** Os Nematoda predominaram na primeira semana, com os Rotifera dominando a partir da segunda semana de experimento. Não observamos diferenças na estrutura taxonômica da comunidade de Nematoda ao longo das semanas. Entretanto, houve um aumento na complexidade funcional da comunidade de Nematoda ao longo do tempo, conforme indicado pelo índice de maturidade e pela estrutura trófica. Os colonizadores/persistentes surgiram rapidamente na primeira semana. Os comedores de depósito dominaram, mas observou-se um aumento na diversidade trófica com a presença crescente dos mastigadores ao longo das semanas. **Conclusões:** Este estudo destaca que as características funcionais dos Nematoda representam uma ferramenta robusta para avaliar a sucessão ecológica em ambientes lânticos de água doce no semiárido tropical.

**Palavras-chave:** índice de maturidade; estrutura trófica; Caatinga; meiobentos.

## 1. Introduction

Colonization is a process by which available habitats are occupied and occurs when pioneer species establish, replacing each other in an ecological succession (Bush et al., 1995; Fastie, 1995; Costa et al., 2016). With the progressive growth of the human population, aquatic ecosystems have been experiencing a high production of artificial substrates of all kinds, such as bulkheads, pontoons, artificial reefs, and garbage disposal (Atilla et al., 2003; Brown, 2005; García-Gómez et al., 2021). Many types of artificial substrata have been used to investigate the colonization and succession of benthic assemblages on marine (Fonsêca-Genevois et al., 2006; Rule & Smith, 2007; Spagnolo et al., 2014) and estuarine ecosystems (Atilla, 2000; Atilla et al., 2003, 2005). However, few studies with such approach were developed in freshwater ecosystems (Peters et al., 2005, 2007), and none on Brazilian tropical semiarid. These regions include small natural shallow lakes, artificial reservoirs, intermittent rivers and streams, which function as a constantly changing mosaic between dry and rainy seasons (Barbosa et al., 2012). Therefore, studying the dynamics of semiarid benthic communities during the colonization and succession processes is crucial for understanding their resilience in the face of extreme disturbances (Ferreira et al., 2015).

The meiobenthos has a short life cycle and high capacity for resilience and, consequently, for quickly

colonizing various habitats (Robertson, 2000), such as unconsolidated soft bottom substrates (Zhou, 2001), natural (Ptatscheck & Traunspurger, 2014) and artificial hard substrates (Freixa et al., 2023). Freshwater meiofaunal organisms are closely related to biofilm, which directly influence on the establishment and succession of species in different types of substrata (Peters et al., 2007; Majdi et al., 2012). The colonization of these small invertebrates commonly occurs after an exponential increase of the algal or heterotrophic microorganisms' biomass and detritus that pave the substrata and make them an available habitat for benthic invertebrates (Costa et al., 2016; Freixa et al., 2023).

Nematode commonly is the most representative meiofaunal taxa in lentic ecosystems, typically with high density and diversity (Abebe et al., 2008; Wilden et al., 2020). They are microscopic animals with short life cycle, limited locomotion capacity, and no larval stages (Zeppilli et al., 2015; Netto & Fonseca, 2017; Ptatscheck & Traunspurger, 2020). These peculiar characteristics make them typically considered organisms with low dispersion ability (Boeckner et al., 2009; Ptatscheck & Traunspurger, 2020) and, consequently, low colonization potential. However, some studies have shown that some species have morpho-functional characters resulting in a higher colonization ability (Tita et al., 1999; Boeckner et al., 2009; Thomas & Lana, 2011). Thus, in addition to the traditional taxonomic approach, evaluating the biology and

functional traits is a powerful tool for assessing the assemblage structure and/or dynamics of the meiobenthos, particularly related to the process of colonization and ecological succession (Ettema & Bongers, 1993).

Two important and widely used functional traits of the Nematode are their life-history and trophic structure (Traunspurger, 2014; Sroczynska et al., 2021). The former refers to a semi-quantitative approach that classifies these animals on a c-p scale, ranging from 1 (extreme colonizer) to 5 (extreme persistent), which refer to a r and k strategists. It uses the abundances of Nematoda classified within this scale to estimate a maturity index (MI) for a given assemblage. This index has been widely used in environmental monitoring studies (Bongers, 1990, 1999; Netto & Valgas, 2010; Jouili et al., 2017). However, it has been sparsely explored to evaluate colonization and succession of freshwater assemblages (Bongers, 1990; Ettema & Bongers, 1993; Steel et al., 2010). Free-living aquatic nematodes may feed on a diverse array of resources, such as bacteria and Archaea, protists, fungi, particulate and dissolved organic matter, and act as both predator and prey for many different metazoans, including other nematodes (Moens et al., 2014). This may be advantageous for colonize another environment. In freshwater environments, for instance, epistrate, detritus and deposit feeders are most abundant in periphyton dwelling on artificial substrate (Vidaković et al., 2011), forming a consolidated structure for chewers (Majdi et al., 2012).

The high abundance and diversity of Nematoda on benthic ecosystems, their ecological plasticity, and the low cost to perform samplings and experiments make them good model organisms for studies evaluating colonization and succession (Pinto et al., 2013; Costa et al., 2016). In this study, we evaluated the colonization and succession of semiarid meiofauna on artificial substrata (ceramic plates), particularly focusing on functional traits of Nematoda. Our main goals were to test the following hypothesis: i) although meiofauna are microscopic organisms with limited active dispersion, they rapidly colonize new substrates with increasing abundance, richness and diversity; ii) functional freshwater Nematode traits are a good tool for view an early succession on hard artificial substrate in a lentic reservoir. We considered that after introduction of artificial substrates, the ecological succession is reflected by the increase of the maturity index value (Bongers, 1990; Ettema &

Bongers, 1993; Steel et al., 2010) and the trophic structure of the assemblage changes through the succession, deposit feeders and epistrate feeders are expected in the early stages, while chewers tend to appear latte (Peters et al., 2005).

## 2. Material and Methods

### 2.1. Study site

The study area is in a mountain region, 667 m above sea level. The climatic and topographic characteristics are typical of a highland swamp, with mean air temperature and rainfall of 26 °C and 800 mm, respectively, with April as the typical rainier month when rainfall averages 72 mm (Andrade-Lima, 1982; Prado, 2003; Barbosa et al., 2012).

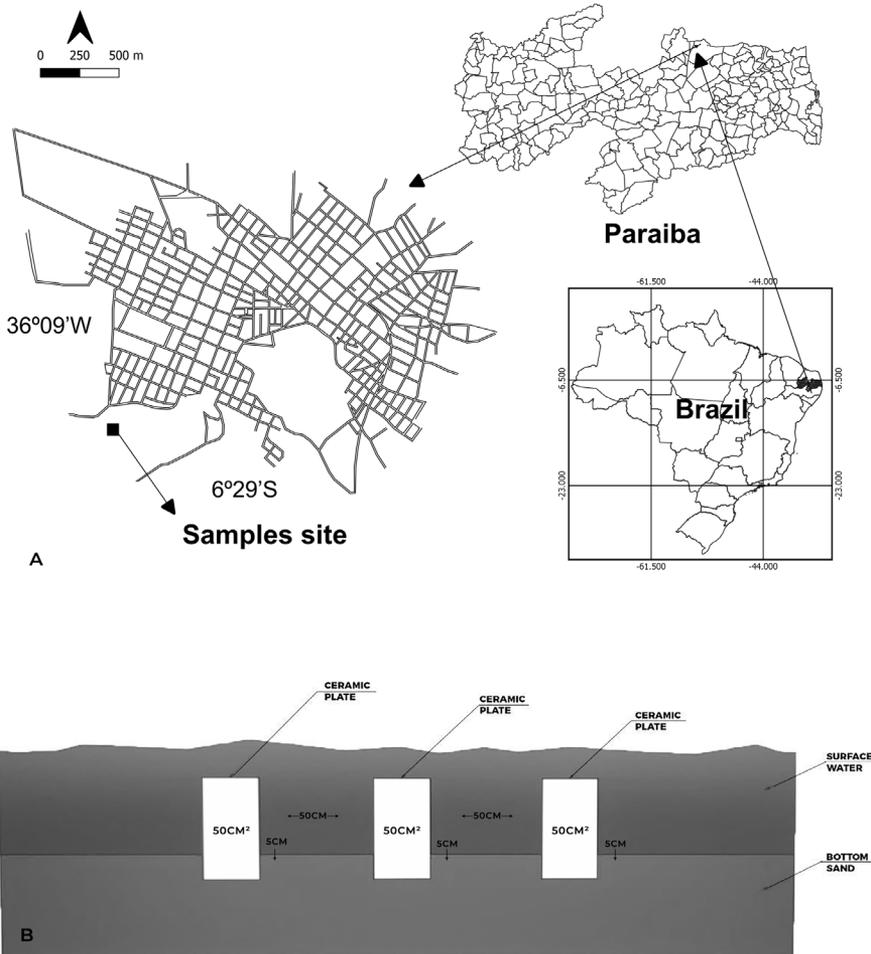
The experiment was developed in the reservoir “Olho d’água da Bica” in the Horto Florestal, Cuité – PB (NE Brazil; Figure 1A). It is a small body of water with an area ~200 m<sup>2</sup> and <2 m depth. This reservoir is preserved for Universidade Federal de Campina Grande (UFCG). This aquatic environment is atypical in the semiarid since unlike most other regional water bodies, it is constantly supplied by a spring. Thus, it rarely dries out completely during dry seasons, only reducing the water level.

### 2.2. Experimental design and sampling

The experiment was developed over 9 weeks, between March 17 and May 12, 2016, with weekly samplings. We used 27 ceramic plates as artificial substrata, each with 200 cm<sup>2</sup> (Figure 1B). These plates were vertically inserted in the sediment at 5 cm depth, with an inserted area of 50 cm<sup>2</sup>. The 27 plates were randomly installed, ~50 cm apart from each other. In the first day, March 17, the plates were installed and from March 24 three plates (replicates) were sampled weekly. On May 12, all plates were sampled in a total of nine weeks. Each plate sampled was put in plastic bags and taken to the laboratory. We also sampled ~100 g of the sediment adjacent to the plates for organic matter analyses (Walkley & Black, 1934). Water temperature (°C), dissolved oxygen (mg L<sup>-1</sup>), pH and salinity were measured weekly using a digital multiprobe (Alfakit, AT-160, Florianópolis, Brazil).

### 2.3. Samples processing

At the laboratory, the plate surfaces were scratched using a spatula. The material from this scratching was washed manually and centrifuged, and the supernatant was poured onto a 45 µm mesh size sieve to retain meiofauna. The samples



**Figure 1.** (A) Study Area and Experimental Setup Location in “Horto Florestal Olho D’água da Bica”, Paraíba, Northeast Brazil; (B) Illustration of Artificial Substrate sample, consisting of 27 ceramic plates vertically inserted in the sediment.

were fixed in 4% formalin solution. The meiofaunal higher taxa were counted under a compounded stereomicroscope using a Dolffus plate with 200 squares. All Nematoda individuals found were sorted out and put on vials with 99% formalin solution (4%) and 1% glycerin. The Nematoda were later diaphanized (de Grisse, 1969) and permanent slides mounted (Cobb, 1917).

#### 2.4. Nematode analysis

The nematodes were identified to the genus level using an optical microscope (Type SZ61, Olympus, Tokyo, Japan) and a pictorial identification key of freshwater Nematoda (Zullini, 2010). Because some marine genera were found (see Barros et al., 2021 for more details), keys for marine nematodes were also used (Platt & Warwick, 1983; Warwick et al., 1998). Each individual was further sorted as juvenile, male, female or gravid female.

We evaluated the functional traits trophic guild and life-history. The trophic structure takes into consideration the buccal morphology of the Nematoda, classifying them as deposit feeders (bacteria feeding; small or absent buccal cavity), epistrate-feeder (small teeth), chewers (omnivores and predator; wide and sclerotized buccal cavity), and suction-feeder (fungi, plant, root, omnivore; with buccal stylet) (Traunspurger et al. 1997; Traunspurger, 2014). The life-history was expressed by Maturity Index (MI) (Bongers, 1990). The MI is extracted from the nematode life history using the following equation:  $MI = \sum v(i) * f(i)$ , where  $v(i)$  is the c-p value of the genus and  $f(i)$  is the relative abundance (%) of the genus in the sample (Bongers, 1990, 1999; Bongers et al., 1995).

#### 2.5. Statistical analysis

The statistical differences in meiofauna abundance throughout the colonization weeks were

assessed through a one-way Analysis of Variance (ANOVA). To examine differences in richness and diversity of both meiofauna and nematofauna, classical ecological indices such as Margalef richness (d), Shannon diversity (H'), and Pielou's evenness (J) were employed (Shannon, 1948; Margalef, 1963; Pielou, 1966). Weekly differences in richness and diversity metrics were tested using Analysis of Variance (ANOVA), followed by a post-hoc comparison with Tukey's HSD test ( $\alpha = 0.05$ ). The ANOVA was computed using the Car package in the R environment (Fox & Weisberg, 2019).

Differences in the Nematode assemblage structure throughout the weeks were evaluated using pairwise Permutational Multivariate Analysis of Variance (PERMANOVA) based on the Bray-Curtis distance. Pairwise PERMANOVA analyses were conducted using the pairwise Adonis package in the R environment (Martinez Arbizu, 2019). Levene's test for homogeneity and Shapiro-Wilk normality test were considered for choosing between parametric or non-parametric tests.

### 3. Results

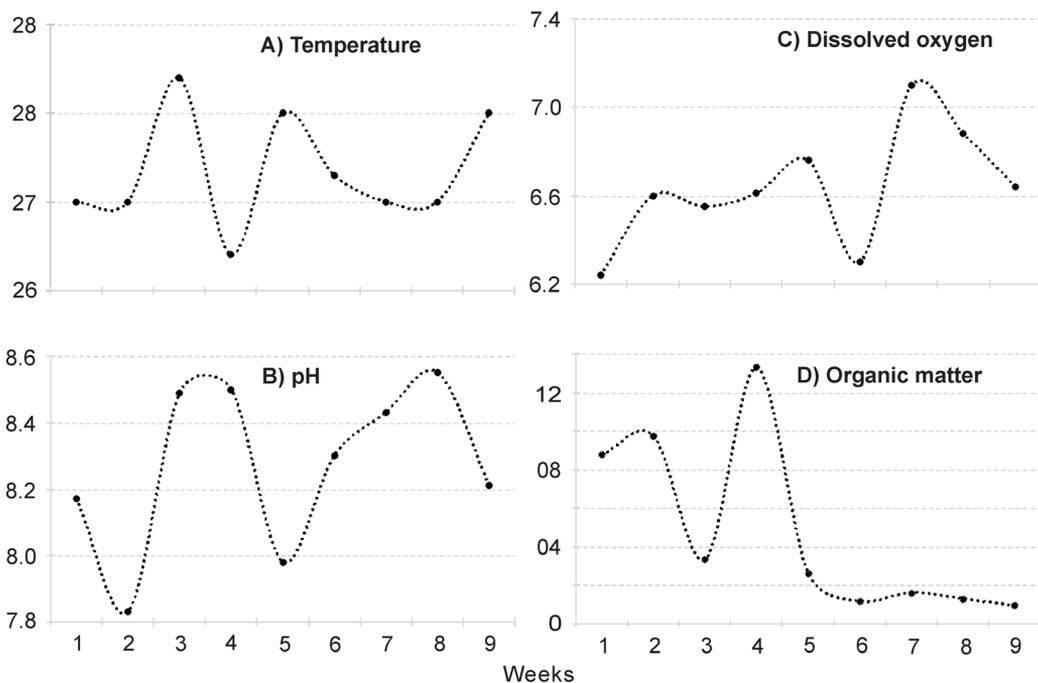
#### 3.1. Environmental variables

Temperature varied little throughout the nine weeks, ranging from 26.4 to 28.4 °C

(mean  $\pm$  standard deviation =  $27.23 \pm 0.59$  °C; Figure 2A). The pH values were typical of an alkaline environment, averaging  $8.27 \pm 0.23$  (Figure 2B). Dissolved oxygen averaged  $6.63 \pm 0.25$  mg L<sup>-1</sup>, ranging from 6.2 mg L<sup>-1</sup> in the first week to 7.1 mg L<sup>-1</sup> in the seventh (Figure 2C). The organic matter content was erratic in the sediment and diminished considerably from the fifth week on values were between 8.8% and 13.3% in the first four weeks (3<sup>rd</sup> week except) and always lower than 1.2% between 6-9<sup>th</sup> weeks (Figure 2D).

#### 3.2. Meiofaunal colonization and succession on artificial substrates

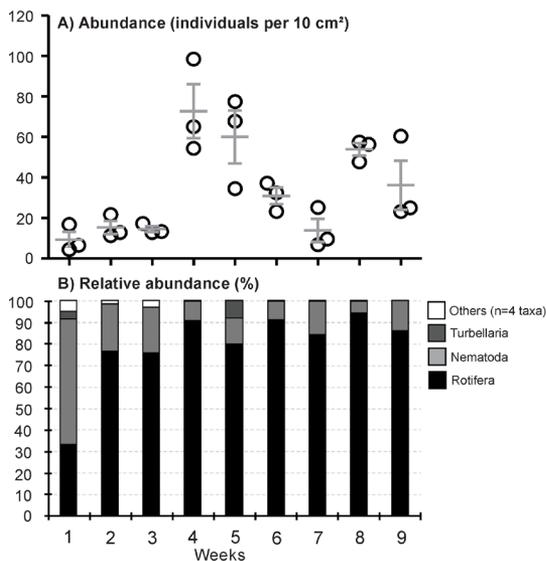
Through the nine weeks sampled, we found seven meiofaunal higher taxa, with higher values ( $3.6 \pm 0.6$ ) in the first week and lowest in weeks six and nine (2 taxa; Table 1). The Shannon diversity was statistically different across weeks (ANOVA, F value= 3.595, p = 0.0115), unlike Margalef's richness, which did not differ statistically (ANOVA, F value= 0.5167, p = 0.8285) throughout the colonization weeks. Meiofaunal density ranged from 6.8 to 98.6 ind.10 cm<sup>-2</sup>, with significant (ANOVA, F value= 8.34, p = 0.0001; Table 1) variations through the colonization and succession. Lower values of abundance were found in the first week ( $9.3 \pm 6.7$  ind.10 cm<sup>-2</sup>) and higher in the 4 and 5<sup>th</sup>



**Figure 2.** Environmental variables. (A) Temperature (°C); (B) Dissolved Oxygen (mg L<sup>-1</sup>); (C) pH; (D) Organic matter (%).

weeks ( $72.7 \pm 23.0$  and  $60.0 \pm 22.5$  ind.  $10 \text{ cm}^{-2}$ , respectively) (Table 1; Figure 3A).

Overall, the Rotifera were the dominant taxa, representing 85% of total organisms sampled, followed by Nematoda (12.4%). Nematodes dominated in the first week (58.2%), but from the second week on they did not exceed 22%, when rotifers became predominant (75.6-94.4%; Figure 3B). Turbellaria represented up to 8.1% in the 5<sup>th</sup> week. Other taxa represented <2% each, occurring only during the three initial weeks, at the beginning of the colonization process. Only for Rotifera (ANOVA, F value= 0.983,  $p = 0.00012$ ; Table 1) and Ostracoda (ANOVA, F value = 4.778,  $p = 0.002$ ; Table 1) weekly densities were significantly different.

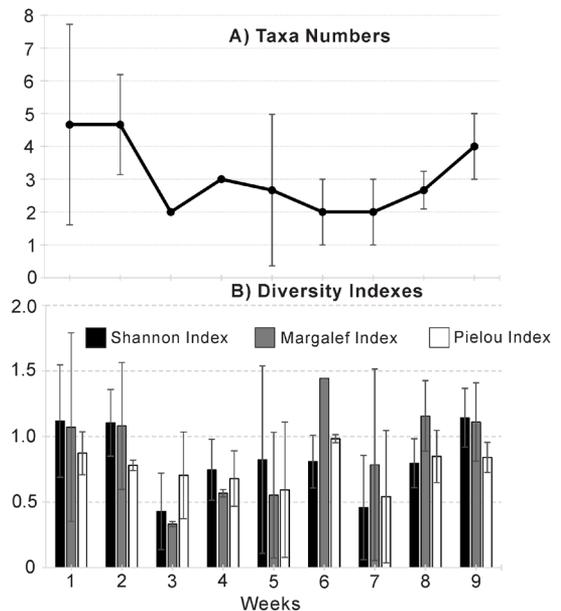


**Figure 3.** Total (A) and relative abundances (%) (B) of meiofauna in artificial substrates.

### 3.3. Nematode colonization and succession and sex/age on artificial substrates

We found 21 genera of 13 families of Nematoda (Table 2). The highest value occurred in the 1<sup>st</sup> week, when up to eight genera were found in a replicate (average  $4.6 \pm 3.0$ ), and lower between weeks 3-8, with averages always <3 genera (Figure 4A). Shannon and Margalef indexes did not present a clear pattern through the weeks (ANOVA, F value = 1.714,  $p = 0.163$ ).

The nematofauna community structure did not change significantly comparing the pairwise weeks (PERMANOVA, Pseudo F value = 3.898  $p > 0.05$ ). The most abundant genera were *Monhystrella*,



**Figure 4.** Number of individuals (A) and diversity indexes (B) of Nematoda genera in artificial substrate.

**Table 1.** Meiofauna abundance with mean densities (individuals per  $10 \text{ cm}^2$ ) and the standard deviations of each taxon along the weekly samples.

Weeks	Total meiofauna	Nematoda	Rotifera	Ostracoda	Turbellaria	Copepoda	Oligochaeta	Acari
1	$9.3 \pm 6.67$	$5.46 \pm 3.68$	$3.13 \pm 2.61$	$0.26 \pm 0.09$	$0.33 \pm 0.47$	$0.13 \pm 0.18$	0	$0.06 \pm 0.09$
2	$15.33 \pm 5.64$	$2.33 \pm 2.45$	$12.73 \pm 5.98$	0	0	0	$0.26 \pm 0.37$	0
3	$14.53 \pm 2.50$	$3.06 \pm 0.24$	$11 \pm 2.26$	$0.33 \pm 0.24$	0	0	$0.13 \pm 0.18$	0
4	$72.73 \pm 23.04$	$6.4 \pm 1.07$	$66.06 \pm 19.59$	$0.26 \pm 0.09$	0	0	0	0
5	$60 \pm 22.53$	$7.13 \pm 0.75$	$48 \pm 16.93$	0	$4.86 \pm 6.88$	0	0	0
6	$30.93 \pm 7.11$	$2.66 \pm 2.20$	$28.2 \pm 5.37$	0	0	0	$0.06 \pm 0.09$	0
7	$13.86 \pm 9.91$	$2.13 \pm 0.80$	$11.66 \pm 7.73$	0	0	0	$0.06 \pm 0.09$	0
8	$53.93 \pm 5.34$	$2.86 \pm 0.83$	$50.93 \pm 4.21$	0	0	0	$0.13 \pm 0.18$	0
9	$36.20 \pm 20.97$	$5.06 \pm 2.37$	$31.13 \pm 14.79$	0	0	0	0	0
One-way PERMANOVA	<b>&lt;0.05</b>	>0.05	<b>&lt;0.05</b>	<b>&lt;0.05</b>	>0.05	>0.05	>0.05	>0.05

Differences are considered significant if  $p < 0.05$  (in bold).

**Table 2.** List of nematode family and genera, feeding habits and colonizer/persister (c-p) values with density mean (ind. 10 cm<sup>2</sup>) and  $\pm$  standard deviation for nine weeks on artificial substrate.

Genera	Feeding Habits	c-p Values	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9
<b>Oncholaimidae</b>											
<i>Oncholaimus</i> Dujardin, 1845	CF	4	0.2 $\pm$ 0.28	0.06 $\pm$ 0.09	0	0.2 $\pm$ 0.28	0	0.2 $\pm$ 0	0.2 $\pm$ 0	0	0.73 $\pm$ 0.41
<i>Viscosia</i> de Man, 1890	CF	3	0	0	0	0	0	0.6 $\pm$ 0.9	0	0	1.06 $\pm$ 1.36
<b>Triploididae</b>											
<i>Bathylaimus</i> Cobb, 1894	EF	2	0	0.13 $\pm$ 0.18	0	0	0	0	0	0	0
<b>Prismatolaimidae</b>											
<i>Prismatolaimus</i> de Man, 1880	CF	3	0.13 $\pm$ 0.18	0	0	0	0	0	0	0	0
<b>Dorylaimidae</b>											
<i>Crocodyrilymna</i> Andrassy, 1988	SF	4	0.33 $\pm$ 0.47	0.06 $\pm$ 0.09	0	0	0	0	0	0	0
<i>Drepanodorylaimus</i> Jaitrapuri, 1966	SF	4	0	0	0.53 $\pm$ 0.61	0	0	0	0	0	0
<b>Quadianematidae</b>											
<i>Chrysonema holsaticum</i> (Schneider, 1925) Andrassy, 1990	SF	5	0	0	0	0.46 $\pm$ 0.33	0.4 $\pm$ 0.56	0	0.06 $\pm$ 0.09	0.13 $\pm$ 0.09	0.33 $\pm$ 0.33
<b>Chromadoridae</b>											
<i>Prochromadorella</i> Micoletzky, 1924	EF	2	0	0	0	0	0	0.06 $\pm$ 0.09	0	0	0
<i>Dichromadora</i> Kreis, 1929	EF	2	0	0.06 $\pm$ 0.09	0	0	0	0	0	0	0
<i>Chromadorita</i> Filipjev, 1922	EF	3	0	1.46 $\pm$ 1.08	0	0	0	0	0	0	0
<b>Cyatholaimidae</b>											
<i>Paracyatholaimus</i> Micoletzky, 1922	EF	3	0.6 $\pm$ 0.58	0	0	1.66 $\pm$ 1.24	0.4 $\pm$ 0.56	0	0	0	0
<b>Desmodoridae</b>											
<i>Paradesmodora</i> Schuurmans, 1950	EF	3	0	0	0	0.06 $\pm$ 0.09	0	0	0	0	0
<i>Prodesmodora</i> Micoletzky, 1923	SF	4	0	0.73 $\pm$ 1.03	0	0	0	0	0	0	0
<b>Monhysteridae</b>											
<i>Monhystera</i> Bastian, 1865	DF	1	0.53 $\pm$ 0.75	0.93 $\pm$ 1.31	0	0	1.2 $\pm$ 1.69	0.06 $\pm$ 0.09	0.53 $\pm$ 0.61	0.73 $\pm$ 0.49	1.13 $\pm$ 0.49
<i>Monhystrella</i> Cobb, 1918	DF	1	2.8 $\pm$ 1.85	1.46 $\pm$ 1.79	3.13 $\pm$ 0.24	4.46 $\pm$ 2.04	1.4 $\pm$ 1.3	0.13 $\pm$ 0.18	0	0	0.46 $\pm$ 0.65
<b>Xylidae</b>											
<i>Deptonema</i> Cobb, 1920	DF	2	0.46 $\pm$ 0.33	0.6 $\pm$ 0.58	0	0	1.06 $\pm$ 1.11	0	0	0	0
<i>Pseudosteneria</i> Wieser, 1956	EF	3	0	0	0.46 $\pm$ 0.65	0	0	0	0	0.06 $\pm$ 0.09	0
<b>Linhomoeidae</b>											
<i>Teschellingia</i> de Man, 1888	DF	3	0	0	0	0	0	0	0	0.2 $\pm$ 0.16	0
<b>Axonolaimidae</b>											
<i>Axonolaimus</i> de Man, 1889	EF	2	0	0.13 $\pm$ 0.18	0	0	0	0	0	0	0
<b>Chronogastridae</b>											
<i>Chronogaster</i> Cobb, 1913	DF	3	0.4 $\pm$ 0.28	0.53 $\pm$ 0.75	0	0	0.53 $\pm$ 0.75	0	0	0	0
<b>Diplogastridae</b>											
<i>Rhabditoides</i> Goodey, 1929	DF	1	0.06 $\pm$ 0.09	0	0	0	0	0	0	0	0

CF = Chewers feeding/Omnivores; EF = Epistrate feeding; DF = Deposit feeding; SF = Suction feeding/Omnivores.

*Monhystera*, *Paracyatholaimus*, and *Daptonema*, representing 94.11, 77.7, 51.7, and 31.7%, respectively. *Monhystrella* dominated through the first six weeks, while *Monhystera* dominated at the end of the experiment (7-9<sup>th</sup> weeks); *Paracyatholaimus* appeared sparsely in some weeks and *Daptonema* appeared in weeks 1, 2 and 5, completely disappearing later (Figure 5A). Each of the other 17 genera represented <5% of total Nematoda abundance, but altogether summed 28%. Among these, stand out *Oncholaimus* and *Prismatolaimus*, abundant in weeks 6, 7, and 9 and *Viscosia* in the weeks 6 and 9 (Figure 5B).

Juveniles dominated in all abundant genera through most of the experiment (Figure 6). Among adults, males tended to dominate in all abundant genera (Figure 6). Males of *Monhystrella* reached up to 4 ind. 10 cm<sup>-2</sup> in the 2<sup>nd</sup> week when dominated the population (Figure 6A). Likewise, for *Monhystera* and *Daptonema* juveniles dominated most of the time, while males dominated adult population followed by gravid females (10-25%; Figures 6B and 6D). Juveniles also dominated the *Paracyatholaimus* population, while non-gravid females were rare, representing <15% of the total population (Figure 6C).

### 3.4. Nematode functional traits colonization and succession on artificial substrates

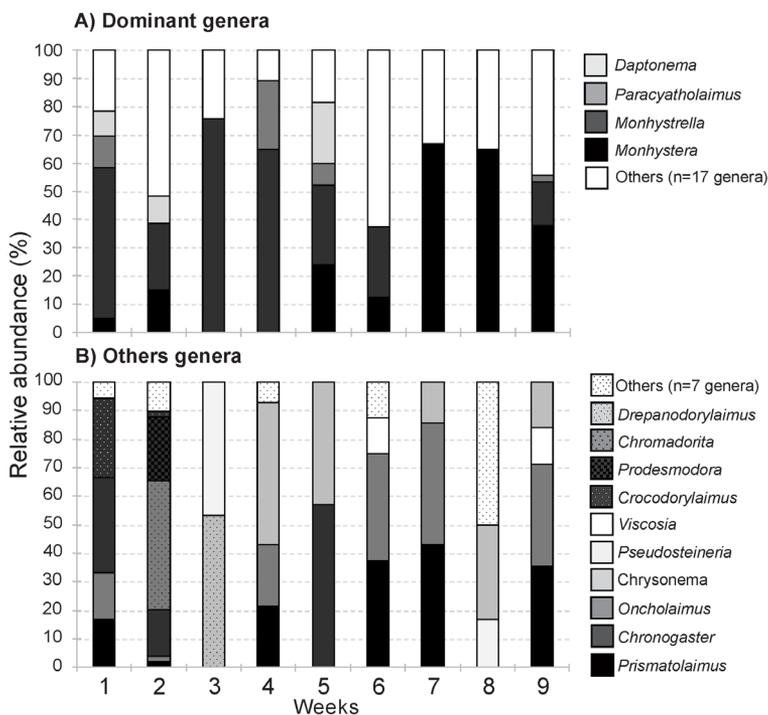
There was a clear tendency to increase the complexity of the life-history and trophic structure

of the nematode assemblages. This was reflected in the increase of the MI and in the relative contribution of chewers, particularly between the 6-9<sup>th</sup> weeks (Figures 7 and 8). Deposit feeder represented 67% of nematode abundance, dominating all weeks but the 6<sup>th</sup> and 9<sup>th</sup> when the chewers dominated (47-57%). Suction feeders represented <10%, except when they peaked in the 3<sup>rd</sup> week (24.1%). Epistrate feeders were particularly important in the 2<sup>nd</sup> and 4<sup>th</sup> weeks, representing 40.8 and 25.2%, respectively (Figure 7). The predator/omnivores were more abundant in the weeks 6, 7, 9 (up to ~60% in the 6<sup>th</sup> week).

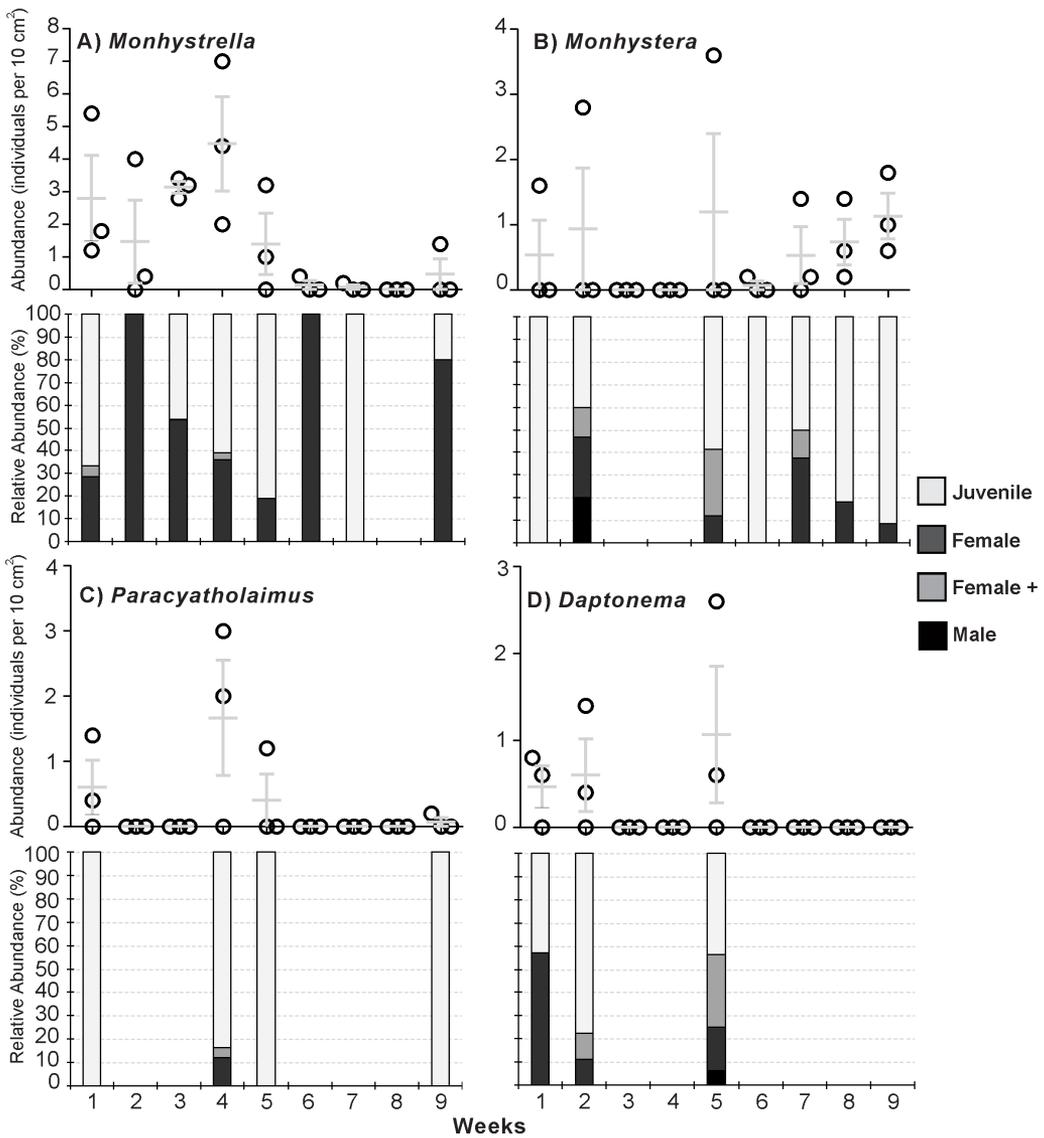
The assemblage was dominated by the nematodes c-p 1 and 2, summing up 68.5% of total nematodes (Figure 8). Individuals c-p 3 occurred mostly in low abundance but reached ~50% in the 2<sup>nd</sup> week. The extreme-persistent (c-p 4, 5) were abundant from the 6<sup>th</sup> week, when MI increased considerably, reaching a weekly average of  $2.8 \pm 1.1$  (Figure 8).

## 4. Discussion

In the present study, we examined the pattern of an early colonization and ecological succession of invertebrates on artificial ceramic substrates in a lentic freshwater reservoir in Brazilian semi-arid. We used meiofauna and nematofauna as parameters, guided by the following hypotheses:

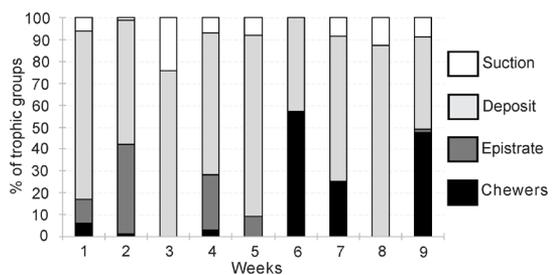


**Figure 5.** Relative abundance (%) of most abundant (A) and less abundant (B) Nematoda genera in artificial substrate.



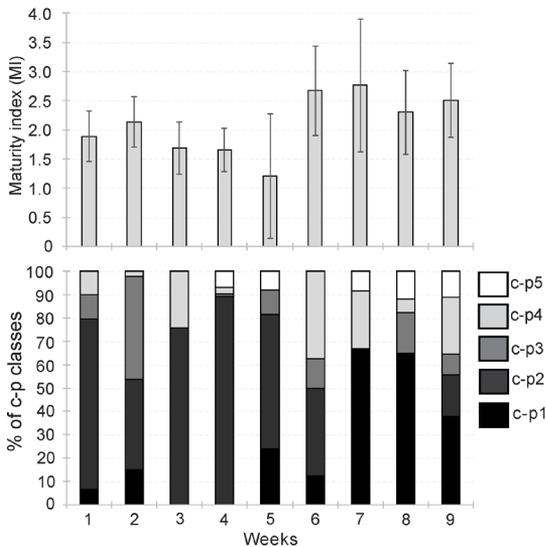
**Figure 6.** Nematoda abundance and sex/age of most abundant genera in artificial substrate.

i) despite meiofauna being microscopic organisms with limited active dispersion, they rapidly colonize new substrates, exhibiting increased abundance, richness, and diversity; ii) functional traits of freshwater nematodes are a good tool for observing early succession on hard artificial substrates in a lentic reservoir. We posited that after the introduction of artificial substrates, an early ecological succession is reflected by an increase in the maturity index value (Bongers, 1990; Ettema & Bongers, 1993; Steel et al., 2010), and the trophic structure of the assemblage changes throughout the succession, with deposit feeders and epistrate feeders expected in the initial stages, while omnivorous and chewers tend to appear later (Peters et al., 2005).



**Figure 7.** Relative abundance (%) of Nematoda trophic groups in artificial substrate.

The meiofauna rapidly colonized the ceramic plates within the first week. Various studies indicate that the dispersion and, consequently,



**Figure 8.** Relative abundance (%) of colonizer/persister (c-p) groups (A) and maturity index (B) in artificial substrate.

colonization of meiofauna depend not only on their locomotion capacity (Soetaert et al., 2002; Thomas & Lana, 2011) but also on substrate pavement by microorganisms forming the biofilm (Fonsêca-Genevois et al., 2006). The rapid colonization (within the first week) by meiofauna organisms suggests their active ability to colonize artificial substrates in lentic environments. This contrasts with the notion that these animals have limited dispersion capacity (Fonsêca-Genevois et al., 2006; Ptatscheck & Traunspurger, 2020) and, consequently, a low potential to colonize new substrates in lentic ecosystems. Therefore, we accept the first hypothesis that meiofauna rapidly colonizes new substrates in lentic environments, despite being microscopic organisms with limited active dispersion.

The nematodes likely colonized the ceramic plates through active transport. Their adhesive capacity to hard substrates and the lentic environment facilitates the anchoring of Nematoda (Ptatscheck & Traunspurger, 2020). Swimming in the water column and crawling through sediment are known forms of active, small-scale transport for many nematodes (Gallucci et al., 2008; Thomas & Lana, 2011). These organisms probably employed vertical movements to reach the ceramic plates. For instance, approximately 62% of Nematoda use these mechanisms to migrate to new habitats (Williams & Hynes, 1976; Benzie, 1984). However, the Nematoda assemblages do not fully mirror the adjacent natural substrates (Barros, 2018).

Differences in the community profile between the two habitats (natural and artificial) may support the active dispersal strategy and the search for available habitats in intermittent or semi-intermittent reservoirs in the semiarid region as a means of survival or preference to dwelling in soft or hard substrate.

In this study, the community structure developed in two main phases: i) an initial phase of higher diversity due to the rapid colonization of the seven higher taxa of meiofauna (weeks 1-3); ii) a second phase with reduced richness (weeks 4-9), accompanied by a progressive increase in the abundance of rotifers, which came to represent over 90% of the entire colonizing meiofauna (Table 1; Figure 3). The characteristics of these two groups differ in habitat preference. For instance, Nematoda possess morphological adaptations allowing them to exploit resources in soft substrates (Tita et al., 1999) and tolerate anoxic conditions within sediment (Soetaert et al., 2002). Rotifers, especially bdelloids, avoid environments with low oxygen conditions found in soft substrates, instead colonizing the shallower layers of sediment (Madaliński, 1961). As primary colonizers, rotifers quickly choose their habitat; within 12 hours, these animals colonize defaunated environments (Smith & Brown, 2006), appearing to be fugitive or invasive species (Pianka, 1970). Rotifers mature quickly and exhibit high fecundity, with a single female capable of producing 1-2 eggs every 2-6 days (Pennak, 1989).

#### 4.1. Colonization and succession of Nematoda and *sex/lage* on artificial substrates

The diversity indexes of Nematoda assemblages did not show a clear trend of temporal fluctuations or ecological succession throughout the experiment. Due to the lack of three-dimensional habitat provided by hard substrates, this absence of patterns in the evaluated timeframe is common (Peters et al., 2005, 2007). However, in some artificial substrate assemblages, the number of nematode genera tended to increase after one week of colonization (Fonsêca-Genevois et al., 2006). Additionally, a small number of genera accounted for high abundance, while the majority experienced wide fluctuations and low abundance on ceramic plates (Figures 5A and B). These scenarios of abundance and diversity lead us to raise the following points about the colonization and ecological succession of these organisms on artificial substrates: i) Nematoda assemblages continue to colonize and develop in the early stages of ecological succession in Caatinga

reservoirs; ii) the colonization process within the analyzed timeframe here (9 weeks) is characterized by a few abundant taxa and numerous less abundant taxa.

It is well-known that nematodes rapidly colonize (approximately five days) new substrates (Smith & Brown, 2006). The dispersal capability of genus/species is crucial for establishing in a new habitat (Ptatscheck & Traunspurger, 2020). *Monhystera*, the dominant genus in the current study, has both short and long-distance swimming capabilities, depending on the species (Riemann & Schrage, 1978; Vranken et al., 1981). However, we must consider the life stages and preference of these organisms in sediment layers. Adults of the genus prefer deeper sediment layers (Traunspurger, 1996), which may be a limiting factor for migrating in large numbers to new habitats and decreasing the reproduction rate during ecological succession on artificial substrates. Indeed, the abundance of *Monhystera* has significantly increased in the last three weeks and can be explained by its feeding preference, reproductive rate, and short-distance swimming ability. In terms of diversity, the development of nematofauna differed from the work of Peters et al. (2005), who found low diversity in the early days of colonization and a progressive increase after the first week. Here, we found a higher number of genera in the first two weeks and a decrease until week 7. The increasing diversity trend from week 8 suggests that the nine weeks of the experiment consist of early stages of ecological succession.

The colonization process in the biofilm is continuous. However, the community formation dynamics in the biofilm vary depending on the substrate type (e.g., roughness, heterogeneity) and the season of the year (Pieczyńska, 1964). The semiarid region of the Caatinga has a distinctive seasonal dynamic, characterized by prolonged periods of drought. In such situations, the availability and colonization of a new microhabitat can be an alternative for maintaining biodiversity in the semiarid region. Specifically, the high diversity observed at the beginning of ecological succession suggests a resilience strategy of the nematofauna in the typical dry conditions of the Caatinga biome.

Among the most abundant genera, juveniles predominantly dominated most of the time, as expected, with some exceptions (Figure 5). The family Monhysteridae, represented here by the genera *Monhystera* and *Monhystrella*, has a significant portion of the population inhabiting

the superficial sediment layer, and the gestation period varies from a few weeks (Traunspurger, 1996). These are characteristics of individuals capable of establishing themselves in defaunated environments during the early stages of ecological succession (Derycke et al., 2013). Among adults, males predominated in populations, especially for *Monhystrella*, followed by gravid females (Figure 5A). This dynamic suggests high rates of sexual reproduction. However, specific data would be needed to confirm the reproductive mechanisms adopted by the genera over the colonization period, as the diversity of life strategies among different species within the same genus is often high (Gerlach & Schrage, 1971; Traunspurger, 1996).

#### 4.2. Are functional freshwater Nematode traits a good tool for view an early succession on hard artificial substrate in a reservoir of Brazilian semiarid?

The analysis of community functional traits (trophic structure and life history) indicates an increase in functional complexity, with a tendency toward an increase in the maturity index during the plate succession process, along with a rise in the relative abundance of shredders, especially from the sixth week of the experiment (Figures 7 and 8). Therefore, we accept our second hypothesis and confirm the efficiency of the index in monitoring ecological succession (Bongers, 1990; Ettema & Bongers, 1993; Steel et al., 2010), which indicates the maturation of the community (Margalef, 1963), as expected (Ettema & Bongers, 1993). However, our results did not show a clear substitution of one c-p group for another, as hypothesized by Bongers (1990), but rather an increase in the representation of genera such as *Oncholaimus* (c-p 4; shredders) and *Chrysonema* (c-p 5; suction feeders), contributing to the increase in the maturity index.

The colonizers (c-p 2) were abundant throughout the experimental period, with a higher contribution from the genera *Monhystera*, *Monhystrella*, and *Daptonema*. These genera dominated the Nematoda community at the beginning of ecological succession and organic enrichment (Figures 3 and 8). In fact, colonizers benefit from an environment rich in organic matter and commonly dominate such conditions (Bongers & Ferris, 1999). These individuals form the basis for the (re)establishment of the fauna, keeping it abundant during a long period (60 weeks) of habitat restructuring (Ettema & Bongers, 1993), as observed over the nine weeks of the experiment

conducted here. The deposit feeders dominated the ceramic plates throughout the experiment (Figure 7), as commonly found in natural and artificial hard substrates in freshwater environments (Peters et al., 2005; Traunspurger et al., 2020). These Nematoda are mainly associated with high levels of eutrophication (Ristau et al., 2015). The abundant presence of epistrates in the early colonization weeks reinforces the close relationship between Nematoda and the biofilm, a likely primary food source for these initial colonizers (Majdi et al., 2012). The microfauna present in the biofilm is vital for the colonization of hard artificial substrates, providing food resources and paving the substrate for epistrate feeders (Weitere et al., 2018). Additionally, this community maintains an open energy flow system with larger organisms of the macrofauna (Majdi & Traunspurger, 2015).

Although the literature on the ecology and taxonomic diversity of meiofauna organisms, particularly Nematoda, is extensive (Abebe et al., 2008; Ristau et al., 2015; Decraemer & Backeljau, 2015), little is known about the relationships between the mechanisms involved in dispersion at small spatial scales and the morphological and behavioral characteristics (Thomas & Lana, 2011). This lack of knowledge is closely related to the challenges of experimentally studying microscopic organisms both in the field (Thomas & Lana, 2011) and in the laboratory (Palmer, 1988). The microscopic sizes of these animals make handling and identification challenging down to the species level, contributing to a shortage of specialists in the field (Derycke et al., 2008; Fonseca et al., 2014).

Some studies have emphasized the importance of experimental utilization of Nematoda colonization on artificial substrates as a means of environmental assessment and monitoring (Mirto & Danovaro, 2004; Costa et al., 2016; Freixa et al., 2023). However, there are still few studies that have tested the efficiency of the maturity index as a monitoring tool for these ecological processes (Bongers, 1990; Ettema & Bongers, 1993; Steel et al., 2010), especially in lentic aquatic ecosystems in semi-aquatic regions of arid tropical areas. The current study demonstrated that the processes of colonization and ecological succession were clearly visualized through the functional characteristics of the Nematoda community, confirming the maturity and trophic index as robust tools for monitoring these processes. We suggest further studies, combining functional traits (Justino et al.,

2023) and the use of metrics such as redundancy and functional vulnerability (Magneville et al., 2022) during an early stage of ecological succession to deepen the understanding of the relationships between these functional traits and the formation of assemblages in ecological succession.

## Acknowledgements

We appreciated the contribution of Hyabbi Lima for the map and figure elaboration, and Maxsuel Silva for the help in the samplings. FLOB was supported by PhD (CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; process number: 88887.689208/2022-00) scholarship program.

## References

- Abebe, E., Decraemer, W., & De Ley, P., 2008. Global diversity of nematodes (Nematoda) in freshwater. *Hydrobiologia* 595(1), 67-78. <http://doi.org/10.1007/s10750-007-9005-5>.
- Andrade-Lima, D., 1982. Present day forest refuges in Northeastern Brazil. In: Prance, G.T., ed. *Biological diversification in the tropics*. New York: Columbia University, 245-254.
- Atilla, N., 2000. Meiofaunal colonization of artificial substrates in an estuarine embayment. *Mar. Ecol. (Berl.)* 21(1), 69-83. <http://doi.org/10.1046/j.1439-0485.2000.00700.x>.
- Atilla, N., Fleeger, J.W., & Finelli, C.M., 2005. Effects of habitat complexity and hydrodynamics on the abundance and diversity of small invertebrates colonizing artificial substrates. *J. Mar. Res.* 63(6), 1151-1172. <http://doi.org/10.1357/002224005775247580>.
- Atilla, N., Wetzel, M.A., & Fleeger, J.W., 2003. Abundance and colonization potential of artificial hard substrate-associated meiofauna. *J. Exp. Mar. Biol. Ecol.* 287(2), 273-287. [http://doi.org/10.1016/S0022-0981\(02\)00569-5](http://doi.org/10.1016/S0022-0981(02)00569-5).
- Barbosa, J.E.D.L., Medeiros, E.S.F., Brasil, J., Cordeiro, R.D.S., Crispim, M.C.B., & Silva, G.H.G.D., 2012. Aquatic systems in semiarid Brazil: limnology and management. *Acta Limnol. Bras.* 24(1), 103-118. <http://doi.org/10.1590/S2179-975X2012005000030>.
- Barros, F.L.O., 2018. Colonização meiofaunística e nematofaunística em substrato artificial em um ecossistema lêntico [Monografia]. Campina Grande: Universidade Federal de Campina Grande.
- Barros, F.L.O., Silva, M.C.D., Castro, F.J.V.D., & Nogueira Júnior, M., 2021. Marine free-living nematodes in semiarid inland waters. *Acta Limnol. Bras.* 33, e15. <http://doi.org/10.1590/s2179-975x6520>.

- Benzie, J.A., 1984. Zooplankton of an Australian high alpine lake, Lake Cootapatamba, Kosciusko range. *Mar. Freshw. Res.* 35(6), 691-702. <http://doi.org/10.1071/MF9840691>.
- Boeckner, M.J., Sharma, J., & Proctor, H.C., 2009. Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low-and high-energy environments. *Hydrobiologia* 624(1), 91-106. <http://doi.org/10.1007/s10750-008-9669-5>.
- Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83(1), 14-19. PMID:28313236. <http://doi.org/10.1007/BF00324627>.
- Bongers, T., 1999. The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. *Plant Soil* 212(1), 13-22. <http://doi.org/10.1023/A:1004571900425>.
- Bongers, T., De Goede, R.G.M., Korhals, G.W., & Yeates, G.W., 1995. Proposed changes of cp classification for nematodes. *Russ. J. Nematol.* 3(1), 61-62.
- Bongers, T., & Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. *Trends Ecol. Evol.* 14(6), 224-228. PMID:10354624. [http://doi.org/10.1016/S0169-5347\(98\)01583-3](http://doi.org/10.1016/S0169-5347(98)01583-3).
- Brown, C.J., 2005. Epifaunal colonization of the Loch Linnhe artificial reef: influence of substratum on epifaunal assemblage structure. *Biofouling* 21(2), 73-85. PMID:16167388. <http://doi.org/10.1080/08927010512331344197>.
- Bush, M.B., Whittaker, R.J., & Partomihardjo, T., 1995. Colonization and succession on Krakatau: an analysis of the guild of vining plants. *Biotropica* 27(3), 355-372. <http://doi.org/10.2307/2388921>.
- Cobb, N.A., 1917. A genus of free-living predatory Nematodes: contributions to a science of Nematology VI: (with 75 Illustration in the text). *Soil Sci.* 3(5), 431-486. <http://doi.org/10.1097/00010694-191705000-00004>.
- Costa, A.B.H.P., Valença, A.P.M.C., & Santos, P.J.P., 2016. Is meiofauna community structure in Artificial Substrate Units a good tool to assess anthropogenic impact in estuaries? *Mar. Pollut. Bull.* 110(1), 354-361. PMID:27315755. <http://doi.org/10.1016/j.marpolbul.2016.06.041>.
- de Grisse, A.T., 1969. Redescription ou modification de quelques techniques utilisées dans l'étude des nématodes phytoparasitaires. *Meded. Fac. Landbouwwet. Rijksuniv. Gent* 34, 35.
- Decraemer, W., & Backeljau, T., 2015. Utility of classical  $\alpha$ -taxonomy for biodiversity of aquatic nematodes. *J. Nematol.* 47(1), 1-10. PMID:25861112.
- Derycke, S., Backeljau, T., & Moens, T., 2013. Dispersal and gene flow in free-living marine nematodes. *Front. Zool.* 10(1), 1. <http://doi.org/10.1186/1742-9994-10-1>.
- Derycke, S., Fonseca, G., Vierstraete, A., Vanfleteren, J., Vincx, M., & Moens, T., 2008. Disentangling taxonomy within the *Rhabditis (Pellioiditis) marina* (Nematoda, Rhabditidae) species complex using molecular and morphological tools. *Zool. J. Linn. Soc.* 152(1), 1-15. <http://doi.org/10.1111/j.1096-3642.2007.00365.x>.
- Ettema, C.H., & Bongers, T., 1993. Characterization of nematode colonization and succession in disturbed soil using the Maturity Index. *Biol. Fertil. Soils* 16(2), 79-85. <http://doi.org/10.1007/BF00369407>.
- Fastie, C.L., 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76(6), 1899-1916. <http://doi.org/10.2307/1940722>.
- Ferreira, R.C., Nascimento-Junior, A.B., Santos, P.J.P., Botter-Carvalho, M.L., & Pinto, T.K., 2015. Responses of estuarine nematodes to an increase in nutrient supply: an in situ continuous addition experiment. *Mar. Pollut. Bull.* 90(1-2), 115-120. PMID:25499965. <http://doi.org/10.1016/j.marpolbul.2014.11.012>.
- Fonseca, G., Norenburg, J., & Di Domenico, M., 2014. Diversity of marine meiofauna on the coast of Brazil. *Mar. Biodivers.* 44(3), 459-462. <http://doi.org/10.1007/s12526-014-0261-0>.
- Fonseca-Genevois, V.D., Somerfield, P.J., Neves, M.H.B., Coutinho, R., & Moens, T., 2006. Colonization and early succession on artificial hard substrata by meiofauna. *Mar. Biol.* 148(5), 1039-1050. <http://doi.org/10.1007/s00227-005-0145-8>.
- Fox, J., & Weisberg, S., 2019. *car: Companion to Applied Regression*. Vienna: R Foundation for Statistical Computing. Retrieved in 2023, July 7, from <https://CRAN.R-project.org/package=car>
- Freixa, A., Ortiz-Rivero, J., & Sabater, S., 2023. Artificial substrata to assess ecological and ecotoxicological responses in river biofilms: use and recommendations. *MethodsX* 10, 102089. PMID:36915862. <http://doi.org/10.1016/j.mex.2023.102089>.
- Gallucci, F., Moens, T., Vanreusel, A., & Fonseca, G., 2008. Active colonisation of disturbed sediments by deep-sea nematodes: evidence for the patch mosaic model. *Mar. Ecol. Prog. Ser.* 367, 173-183. <http://doi.org/10.3354/meps07537>.
- García-Gómez, J.C., Garrigós, M., & Garrigós, J., 2021. Plastic as a vector of dispersion for marine species with invasive potential: a review. *Front. Ecol. Evol.* 9, 629756. <http://doi.org/10.3389/fevo.2021.629756>.
- Gerlach, S.A., & Schrage, M., 1971. Life cycles in marine meiobenthos. Experiments at various temperatures with *Monhystera disjuncta* and *Theristus pertenuis*

- (Nematoda). *Mar. Biol.* 9(3), 274-280. <http://doi.org/10.1007/BF00351390>.
- Jouili, S., Essid, N., Semprucci, F., Boufahja, F., Nasri, A., Beyrem, H., & Mahmoudi, E., 2017. Environmental quality assessment of El Bibane lagoon (Tunisia) using taxonomic and functional diversity of meiofauna and nematodes. *J. Mar. Biol. Assoc. U. K.* 97(8), 1593-1603. <http://doi.org/10.1017/S0025315416000990>.
- Justino, J.T., Demetrio, G.R., Neres, P.F., Meneses, D., & Pinto, T.K., 2023. A functional perspective of nematode assemblages as proxy of quality in tropical estuarine tidal flats. *Mar. Environ. Res.* 186, 105922. PMID:36812839. <http://doi.org/10.1016/j.marenvres.2023.105922>.
- Madaliński, K., 1961. Moss dwelling Rotifers of Tatra streams. *Pol. Arch. Hydrobiol.* 9(22), 243-263.
- Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., & Villéger, S., 2022. mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography* 2022(1), ecog.05904. <http://doi.org/10.1111/ecog.05904>.
- Majdi, N., & Traunspurger, W., 2015. Free-living nematodes in the freshwater food web: a review. *J. Nematol.* 47(1), 28-44. PMID:25861114.
- Majdi, N., Tackx, M., Traunspurger, W., & Buffan-Dubau, E., 2012. Feeding of biofilm-dwelling nematodes examined using HPLC-analysis of gut pigment contents. *Hydrobiologia* 680(1), 219-232. <http://doi.org/10.1007/s10750-011-0920-0>.
- Margalef, R., 1963. On certain unifying principles in ecology. *Am. Nat.* 97(897), 357-374. <http://doi.org/10.1086/282286>.
- Martinez Arbizu, P., 2019. pairwiseAdonis: Pairwise multilevel comparison using adonis. 2017. R package version 00, 1. São Francisco: GitHub, Inc.
- Mirto, S., & Danovaro, R., 2004. Meiofaunal colonisation on artificial substrates: a tool for biomonitoring the environmental quality on coastal marine systems. *Mar. Pollut. Bull.* 48(9-10), 919-926. PMID:15111039. <http://doi.org/10.1016/j.marpolbul.2003.11.016>.
- Moens, T., Vafeiadou, A.M., De Geyter, E., Vanormelingen, P., Sabbe, K., & De Troch, M., 2014. Diatom feeding across trophic guilds in tidal flat nematodes, and the importance of diatom cell size. *J. Sea Res.* 92, 125-133. <http://doi.org/10.1016/j.seares.2013.08.007>.
- Netto, S.A., & Fonseca, G., 2017. Regime shifts in coastal lagoons: evidence from free-living marine nematodes. *PLoS One* 12(2), e0172366. PMID:28235030. <http://doi.org/10.1371/journal.pone.0172366>.
- Netto, S.A., & Valgas, I., 2010. The response of nematode assemblages to intensive mussel farming in coastal sediments (Southern Brazil). *Environ. Monit. Assess.* 162(1-4), 81-93. PMID:19238569. <http://doi.org/10.1007/s10661-009-0777-0>.
- Palmer, M. A. (1988). Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Marine Ecology Progress Series*, 48(1), 81-91.
- Pennak, R.W., 1989. Eubranchiopoda (Fairy, Tadpole, and Clam Shrimps). In: Pennak, R.W., ed. *Freshwater Invertebrates of the United States: protozoa to mollusca*. New York: John Wiley & Sons, 3 ed.
- Peters, L., Traunspurger, W., Wetzel, M.A., & Rothhaupt, K.O., 2005. Community development of free-living aquatic nematodes in littoral periphyton communities. *Nematology* 7(6), 901-916. <http://doi.org/10.1163/156854105776186352>.
- Peters, L., Wetzel, M.A., Traunspurger, W., & Rothhaupt, K.O., 2007. Epilithic communities in a lake littoral zone: the role of water-column transport and habitat development for dispersal and colonization of meiofauna. *J. N. Am. Benthol. Soc.* 26(2), 232-243. [http://doi.org/10.1899/0887-3593\(2007\)26\[232:ECIALL\]2.0.CO;2](http://doi.org/10.1899/0887-3593(2007)26[232:ECIALL]2.0.CO;2).
- Pianka, E.R., 1970. On r-and K-selection. *Am. Nat.* 104(940), 592-597. <http://doi.org/10.1086/282697>.
- Pieczynska, E., 1964. Investigations on colonization of new substrates by nematodes (Nematoda) and some other periphyton organisms. *Ekol. Pol. A* 12(13), 185-234.
- Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13, 131-144. [http://doi.org/10.1016/0022-5193\(66\)90013-0](http://doi.org/10.1016/0022-5193(66)90013-0).
- Pinto, T.K., Austen, M.C., Warwick, R.M., Somerfield, P.J., Esteves, A.M., Castro, F.J., Fonseca-Genevois, V.G., & Santos, P.J.P., 2013. Nematode diversity in different microhabitats in a mangrove region. *Mar. Ecol.* 34(3), 257-268. <http://doi.org/10.1111/maec.12011>.
- Platt, H.M., & Warwick, R.M., 1983. A synopsis of the free-living marine nematodes, part I. British enoplids. Cambridge: Cambridge University Press.
- Prado, D., 2003. As caatingas da América do Sul. In: Leal, I.R., Tabarelli, M., & Silva, J.M.C., eds. *Ecologia e conservação da Caatinga*. Recife: Editora Universitária da UFPE, 3-73.
- Ptatscheck, C., & Traunspurger, W., 2014. The meiofauna of artificial water-filled tree holes: colonization and bottom-up effects. *Aquat. Ecol.* 48(3), 285-295. <http://doi.org/10.1007/s10452-014-9483-2>.
- Ptatscheck, C., & Traunspurger, W., 2020. The ability to get everywhere: dispersal modes of free-living, aquatic nematodes. *Hydrobiologia* 847(17), 3519-3547. <http://doi.org/10.1007/s10750-020-04373-0>.
- Riemann, F., & Schrage, M., 1978. The mucus-trap hypothesis on feeding of aquatic nematodes and

- implications for biodegradation and sediment texture. *Oecologia* 34(1), 75-88. PMID:28309389. <http://doi.org/10.1007/BF00346242>.
- Ristau, K., Spann, N., & Traunspurger, W., 2015. Species and trait compositions of freshwater nematodes as indicative descriptors of lake eutrophication. *Ecol. Indic.* 53, 196-205. <http://doi.org/10.1016/j.ecolind.2015.01.010>.
- Robertson, A.L., 2000. Lotic meiofaunal community dynamics: colonisation, resilience and persistence in a spatially and temporally heterogeneous environment. *Freshw. Biol.* 44(1), 135-147. <http://doi.org/10.1046/j.1365-2761.2000.00595.x>.
- Rule, M.J., & Smith, S.D., 2007. Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs. *J. Exp. Mar. Biol. Ecol.* 345(1), 38-51. <http://doi.org/10.1016/j.jembe.2007.01.006>.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27(3), 379-423. <http://doi.org/10.1002/j.1538-7305.1948.tb01338.x>.
- Smith, F., & Brown, A.V., 2006. Effects of flow on meiofauna colonization in artificial streams and reference sites within the Illinois River, Arkansas. *Hydrobiologia* 571(1), 169-180. <http://doi.org/10.1007/s10750-006-0237-6>.
- Soetaert, K., Muthumbi, A., & Heip, C., 2002. Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns. *Mar. Ecol. Prog. Ser.* 242, 179-193. <http://doi.org/10.3354/meps242179>.
- Spagnolo, A., Cuicchi, C., Punzo, E., Santelli, A., Scarcella, G., & Fabi, G., 2014. Patterns of colonization and succession of benthic assemblages in two artificial substrates. *J. Sea Res.* 88, 78-86. <http://doi.org/10.1016/j.seares.2014.01.007>.
- Sroczyńska, K., Chainho, P., Vieira, S., & Adao, H., 2021. What makes a better indicator? Taxonomic vs functional response of nematodes to estuarine gradient. *Ecol. Indic.* 121, 107113. <http://doi.org/10.1016/j.ecolind.2020.107113>.
- Steel, H., de la Peña, E., Fonderie, P., Willekens, K., Borgonie, G., & Bert, W., 2010. Nematode succession during composting and the potential of the nematode community as an indicator of compost maturity. *Pedobiologia* 53(3), 181-190. <http://doi.org/10.1016/j.pedobi.2009.09.003>.
- Thomas, M.C., & Lana, P.C., 2011. A new look into the small-scale dispersal of free-living marine nematodes. *Zoologia* 28(4), 449-456. <http://doi.org/10.1590/S1984-46702011000400006>.
- Tita, G., Vincx, M., & Desrosiers, G., 1999. Size spectra, body width and morphotypes of intertidal nematodes: an ecological interpretation. *J. Mar. Biol. Assoc. U. K.* 79(6), 1007-1015. <http://doi.org/10.1017/S0025315499001241>.
- Traunspurger, W., 1996. Autecology of *Monhystera paludicola* De Man, 1880-seasonal, bathymetric and vertical distribution of a free-living Nematode in an Oligotrophic Lake. *Int. Rev. Ges. Hydrobiol.* 81(2), 199-211. <http://doi.org/10.1002/iroh.19960810205>.
- Traunspurger, W., 2014. Ecology of Freshwater Nematodes. In: Schimdt-Rhaesa, A., ed. *Handbook of zoology: Gastrotricha, Cycloneuralia and Gnathifera*. Berlin: NHBS Ltd., 153-170, vol. 3.
- Traunspurger, W., Bergtold, M., & Goedkoop, W., 1997. The effects of nematodes on bacterial activity and abundance in a freshwater sediment. *Oecologia* 112(1), 118-122. PMID:28307367. <http://doi.org/10.1007/s004420050291>.
- Traunspurger, W., Wilden, B., & Majdi, N., 2020. An overview of meiofaunal and nematode distribution patterns in lake ecosystems differing in their trophic state. *Hydrobiologia* 847(12), 2665-2679. <http://doi.org/10.1007/s10750-019-04092-1>.
- Vidaković, J., Palijan, G., & Cerba, D., 2011. Relationship between nematode community and biomass and composition of periphyton developing on artificial substrates in floodplain lake. *Pol. J. Ecol.* 59(3), 577-588.
- Vranken, G., Thielemans, L.K., Heip, C., & Vanduycke, M., 1981. Aspects of the life cycle of *Monhystera parelegantula* (Nematoda, Monhysteridae). *Mar. Ecol. Prog. Ser.* 6, 67-72. <http://doi.org/10.3354/meps006067>.
- Walkley, A., & Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter, and proposed modification of the chromic acid titration method. *Soil Sci.* 37(1), 29-38. <http://doi.org/10.1097/00010694-193401000-00003>.
- Warwick, R.M., Platt, H.M., & Somerfield, P.J., 1998. Free-living marine nematodes. Part III. British Monhysterids. Shrewsbury: The Linnean Society of London and The Estuarine and Coastal Science Association, 296 p., Synopses of the British Fauna (New Series).
- Weitere, M., Erken, M., Majdi, N., Arndt, H., Norf, H., Reinshagen, M., Traunspurger, W., Walterscheid, A., & Wey, J.K., 2018. The food web perspective on aquatic biofilms. *Ecol. Monogr.* 88(4), 543-559. <http://doi.org/10.1002/ecm.1315>.
- Wilden, B., Tasevska, O., & Traunspurger, W., 2020. A comparison of benthic meiofaunal communities in the oldest European lake. *J. Great Lakes Res.* 46(5), 1146-1155. <http://doi.org/10.1016/j.jglr.2020.01.018>.
- Williams, D.D., & Hynes, H.B.N., 1976. The recolonization mechanisms of stream benthos. *Oikos* 27(2), 265-272. <http://doi.org/10.2307/3543905>.

- Zeppilli, D., Sarrazin, J., Leduc, D., Arbizu, P.M., Fontaneto, D., Fontanier, C., Gooday, A.J., Kristensen, R.M., Ivanenko, V.N., Sørensen, M.V., Vanreusel, A., Thébault, J., Mea, M., Allio, N., Andro, T., Arvigo, A., Castrec, J., Danielo, M., Foulon, V., Fumeron, R., Hermabessiere, L., Hulot, V., James, T., Langonne-Augen, R., Le Bot, T., Long, M., Mahabror, D., Morel, Q., Pantalos, M., Pouplard, E., Raimondeau, L., Rio-Cabello, A., Seite, S., Traisnel, G., Urvoy, K., Van Der Stegen, T., Weyand, M., & Fernandes, D., 2015. Is the meiofauna a good indicator for climate change and anthropogenic impacts? *Mar. Biodivers.* 45(3), 505-535. <http://doi.org/10.1007/s12526-015-0359-z>.
- Zhou, H., 2001. Effects of leaf litter addition on meiofaunal colonization of azoic sediments in a subtropical mangrove in Hong Kong. *J. Exp. Mar. Biol. Ecol.* 256(1), 99-121. PMID:11137508. [http://doi.org/10.1016/S0022-0981\(00\)00310-5](http://doi.org/10.1016/S0022-0981(00)00310-5).
- Zullini, A., 2010. Identification manual for freshwater Nematode Genera. Italian: Università di Milano Bicocca, 112 p.

Received: 07 July 2023

Accepted: 24 June 2024

**Associate Editor:** Priscilla de Carvalho.