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Rethinking ecotoxicological paradigms: microbial-mediated tolerance and life-history trade-offs of *Folsomia candida* in hydrocarbon-contaminated groundwater

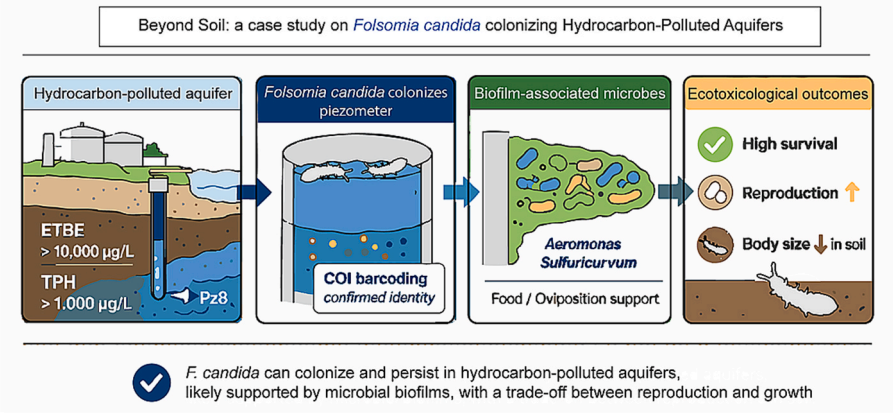
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HIGHLIGHTS

- *Folsomia candida* successfully colonizes hydrocarbon-polluted groundwater aquifers.
- The species shows high tolerance to ETBE concentrations.
- Polluted water significantly increases reproductive output compared to pure water.
- Trade-offs occur between increased reproduction and reduced somatic growth in soil.

GRAPHICAL ABSTRACT



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ABSTRACT

The ecological relevance of soil invertebrates in contaminated groundwater systems remains largely unexplored, particularly under chronic exposure to petroleum-derived compounds. Here, we provide the first evidence of stable colonization and functional persistence of the model collembolan *Folsomia candida* within a hydrocarbon-polluted aquifer in Gaeta (central Italy). Long-term monitoring (2019–2023) revealed persistent groundwater contamination, with ethyl tert-butyl ether (ETBE) > 10,000 µg/L and total petroleum hydrocarbons (TPH) > 1000 µg/L. Despite these extreme conditions, *F. candida* populations were consistently detected on the water surface of quiescent piezometers and taxonomically confirmed via COI DNA barcoding. To disentangle tolerance and potential adaptive responses, we performed ecotoxicological bioassays using three populations (laboratory control, native contaminated population, and a depurated lineage) across aqueous and soil exposure scenarios with site-specific groundwater. Survival remained high (>70%) across all treatments which indicates a limited

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acute toxicity of ETBE-dominated mixtures. In contrast, reproduction was significantly stimulated under contaminated conditions, suggesting a shift from toxic to trophic effects mediated by hydrocarbon-associated microbial communities, including *Aeromonas* and *Sulfuricurvum*, likely providing both nutritional subsidy and oviposition substrates. However, under soil conditions, this enhanced reproductive output was coupled with reduced body length, revealing a contamination-driven life-history trade-off between reproduction and somatic growth. These results demonstrate that organism–microbe–contaminant interactions can modulate ecotoxicological outcomes beyond direct toxicity paradigms, enabling persistence and even functional exploitation of polluted environments. Our findings redefine the ecological boundaries of Collembola and support their use as bioindicators of hydrocarbon contamination pathways across terrestrial and groundwater interfaces, with implications for risk assessment frameworks in subsurface ecosystems.

1. Introduction

Collembola, a diverse and abundant group of soil-dwelling arthropods, plays an essential role in ecosystem functioning. As microbivorous and detritivorous, they are pivotal in nutrient cycling, organic matter decomposition, and the maintenance of soil structure. These organisms exhibit high sensitivity to environmental changes, making them valuable bioindicators of soil health. Over the years, extensive research has documented their responses to various contaminants, particularly pesticides and heavy metals, which often alter their community composition and abundance (e.g. (Chernova and Kuznetsova, 2000; Cole et al., 2001; Rebecchi et al., 2000),). These changes, in turn, can have cascading effects on soil ecosystem processes. Interestingly, while many collembolan species are sensitive to soil contamination, others have demonstrated remarkable tolerance and adaptability. For example, some species can survive in extreme and heavily polluted environments, including soils contaminated with metals and hydrocarbons, potentially exploiting these habitats as ecological niches (Potapov et al., 2020; Remelli et al., 2024). The presence of such tolerant species highlights the potential of soil fauna to play a role in mitigating contamination effects, possibly through interactions with microbial communities that degrade organic pollutants (De Marco et al., 2004). This aspect is particularly relevant in the context of gasoline ether oxygenates, such as ethyl tert-butyl ether (ETBE) and methyl tert-butyl ether (MTBE), which are widely used as fuel additives. These compounds pose significant threats to soil and groundwater quality due to their persistence and high solubility (McGregor, 2007; Nihlen et al., 1998).

In recent years, ether oxygenates such as ETBE have gained prominence in several European markets due to their advantageous properties and compatibility with renewable energy sources (Kulkarni et al., 2018; Stupp, 2007; van der Waals et al., 2019). Compared to MTBE, ETBE offers superior performance as an octane enhancer, improving gasoline combustion efficiency while reducing vehicular emissions (Thornton et al., 2020; Umar et al., 2009). Furthermore, ETBE demonstrates environmental benefits over ethanol, emitting less CO_2 per unit of energy and generating lower greenhouse gas emissions (Croezen and Kampman, 2009). Despite its widespread occurrence and mobility in groundwater (Kulkarni et al., 2018), ETBE remains poorly characterized from an ecotoxicological perspective. Existing frameworks are largely based on chemical thresholds, with a critical lack of data on organism-level responses, particularly for Collembola under groundwater exposure. This limitation may lead to an incomplete assessment of environmental risk, as interactions between contaminants, microbial communities, and soil invertebrates can fundamentally alter toxicity outcomes, shifting from inhibitory to trophic or adaptive responses.

Soil ecotoxicological tests based on invertebrates serve as a crucial step in assessing soil risks by evaluating biota exposure and determining the impact of soil disturbances on ecosystem services (Aqeel et al., 2014). The bioavailability of contaminants is influenced by their physico-chemical properties, environmental conditions, and the test organisms employed in bioassays. To account for varying exposure pathways, it is recommended to utilize both aqueous and soil media in toxicity assessments (Remelli et al., 2022). The soil-dwelling arthropod *Folsomia candida* (Collembola, Isotomidae) is one of the important organisms used in soil toxicity tests and it is able to survive in aqueous exposure systems for several days (Ardestani and van Gestel, 2013). While the toxicity of MTBE on soil invertebrates is scarcely documented (Dodd and Addison, 2010), no equivalent studies exist for ETBE.

Moreover, critical gaps persist in understanding ETBE's biodegradation under conditions that facilitate MTBE degradation, the role of co-contaminants, and the identity of microorganisms responsible for ETBE biodegradation. Although soils likely harbour diverse methylotrophic bacteria capable of metabolizing ether oxygenates (De Marco et al., 2004), research on ETBE degradation in soils is scarce. Some microorganisms isolated from gasoline- and MTBE-contaminated soils can utilize ETBE as their sole carbon and energy source under aerobic conditions. However, the potential interactions between ETBE and soil fauna, such as Collembola, remain unexplored. The ability of Collembola to thrive in harsh environments suggests a potential for adaptation to chemical stressors, and their possible contributions to contaminant degradation through interactions with microbial communities (Remelli et al., 2020, 2022; Wee et al., 2024). It is plausible that Collembola would not only survives but also interacts with microbial communities influencing the fate of ETBE in the environment, so that understanding their interactions with ETBE is a critical area for future research.

The present study aims to test three main hypotheses using piezometer-contaminated groundwater representative of real field conditions: (i) *Folsomia candida* can maintain survival and reproduction under hydrocarbon-contaminated conditions in both aqueous and soil exposure pathways; (ii) exposure to contaminated groundwater induces differential ecotoxicological responses depending on the exposure matrix (aqueous vs. soil), reflecting changes in contaminant bioavailability and interaction with soil processes; and (iii) populations originating from contaminated environments exhibit enhanced tolerance compared to laboratory cultures, suggesting environmentally induced adaptation or acclimation, which may persist across generations.By addressing these questions, the study aims to gain a deeper understanding of the ecological and physiological mechanisms that may allow *F. candida* to survive in contaminated environments, and to evaluate the potential the potential of this species for monitoring and possibly remediating contaminated soils and groundwater. Furthermore, the findings may provide insights into the broader applicability of soil organisms in bioremediation efforts, particularly in relation to persistent contaminants like ETBE.

2. Materials and methods

2.1. Study area

The study area is located in southern Latium (central Italy), precisely near the Tyrrhenian Sea coast, at the northern edge of the village of Gaeta. The research site is an industrial deposit with the function of hydrocarbons storage and distribution.

The study area is located within a carbonate aquifer system of the Central Apennines (central Italy). The site is developed on Cretaceous limestones characterized by fracturing and locally interbedded clayey-silty layers From a hydrogeological perspective, the aquifer exhibits moderate to high permeability, primarily controlled by fracture

networks and karst features. At the regional scale, groundwater flow is directed from the Apennines toward the Tyrrhenian Sea (NE–SW) (Aquino et al., 2015; Celico, 1983; Celico et al., 2000, 2006, 2010; Fiorillo, 2011; Petrella et al., 2009, 2015; Allocca et al., 2014; De Vita et al., 2018; Petrone et al., 2024).

The hydrogeological context of study area can be included in the overmentioned "limestone aquifer" contexts where usually contrast in permeability between the epikarst and the underlying fractured rocks is not enough to allow water storage in a temporary perched aquifer (Petrella et al., 2007). Additionally, local structural settings could play a key role in permeability distribution, with emphasis on the hydraulic compartmentalization of large aquifer systems, due to low permeability faults zones that act as permeability barriers (Celico et al., 2006; Petrella et al., 2009).

At the regional scale, the groundwater usually flows from the Apennine to the Tyrrhenian Sea, from NE to SW (Capelli et al., 2012) (Fig. 1).

The Coastal Depot has been operational since 1970, serving as a refinery and then as site for the distribution, intermediate storage, and pipeline transfer of petroleum products (gasoline, diesel, and aviation fuel such as ATK) to another petroleum depots. Since March 2001, four wells have been used as hydraulic barriers (Table 1).

Table 1
Characteristics of barrier wells and piezometers.

	Drilling depth (m)	Blind section (m b.g.l.)	Screened interval (m b.g.l.)	Pumping rate (l/min)
Pz3	65	0 —11	11–65	
Pz4	70	0–5	5–70	
Pz5	70	0–7	7–70	
Pz6	70	0–21	21–70	
Pz8	70	0–12	12–70	
Pz9	90	0–49	49–90	
W1	85	0–30	30–85	Negligible
W2	80	0–30	30–80	Negligible
W3	80	0–30	30–80	0.7–15.3
W4	76	0–30	30–76	0.1–12.4

2.2. Hydrogeological investigation

Within the present study, the hydraulic head was measured once (in March 2022) in six piezometers (Pz3, Pz4, Pz5, Pz6, Pz8 and Pz9) drilled within the study area (Fig. 2) using a water level meter, in order to reconstruct the groundwater flow net and assess the effect of the hydraulic barrier from the hydraulic point of view.

The study was developed using the available dataset and the groundwater monitoring network existing up to 2023. The piezometers have different drilling depths, ranging from 65 to 90 m, with fully screened intervals extending from a minimum of 5 to a maximum of 90

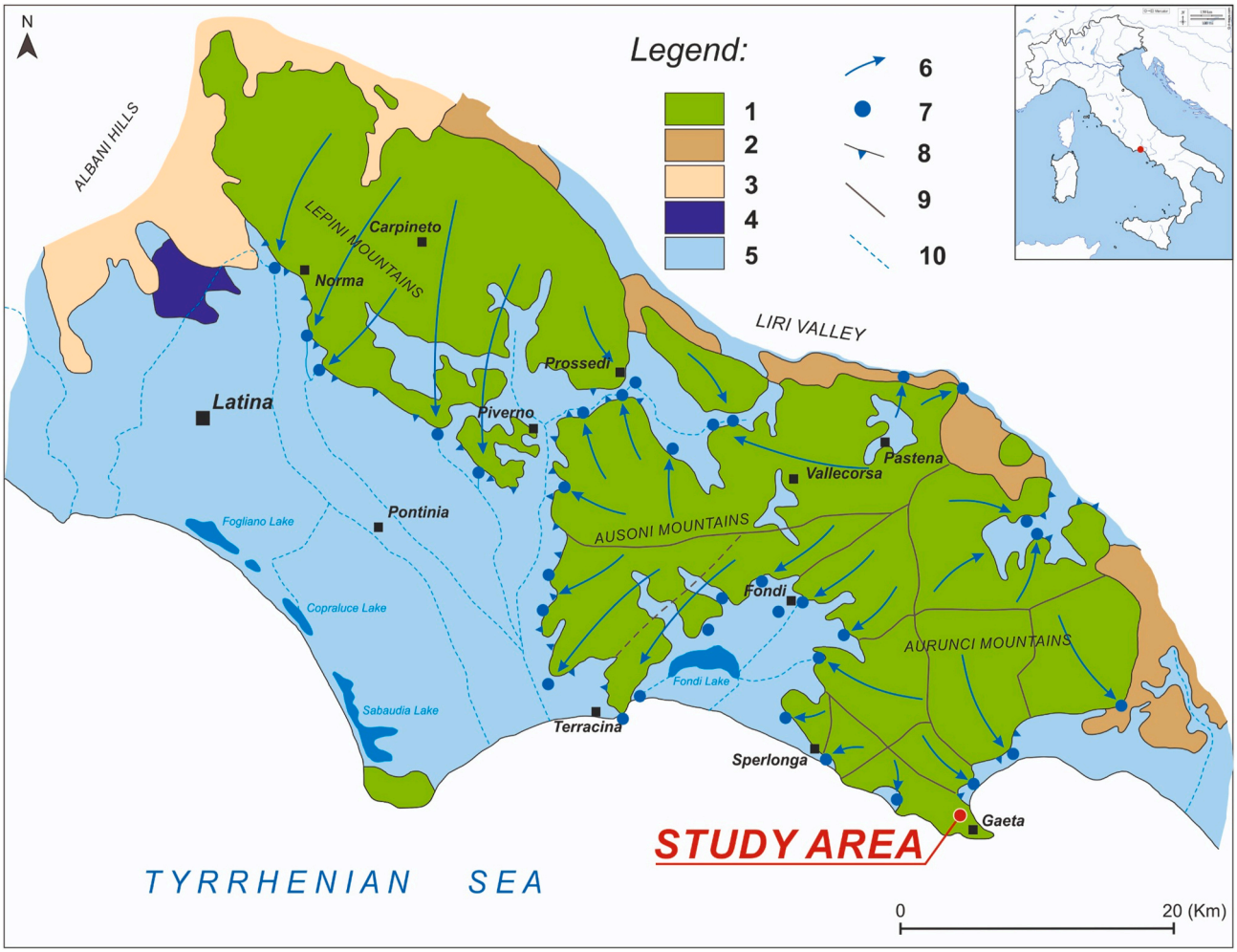


Fig. 1. Hydrogeological setting: 1 - Carbonate aquifer, 2 - Clay, marls and arenites, 3 - Volcanic aquifer, 4 - Travertine aquifer, 5 - Alluvial-detritic aquifer, 6 - Groundwater flow lines, 7 - Main springs, 8 - Limits of the hydraulic interchanges between aquifers (the arrow shows the groundwater flow direction), 9 - Groundwater divide, 10 - Main streams.

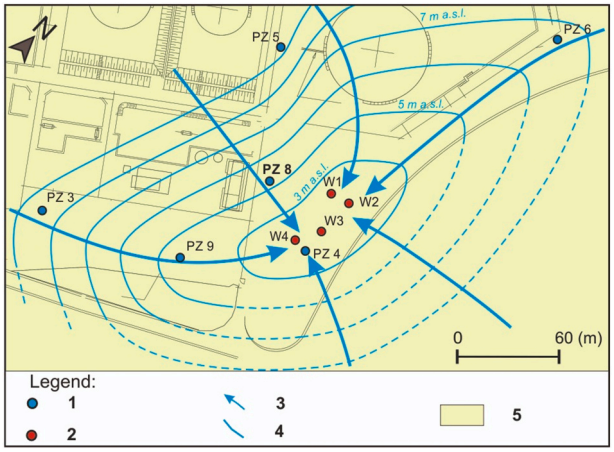


Fig. 2. Groundwater surface contour map of the study site (March 2022): 1 - Piezometer and relative ID, 2 - Well and relative ID, 3 - Groundwater flow line, 4 - Groundwater contour line and relative elevation (m a.s.l.), 5 - Carbonate aquifer.

m below ground. Table 1 summarizes the main characteristics of barrier wells (W1, W2, W3 and W4) and piezometers (Pz3, Pz4, Pz5, Pz6, Pz8, Pz9).

2.3. Chemical analysis of groundwater samples

Groundwater chemical data collected during the 2019–2023 monitoring period (see Table S1 for the exact months of collection) were analyzed to assess the occurrence of Total Petroleum Hydrocarbons (TPH), MTBE and ETBE in Pz3, Pz4, Pz5, Pz6, Pz8, Pz9, W3, and W4. No water samples were collected from wells W1 and W2 due to the presence of Light Non-Aqueous Phase Aqueous s (LNAPLs) in the wells.

2.4. Microbial community characterization

To characterize the microbial communities using Next Generation Sequencing (NGS) technique, a sampling campaign was conducted in March 2022. One liter of water was collected from each monitoring point using sterile PP bottles. The samples were stored and transported in refrigerated containers to the laboratories of the University of Parma within 24 h. The samples were filtered through sterile mixed esters of cellulose filters (S-Pak™ Membrane Filters, 47 mm diameter, 0.22 μm pore size, Millipore Corporation, Billerica, MA, USA). NGS analyses were carried out at the Genprobio S.r.l. Laboratory (Parma, Italy), following the protocol reported by Rizzo et al. (2023).

2.5. DNA barcoding for species identification

In the piezometers Pz8, a colony of Collembola was repeatedly found living on the water surface. In March 2022, approximately one thousand individuals were collected and taken to the Parma laboratory. DNA Barcoding for species identification was conducted on both the Pz8-native specimens and the laboratory cultures (to guarantee their belonging to *F. candida* species). High molecular weight genomic DNA of 6 (3 for native specimens and 3 for laboratory ones) samples were extracted and purified by Wizard genomic DNA Purification kit (Promega, Madison, WI, USA). DNA quality was visually inspected by 1% agarose gel electrophoresis in TAE buffer and by spectrophotometry at 260–280 nm. The extraction procedure yielded not less than 15 ng/ul of HMW (high molecular weight) DNA. Cytochrome C Oxidase 1 (*COI*) gene fragment was amplified using universal primers suggested by (Folmer et al., 1994) LCO1490 5′-GGTCAACAAATCATAAAGATATTGG-3′ and HCO2198 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′. A 25 μL reaction mixture contained 1 U of GoTaq DNA polymerase (Promega, Madison, WI, USA), 1× reaction buffer, 0.2 mM dNTPs, and 10 pmol of each primer was used. The PCR profile was set as follows: 35 cycles of 45s at 95°C, 45s at 48°C, and 45 s at 72°C, after an initial 5 min denaturation step at 95°C and a final extension at 72°C for 10 min.

Amplicons were separated by 2.5% agarose gel electrophoresis and purified using the Qiagen MinElute PCR Purification Kit (QIAGEN, Venlo, The Netherlands). The quality of the purified sample (1 μl) was visualized in 1.5% agarose gel that yielded clear bands. DNA quantity was evaluated using the Qubit dsDNA HS (High Sensitivity) Assay Kit (Invitrogen, Waltham, MA, USA) with a Qubit 3.0 Fluorometer (Life Technologies, Waltham, MA, USA). Forward and Reverse fragments sequencing was performed by Macrogen Europe Lab (Amsterdam, the Netherlands). The obtained sequences were manually corrected using MEGA7 (Kumar et al., 2018) and compared with those available in the NCBI genomic databases (National Institutes of Health, Bethesda, MD, USA) using the BLAST service (National Institutes of Health, Bethesda, MD, USA). Species-level identification was assigned when sequence identity exceeded 98% (Pardo et al., 2018). Identity >98% confirmed *F. candida*.

2.6. *Folsomia candida* laboratory breeding and ecotoxicological tests

Specimens of *Folsomia candida* were obtained from the laboratory cultures at the University of Parma ("Control") and from PZ8. Laboratory cultures have been maintained for at least 20 years under controlled conditions (20 ± 2°C, 50–55% relative humidity, 16:8 h light–dark cycle) and fed weekly with dry yeast. Specimens from PZ8 were divided into two breeding colonies: one reared with PZ8 water, and the other with deionised water (Table 2). All cultures were maintained under these conditions for one year before use in ecotoxicological tests.

Ecotoxicological tests were conducted using water from PZ8, identified as the most contaminated piezometer. Two experimental matrices were tested: soil and aqueous media. For soil tests, Petri dishes were filled with 10 g of ISO 11267 standard soil (ISO 11267:1999, 1999) and moistened to 40–60% water-holding capacity (WHC) with either PZ8 water (Treated) or deionised water (Control). For aqueous media tests, Petri dishes were lined with filter paper soaked with 2 mL of either PZ8 water (Treated) or deionised water (Control). All tests were performed at 20°C under a 16:8 h light–dark cycle.

Ten-day-old juveniles, age-synchronized by removing eggs from deposition cultures, were used. Synchronization was conducted in Petri dishes containing a breeding substrate composed of plaster of Paris and activated carbon powder (8:1 w/w), moistened as appropriate. Survival and reproduction tests followed ISO 11267:1999, adapted to the miniaturized reproduction assay described by Filser et al. (2014). Four adults were introduced per replicate, with five replicates per treatment. The experimental treatments were coded as reported in Table 2.

Egg hatching tests followed the same design, with five eggs added to each Petri dish at the start using a fine brush (Filser et al., 2014; Filser et al., 2014).

During the experiments, springtails were fed weekly with dry yeast, aerated as needed, and watered whenever moisture loss exceeded 2% of the initial WHC. Petri dishes were incubated for 28 days. At the end of the test, adults, juveniles, and hatched eggs were euthanized by freezing. A flotation technique was used for counting, with gentle stirring and the addition of ~0.5 mL black ink to improve contrast. Digital photographs

Table 2
Four treatments used in tests with both soil and elutriate. Reference code: uppercase letters indicate test water, lowercase letters indicate rearing water.

Code	Test water	Origin of Collembola	Rearing water
DCOd	deionised	Control (lab)	deionised
CCOd	Contaminated (PZ8)	Control (lab)	deionised
CPZc	Contaminated (PZ8)	PZ8	contaminated (PZ8)
CPZd	Contaminated (PZ8)	PZ8	deionised

were captured, and surviving adults, juveniles, and hatched individuals were counted.

Body length measurements were performed only on individuals that successfully hatched and survived until the end of the test, using ImageJ software (version 1.53). This ensured that growth measurements reflected the effects of the treatments on viable, developed springtails.

2.7. Statistical analysis

For ecotoxicological tests, data obtained for each endpoint evaluated did not meet the ANOVA assumptions, and the Kruskal–Wallis test was performed for multiple comparisons, followed by Mann-Whitney tests for pairwise comparisons between each independent treatment.

A p-value ≤ 0.05 was considered significant. All analyses were performed using R (v.4.4.0 alpha) (R Core Team2025 R Core Team, 2025).

3. Results

3.1. Hydrogeological investigation

The hydraulic head is located several ten of meters below the ground surface, and the groundwater flow net clearly shows a large well-capture area around the hydraulic barrier and then its efficacy in capturing the contaminated groundwater (Fig. 2).

3.2. Groundwater chemical compounds

Chemical analyses showed different concentration trends of TPH, MTBE and ETBE in the piezometers (Pz3, Pz4, Pz5, Pz6, Pz8, and Pz9) and in the barrier wells (W3 and W4).

During the monitoring period (2019-2023), different exceedances of The Contamination Threshold Concentrations (CSC) were observed. The CSC value is established by Decreto Legislativo 152/2006 and its subsequent amendments and defines the regulatory limit, above which potential environmental contamination is identified. The threshold proposed for TPH is reported in Decreto Legislativo 152/2006 – Allegato 5 - Parte IV - Tabella 2 and is set at 350 μg/l, while for MTBE and ETBE, the limit is set at 40 μg/L by the ISS (in Italian: Istituto superiore di Sanità) with Parere del 12/09/2006 n. 45848. In particular, Table S1 in Supplemental materials report the mean, maximum and minimum concentrations of TPH, MTBE and ETBE detected in the piezometers (Pz3, Pz4, Pz5, Pz6, Pz8, and Pz9) and in the barrier wells (W3 and W4) for each monitoring year. The trend of TPH (μg/L), MTBE (μg/L) and ETBE (μg/L) concentrations, measured at the monitoring points W4, W3, Pz9, Pz8, Pz6, Pz5, Pz4, Pz3, during the 2019-2023 monitoring period, is shown respectively in Figs. 3–5.

TPH concentrations (Fig. 3) show values ranged between several tens and over 10^3 μg/L, which highlights high spatial heterogeneity and a significant temporal variability at the same monitoring point. Within the dataset, points Pz8, W3 and W4 show the highest values, with concentrations on the order of hundreds of μg/L, with some values exceeding 10^3 μg/L. The other monitoring points (Pz3, Pz9, Pz6, Pz5 and Pz4) instead show generally lower concentrations, predominantly between approximately 30 and 200 μg/L, characterized by fluctuations among the different sampling campaigns alternating with frequent non-detections.

Marked spatial and temporal variability in MTBE concentrations are reported in Fig. 4. The most significant MTBE concentrations are predominantly observed at points W3, W4 and Pz8, where concentrations range from several tens of μg/L to maxima reaching hundreds of μg/L. At the other monitoring points (Pz3, Pz4, Pz5 and Pz6), MTBE is generally detected at low levels, often with concentrations below 5 μg/L and many monitoring campaigns reporting concentrations below the limit of quantification (LOQ).

Results show high spatial and temporal variability of ETBE values (Fig. 5), with concentrations ranging from a few units up to several tens of thousands of μg/L. While both W3 and Pz8 showed elevated concentrations, Pz8 was consistently characterized by persistent ETBE levels in the order of several thousand μg/L, with repeated peaks exceeding 10,000 μg/L across multiple sampling campaigns. Point W4 also shows high concentrations in some campaigns, although with greater temporal discontinuity compared to W3 and Pz8. The other monitoring points (Pz3, Pz4, Pz5, Pz6 and Pz9) instead show generally low concentrations, often close to detection limits, or absent.

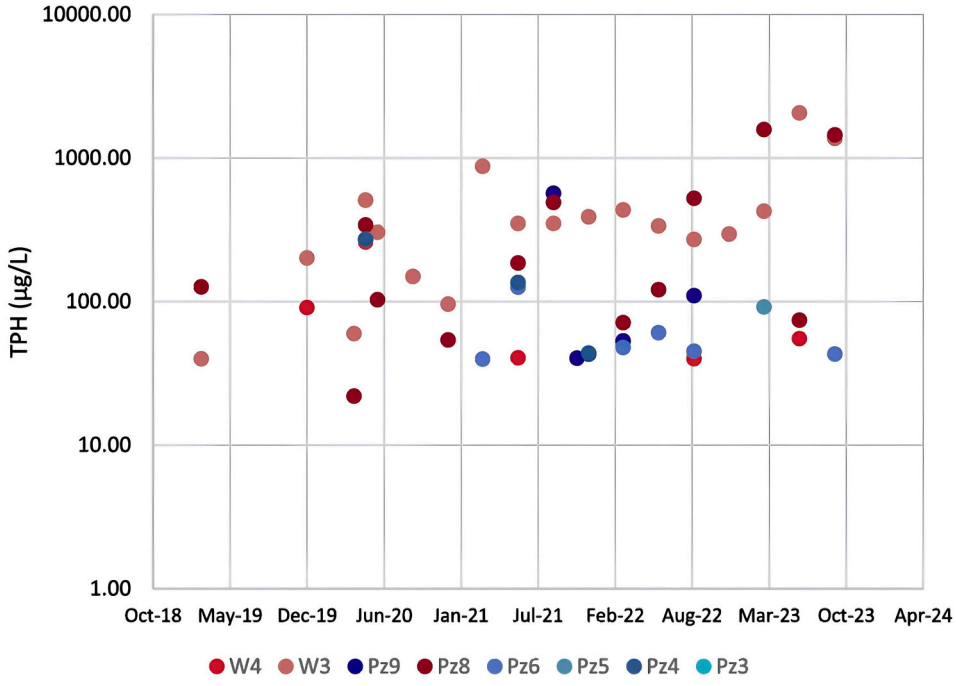


Fig. 3. Temporal variations of TPH concentrations at the monitoring points W4, W3, Pz9, Pz8, Pz6, Pz5, Pz4, Pz3, during the 2019-2023 monitoring period. The data are presented on a logarithmic scale, in order to effectively visualize the wide range of observed concentrations.

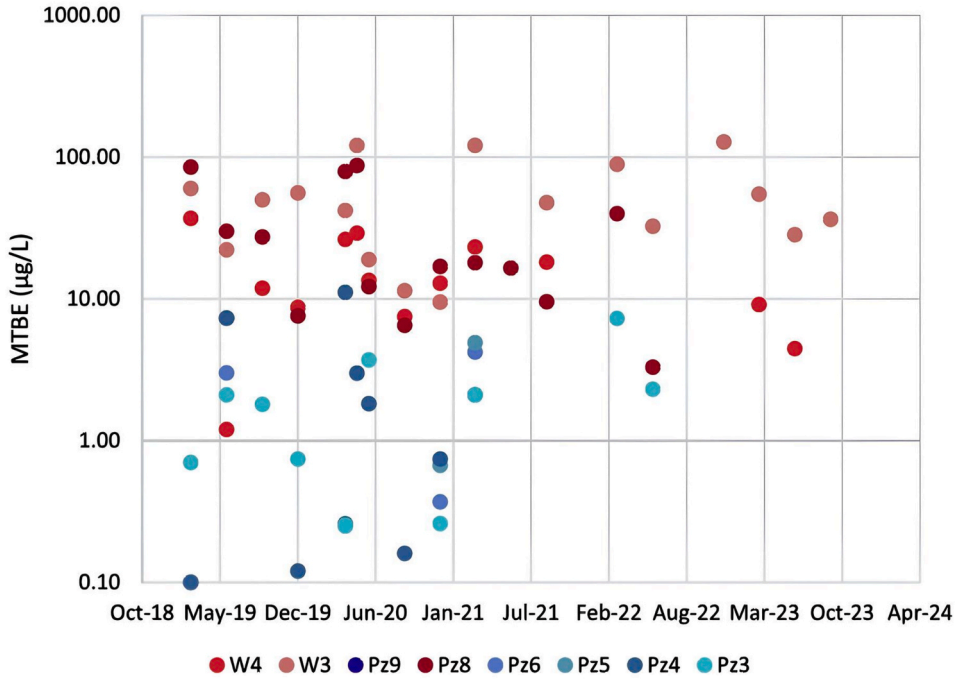


Fig. 4. Temporal variations of MTBE concentrations at the monitoring points W4, W3, Pz9, Pz8, Pz6, Pz5, Pz4, Pz3, during the 2019-2023 monitoring period. The data are presented on a logarithmic scale, in order to effectively visualize the wide range of observed concentrations.

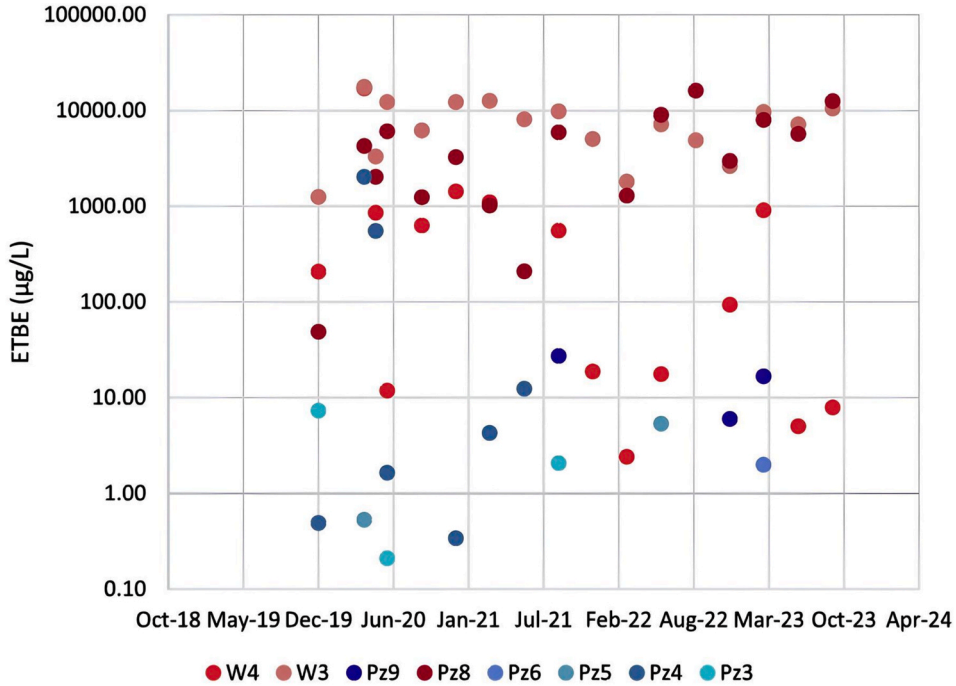


Fig. 5. Temporal variations of ETBE concentrations at the monitoring points W4, W3, Pz9, Pz8, Pz6, Pz5, Pz4, Pz3, during the 2019-2023 monitoring period. The data are presented on a logarithmic scale, in order to effectively visualize the wide range of observed concentrations.

3.3. Microbial community characterization

The 16S rRNA gene sequences generated in this study have been deposited in the NCBI sequence read archive (SRA) under the accession number PRJNA1371911. The results of the NGS analyses show a heterogeneous microbial community with spatial and temporal variations within the site. A generally predominantly aerobic, mesophilic community is present, with the presence of numerous bacterial genera often found in groundwater, such as *Pseudomonas*, *Hydrogenophaga*, and *Sulfuricurvum*. Some genera associated with sulfate oxidation metabolic processes are noted throughout the site, particularly in samples collected in March; their abundance decreases in April. The genera attributable to this group are *Sulfuricurvum* and *Sulfuricella*, which represent almost all of the genera expressed and are also the most prevalent in some samples, with relative abundances ranging between 48% and 76% (PZ5, PZ6, PZ8) for *Sulfuricurvum*.

From the analysis of bacterial genera, the presence of contaminants such as TPH, MTBE, and ETBE does not appear to have influenced the microbial community.

The microbial community in Pz8 exhibited a clear temporal shift, with *Sulfuricurvum* dominating in March (49%) and *Aeromonas* becoming the most abundant genus in April (30%), while *Sulfuricurvum* decreased to 22%(Table S1).

3.4. Molecular identification of Folsomia candida

In the PZ8 piezometer, a colony of Collembola was consistently observed on the water surface. Approximately one thousand individuals were collected in March 2022 and transferred to the laboratory at Parma. To confirm species identity, DNA barcoding of both PZ8-native specimens and laboratory-cultured individuals was performed. High-molecular-weight genomic DNA was extracted and purified, and a fragment of the mitochondrial Cytochrome C Oxidase I (COI) gene was amplified using the universal primers LCO1490 and HCO2198 (Folmer et al., 1994). Sequencing of the purified PCR products and comparison with sequences in the NCBI database (BLAST) confirmed that all specimens, both native and cultured, belonged to the species *Folsomia candida* (sequence identity >98%).

3.5. Ecotoxicological tests: survival and reproduction

The survival and reproduction of *F. candida* under different treatments and matrices are summarized in Fig. 6a and b.

In the aqueous matrix, survival rates were generally high across treatments, with no mortality observed in the DCOd. The survival rate in the CCOd and CPZd treatments remained consistent and like the control, while a significant reduction in survival was recorded for CPZc (Fig. 6a). Reproduction differed significantly among treatments ($p < 0.05$). DCOd no reproduction, while CPZd produced the highest number of juveniles. Juvenile numbers in CCOd and CPZc were significantly lower than in CPZd but higher than in DCOd (Fig. 6b).

In the soil matrix, survival was consistently high across treatments, with the DCOd control group meeting the ISO 11267:1999 validity requirements. However, significant differences were observed in juvenile production (Fig. 6a). Juvenile numbers were the lowest in DCOd, while all Pz8 treatments yielded significantly higher reproduction (Fig. 6b). The highest juvenile production was observed in CPZc, followed closely by CCOd and CPZd.

3.6. Ecotoxicological tests: eggs hatching and growth

In the aqueous matrix, the hatching/survival rates were not significantly different between the treatments (Fig. 7a); with the CPZc treatment exhibiting a higher hatching rate compared to CPZd.

The body length in the aqueous matrix varied minimally across treatments (Fig. 7b).

In the soil matrix, significant differences in body length, but not in hatching/survival rates, were observed among treatments (Fig. 7a and b). The highest hatching/survival rate was found in the CPZd, followed by the DCOd (Fig. 7a) and CPZc. The lowest hatching rate was found in the CCOd. Body length varied significantly, with DCOd showing the longest body dimension, followed by CPZc, CPZd, and CCOd. Post-hoc comparisons indicated that the body length in the soil matrix was significantly lower in the CPZd and CCOd compared to DCOd (Fig. 7b).

4. Discussion

Collembola are widely used as bioindicators due to their sensitivity to environmental stressors, although species-specific responses to contamination range from decline to tolerance or even dominance in polluted soils (Fiera, 2009; Liu et al., 2018; Migliorini et al., 2004). While primarily terrestrial, some species exhibit notable ecological plasticity and dispersal ability, including passive transport via water (Ponge, 2013; Santorufo et al., 2021; Schuppenhauer et al., 2019a; Sterzyńska et al., 2018). In this context, the occurrence of *F. candida* in a hydrocarbon-contaminated piezometer represents a remarkable case of colonization of groundwater-associated habitats, suggesting both tolerance to extreme conditions and the capacity to exploit unconventional ecological niches.

Another issue is how those *F. candida* colonies survive in the piezometer. Collembola are not fully adapted to life in water, but their hydrophobic cuticle and lipid secretions allow them to float and survive on water surfaces (Noble-Nesbitt, 1963). Morphological modifications, such as elongated claws, further facilitate locomotion in humid or aquatic habitats (Schuppenhauer et al., 2019b). The presence of biofilm-forming bacterial, such as *Aeromonas* (Kappachery et al., 2010), likely represents a key ecological driver of *F. candida* persistence in the piezometer. Although a direct trophic link cannot be experimentally confirmed in this study, the occurrence of stable colonies exclusively in Pz8—where microbial biofilm development was observed—suggests a functional association. In contrast, no comparable colonization was detected in other piezometers lacking visible biofilm structures. Microbial biofilms likely provide both a trophic resource and a suitable

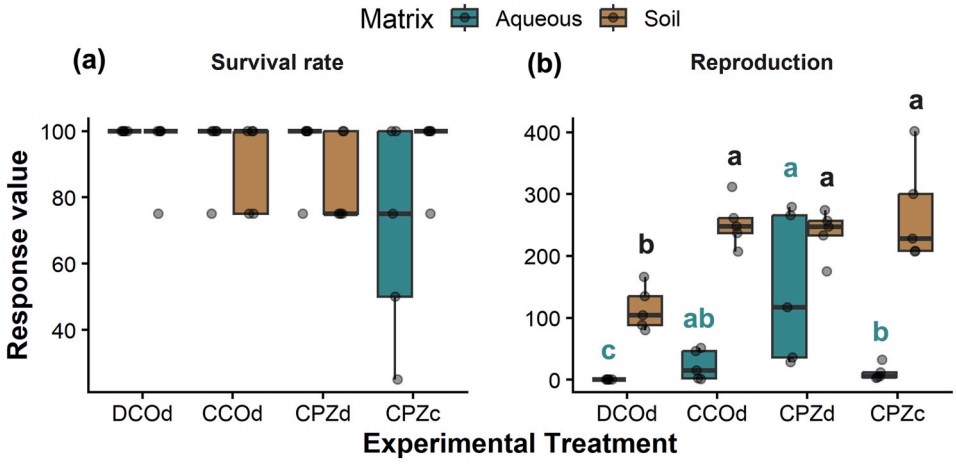


Fig. 6. Fitness parameters and reproductive output of *F. candida* lineages across aqueous and soil matrices. **(a)** Survival rate (%) represents the adult survivorship over the experimental period. **(b)** Reproduction is expressed as the total number of juveniles (offspring) produced per replicate. Boxplots represent the median and IQR; jittered points represent individual replicates (n = 5). Different letters with the same colour mean statistical significance ($p < 0.05$).

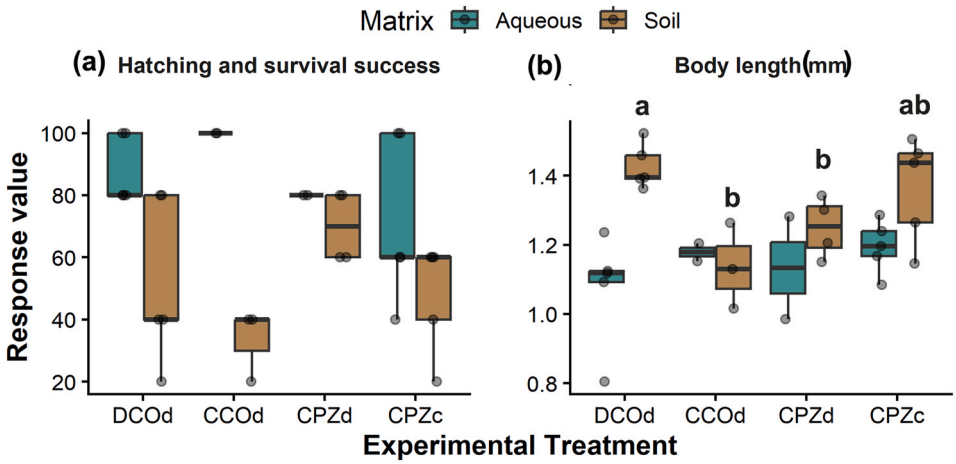


Fig. 7. Ecotoxicological response of *F. candida* exposed to hydrocarbon-polluted groundwater in different experimental matrices. **(a)** Hatching and survival success (%) represents the percentage of individuals successfully completing embryonic development and surviving until the end of the 28-day bioassay. **(b)** Body length mm indicates the somatic growth reached by individuals at the end of the test. Boxplots represent the median (horizontal line) and interquartile range (IQR), while points represent individual replicates (n = 5). Different letters with the same colour mean statistical significance ($p < 0.05$).

oviposition substrate, creating a functional interface between the aquatic environment and the terrestrial ecological requirements of the species. In addition to the bacterial genera detected by 16S rRNA sequencing, unmeasured fungal components of the biofilm may have further contributed to food quality, particularly through sterol-rich biomass that could support reproduction.

In this context, hydrocarbon-associated microbial communities may simultaneously mediate resource availability and habitat structure, supporting feeding, reproduction, and spatial anchoring of *F. candida*. However, this relationship remains correlative and requires targeted experimental validation to disentangle trophic versus structural effects of microbial communities. Although microbial characterization in this study targeted bacterial communities through 16S rRNA gene sequencing, unmeasured fungal components of the biofilm may also have contributed to food quality for *F. candida*. This species is primarily microbivorous and fungivorous, and fungal or yeast-like biomass may supply dietary sterols relevant to Collembola nutrition (LeFait et al., 2019; Menta et al., 2019). Previous work showed that *F. candida* can assimilate and convert yeast-derived ergosterol into cholesterol, supporting the potential nutritional relevance of sterol-containing microbial resources (Chamberlain et al., 2004). Therefore, the enhanced reproduction observed under contaminated conditions may also involve uncharacterized fungal or other microbial components. This interpretation remains hypothetical, as fungi were not directly assessed, and should be verified in future studies using fungal metabarcoding, ergosterol quantification, or controlled feeding assays.Physiological plasticity further supports their persistence. *F. candida*, in particular, is known to survive under hypoxic or even anoxic conditions by shifting its metabolism and increasing lactate production, while also adjusting heart rate to maintain oxygen gradients between tissues and the medium (Marx et al., 2012). These adaptations allow this species to tolerate extremely low oxygen pressures, a trait that is consistent with its presence in the hydrocarbon-polluted piezometer water. In such an environment, where contamination and reduced oxygen availability co-occur, survival requires both physiological adjustments and ecological resilience. Furthermore, the specific occurrence of *F. candida* in Pz8, as opposed to other monitored sites, suggests a synergistic effect between hydrochemical conditions and structural-management factors. From a hydrochemical perspective, the water sampled in Pz8 is largely indistinguishable from that of wells W3 and W4. However, a significant divergence exists in their operational regimes; while Pz8 is utilized exclusively for episodic measurements and sampling, W3 and W4 are active pumping wells. These active sites are characterized by frequent physical turbulence and are subject to both routine and extraordinary maintenance of the pumping apparatus. Such anthropogenic disturbances and mechanical fluctuations likely preclude the establishment of stable colonies, whereas the relatively quiescent environment of Pz8 provides the necessary structural stability for *F. candida* to exploit the available niches. This evidence, together with *F. candida*'s potential to move on the piezometer walls (probably also for egg deposition) and the presence of food from the bacterial community, reinforces that its presence is not incidental.

Ecotoxicological results further highlight the importance of organism–microbe–contaminant interactions. Survival remained high across treatments, confirming the limited acute toxicity of ETBE-dominated mixtures, consistent with previous findings for MTBE (Dodd and Addison, 2010). In contrast, reproduction emerged as the most responsive endpoint and was consistently stimulated under contaminated conditions. This effect is likely driven by microbial communities associated with hydrocarbons, which provide both nutritional subsidies and oviposition substrates, particularly in aqueous conditions where suitable surfaces are otherwise limited. Despite enhanced reproductive output, hatching success did not significantly differ among treatments, and the lowest hatching rates were observed in the same conditions that maximized reproduction. This pattern suggests a trade-off between offspring quantity and quality, where increased reproductive investment occurs at the expense of egg viability.

This trade-off became more evident in the soil matrix, where individuals exposed to contaminated conditions showed reduced body length despite increased reproduction. This pattern indicates a shift in energy allocation under contaminant stress, where resources are preferentially invested in reproduction rather than somatic growth (Lee et al., 2019; Zhang and Qiao, 2020). Such reallocation likely reflects an adaptive strategy in resource-rich but stressful environments, where microbial-derived energy inputs promote reproduction, while physiological costs associated with contaminant exposure constrain growth. Similar hormetic and trophic effects have been reported in organic waste systems, where contaminants simultaneously act as stressors and nutritional subsidies (Domene et al., 2007).

5. Conclusion

Overall, this study demonstrates that *F. candida* can colonize and persist in highly hydrocarbon-contaminated groundwater, revealing an unexpected ecological plasticity in a typically terrestrial taxon. Under ETBE-dominated conditions, reproduction was consistently stimulated,

likely mediated by hydrocarbon-associated microbial communities providing both trophic support and oviposition substrates. However, this positive reproductive response was coupled with reduced body length in soil, indicating a trade-off between reproduction and somatic growth driven by energy reallocation under contaminant stress.

These findings challenge conventional ecotoxicological paradigms based solely on direct toxicity, highlighting the importance of organism–microbe–contaminant interactions in shaping biological responses. In this context, Collembola should be reconsidered not only as indicators of soil quality but also as sensitive bioindicators of contamination pathways across soil–groundwater interfaces.

CRediT authorship contribution statement

Sara Remelli: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Laura Ducci:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Laura Filonzi:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation. **Riccardo Pinardi:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Pietro Rizzo:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Fulvio Celico:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization. **Emanuele Scanferla:** Writing – review & editing, Validation, Supervision, Resources, Methodology. **Marcello Pianu:** Writing – review & editing, Validation, Supervision, Resources, Methodology. **Cristina Menta:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.chemosphere.2026.145072.

Data availability

Data will be made available on request.

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