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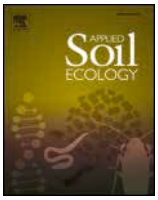

Short communication

# Conservation agriculture buffers the impact of irrigation on soil nematodes: a case study in Southern France

Charlotte Biryol [a,*], Claire Wittling [b], Juan David Dominguez-Bohorquez [b], Sidy Diakhate [c], Stephan Hättenschwiler [d], Grégoire T. Freschet [e], Jean Trap [a,*]

[a] *Eco&Sols, Univ Montpellier, IRD, INRAe, CIRAD, Institut Agro, Montpellier, France*
[b] *G-EAU, Univ Montpellier, INRAE, AgroParisTech, BRGM, CIRAD, Institute Agro, IRD, Montpellier, France*
[c] *Sine-Saloum El-hadj Ibrahima NIASS University (USSEIN), Kaolack, Senegal, UFR (Research Training Unit), Environmental and Social Sciences, Department of Environment Biodiversity and Sustainable Development, Senegal*
[d] *CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France*
[e] *Theoretical and Experimental Ecology Station, CNRS, Moulis, France*

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ABSTRACT

Understanding how crop management influence soil biodiversity is crucial for maintaining soil functions and long-term ecosystem health. Nematodes are key bioindicators of soil quality due to their sensitivity to both soil management and water availability. In Mediterranean regions, where drought events are becoming more frequent and intense under climate change, it is essential to identity practices that can buffer their effects. Here, we assessed the combined effect of crop management and irrigation on soil nematode communities in maize crops in southern France. The experiment compared four treatments: conservation agriculture (CA) *vs.* conventional tillage (CT), each under irrigated and non-irrigated conditions. Soil samples were collected in March 2022 (0–10 cm depth), and soil nematodes were extracted, counted and identified with subsequent calculation of community and functional indices. Total nematode density was 70% higher under CA compared to CT. Irrigation increased total nematode density (+30%) under CA plots, whereas it had a negative effect under CT plots. Under no-irrigation, CA maintained high predator densities and reduced plant-parasitic nematodes compared to CT. Consistently, irrigation under CT favored opportunistic and plant parasite taxa. Overall, our exploratory insights underlined that CA supports a more stable and complex soil food-web, helping to mitigate the disturbing effects of irrigation on soil nematode communities. These findings highlight CA as a promising strategy to enhance soil resilience to drought in Mediterranean agroecosystems. Larger sample sizes and repeated seasonal sampling would be needed to confirm and generalize these patterns.

## 1. Introduction

Agricultural systems are facing major challenges, including the need to increase food production in line with population growth while ensuring the long-term sustainability of cropping practices (Wezel et al., 2014). Rising global temperatures, altered precipitation patterns, and more frequent extreme climatic events are projected to negatively affect crop productivity (Mbow et al., 2019; Farooq et al., 2023). At the same time, the intensification of agricultural practices has accelerated soil degradation through erosion, salinization, acidification, contamination or compaction (Chowdhury et al., 2008; Kremen and Miles, 2012; Mukhopadhyay et al., 2021; Beaumelle et al., 2023; Al-Shammary et al., 2024). In this context, maintaining soil health is critical for sustaining essential ecosystem services such as primary production, nutrient cycling, biodiversity conservation, carbon sequestration, and pest control (Kopittke et al., 2019).

Conservation agriculture (CA) is a set of management principles based on minimal soil disturbance, permanent soil cover and crop diversification which can be implemented across a wide range of cropping systems (Giller et al., 2015; Corsi and Muminjanov, 2019). Cover crops contribute to soil protection, organic matter inputs, and resource continuity for soil biota during intercropping periods (Daryanto et al., 2018; Kim et al., 2020). CA-based management not only improves soil fertility but also enhances water retention and conservation, making CA

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* Corresponding authors.
*E-mail addresses:* charlotte.biryol@outlook.fr (C. Biryol), jean.trap@ird.fr (J. Trap).

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a valuable crop management for coping with water stress (Palm et al., 2014; Pisante et al., 2015; Choudhary et al., 2016). In the Mediterranean region, which suffers from frequent droughts and therefore requires effective water management to sustain agricultural productivity, CA emerges as a promising system (Chartzoulakis and Bertaki, 2015). Moreover, practices such as irrigation can complement CA to further strengthen resilience to climate-induced water stress (Mastrorilli and Zucaro, 2016).

Given their role in the functioning of terrestrial ecosystems (Ferris, 2010), soil nematodes can be used as a biological indicator of soil health (Lu et al., 2020). These ubiquitous and highly abundant organisms exhibit various feeding strategies (Yeates et al., 1993). Microbivorous nematodes play a key role in nutrient cycling by stimulating microbial communities and nutrient mineralization, thereby indirectly supporting plant growth (Ingham et al., 1985; Wilschut and Geisen, 2021; Trap et al., 2025). Omnivore and predator nematodes further contribute to soil functioning by regulating lower trophic levels, including herbivore nematodes, and by enhancing the stability and complexity of soil food-webs (de Vries and Wallenstein, 2017; Topalović and Geisen, 2023). In contrast plant-parasitic nematodes (PPN) are among the most widespread pests and can cause crop production losses (Nicol et al., 2011). Different cropping management can modify the diversity and density of soil nematodes (Puissant et al., 2021). Moreover, nematodes are soil-dwelling worms whose movement, feeding activity and survival rely on water films surrounding soil particles (Young and Robertson, 1998; Yeates et al., 2002; Zheng et al., 2023). Their strong dependence on soil moisture makes them particularly sensitive to water availability and drought conditions (de Vries et al., 2012). In this context, crop management and irrigation emerge as two key drivers shaping soil nematode communities. By creating favorable conditions for the establishment and proliferation of opportunists and PPN, irrigation could lead to imbalances in nematode communities, ultimately affecting soil functioning and crop health (Siebert et al., 2020). While the effect of conservation agriculture and irrigation have been studied separately, their combined influence on nematode trophic balance and soil food-web structure remains poorly understood, particularly under Mediterranean conditions characterized by recurrent drought. Here, we addressed this gap by considering nematode trophic groups and functional indices to assess soil biological resilience to irrigation-driven disturbances. We therefore hypothesize that CA, by maintaining a higher taxonomic and functional diversity of the nematode community, including omnivores and predators feeding on herbivores, may buffer potential imbalances in nematode trophic groups induced by irrigation.

## 2. Materials and methods

The study site is located at the “PRESTI” INRAE experimental platform (“Plateforme de Recherche et experimentation en Sciences et Technologies d'Irrigation; PRESTI, 2025), in southern France, Montpellier (43.647°N, 3.871°E). The annual temperature during the cropping season of the soil sampling year (2022) fluctuated between 17 °C and 30 °C, while the annual precipitation was 115 mm. The soil is a Fluvisol of colluvio-alluvial origin, with a texture comprising 43% silt, 36% sand and 21% clay. Experimental plots were established in autumn 2020 on a 1.5 ha field to study the effect of conversion from traditional homogeneous tillage to conservation agriculture. The plot size ranged from 1000 to 4200 $m^2$. Maize (*Zea mays* L.) was sown under conventional tillage (CT) or conservation agriculture (CA). In the CA fields, maize was planted by direct seeding after the destruction of the winter cover crops (*Vicia faba* L.) using a FACA roller. After the crop harvest, CT plots were ploughed with a rotary harrow and the soil was left bare in winter, while a winter cover crop (a mixture of *Vicia sativa* L., *Phacelia tanacetifolia* Benth. and *Sinapis alba* L.) was implemented in CA (see Dominguez-Bohorquez et al., 2025 for details). Different water management methods were applied to the crops in 2021: no irrigation (rainfed) or sprinkler irrigation (Dominguez-Bohorquez et al., 2025), leading to an additive water input of 210 mm in the CA and 240 mm in CT. These variations in total water input were induced by wind drift losses. In 2022, corresponding to the soil sampling year, no irrigation was performed (Dominguez-Bohorquez et al., 2025). Thus, there were four experimental plots, each with a different treatment condition: CA non-irrigated, CA irrigated, CT non-irrigated and CT irrigated.

Three subplots were established within each treatment condition, spaced approximately 50 m apart. In each sub-plot, three sampling points of an area of 1 $m^2$ were determined with a distance between points of approximately 3 m. At each sampling point, four cylindrical soil cores (5.3 cm in diameter and 10 cm deep) were taken at each corner of 25 cm central square using a stainless-steel auger (SDEC, France) in March 2022. The four soil cores were mixed together, resulting in one composite soil sample per sampling point. This hierarchical sampling resulted in a total of nine replicates per plot, with three replicates nested in each sub-plot and three sub-plots nested per plot. A total of 36 samples were gathered: 2 crop managements × 2 irrigation levels × 9 nested replicates.

Soil samples were then brought back to the laboratory for nematode extraction within 24 h. Nematodes were extracted using the Oostenbrink direct cottonwood filter method (Townshend, 1963) using a 16 cm diameter and 2 cm deep PVC “Petri dish”-Baermann device from 100 g of fresh soil samples for 48 h at 25 °C in the dark. The nematodes were then counted with a stereomicroscope (Olympus BX, Japan) and approximately 200 individuals per sample were randomly selected and identified at the genus or family level with a compound microscope. Taxa were then assigned to trophic groups as described by Yeates et al. (1993), *i.e.* bacterivores, fungivores, herbivores, omnivores and predators, and into the life-history groups from the “colonizer-persistent” scale (Bongers, 1990). We then computed the following metrics: total nematode density, relative density of trophic groups, Shannon diversity (Shannon, 1948), nematode channel ratio (NCR) (Yeates, 2003), indicating the relative dominance of bacterial *versus* fungal decomposition pathways; the maturity index (MI) and plant parasite index (PPI) (Bongers, 1990), reflecting respectively soil food web stability and the potential impact of PPN; and the enrichment index (EI) and structure index (SI) (Ferris et al., 2001), used to infer nutrient availability and the complexity of the soil food web.

All the statistical analyses were performed using R (v.4.4.3; R Core Team, 2025).

Statistical differences among crop management and irrigation treatments were assessed for total nematode and trophic group densities as well as nematofaunal indices using analysis of variance (ANOVA), followed by post-hoc Tukey comparison tests (*lm* function in the *stats* package and *glht* function in the *multcomp* package; Royston, 1982; Hothorn et al., 2008). Model assumptions for normality and homoscedasticity were evaluated using the *shapiro.test* function in the *stats* package and the *leveneTest* function in the *car* package (Fox, 2015). When necessary, data were log-transformed to meet model assumptions. For variables exhibited Poisson-like distribution (*e.g.* predator, omnivore, ectoparasite, semi-endoparasite, sedentary endoparasite nematode densities), non-parametric Kruskal-Wallis test were applied (*krukal* function in the *agricolae* package; De Mendiburu, 2023). The association between nematode taxa and crop management and irrigation levels was evaluated using indicator species analysis (*multipatt* function in the *indicspecies* package; Cáceres and Legendre, 2009). To characterize the multivariate effect of treatments (crop managements and hydric levels) a principal component analysis (PCA) was carried out on the absolute density of the nematode trophic groups, the nematofaunal indices (EI and SI), the Shannon diversity and the 2 most frequent herbivore nematodes (*Pratylenchus* and *Tylenchorhynchus*) using the *ade4* package (*dudi.pca* function; Dray and Dufour, 2007). The effects of crop management and irrigation level on the PCA individual plan were then assessed by performing a permutational multivariate analysis of variance (PERMANOVA) using the *vegan* package (*adonis2* function; Legendre and Anderson, 1999). The model included the interaction between the two fixed factors (crop managements× irrigation levels) and accounted for the nested design by constraining permutations within plot. Euclidean distance was used as the distance measure.

To further investigate the effects of crop management types and irrigation levels on nematode trophic group imbalance, we calculated a nematode balance index representing the relative dominance of non-herbivore taxa. The index was defined as the logarithm of the ratio between the combined density of non-herbivore (bacterivores, fungivores, omnivores and predators) nematodes over herbivores. The nematode balance index was chosen to specifically assess trophic imbalance within the nematode community by contrasting herbivorous nematodes, which are directly linked to plant parasitism, with non-herbivore taxa (bacterivores, fungivores, omnivores and predators), which are primarily involved in decomposition pathways and higher trophic regulation. This index therefore provides an integrative indicator of shifts in food web structure rather than changes in single trophic groups. The logarithmic transformation of the ratio was applied to stabilize variance, reduce skewness inherent to ratio-based metrics, and allow symmetrical interpretation of values around zero. Biologically, positive values indicate a dominance of non-herbivore nematodes and suggest a more structured and functionally complex soil food web, whereas negative values reflect a relative dominance of herbivores, often associated with disturbed or simplified systems. Differences in the balance index among treatments were tested using a linear mixed-effects model (*lmer* function, *lme4* package; Bates et al., 2015), with crop managements and irrigation level as fixed effects and a random effect included to account for spatial structure. The normality and homoscedasticity of the model residuals were checked as previously mentioned. All graphical representations were produced using the *ggplot2* package (Wickham, 2016).

## 3. Results and discussion

In line with our hypothesis, the PCA performed on nematode community and functional indices showed a clear separation between CA and CT, irrespective of irrigation (Fig. 1). This separation was mainly driven by higher loadings of total nematode density, diversity indices, and higher trophic groups along the first axis (Fig. 1, Table 1). CA was positively associated with persistent nematode taxa (*e.g. Aporcelaimus*) and the Structure Index (SI), whereas CT was associated with stress-tolerant microbivorous nematodes (*e.g.*, *Acrobeloides*, *Eucephalobus* and *Aphelenchoides*, Table 2), with the Enrichment Index (EI) and the Plant-Parasitic Index (PPI). The EI reflects the response of opportunistic nematodes to available resources, and the PPI indicates the potential impact of PPN on crops, whereas the SI reflects the structure of the soil food-web (Bongers, 1990; Ferris et al., 2001). Consistent with the multivariate patterns, univariate analyses revealed significantly higher densities of bacterivores and predators and greater Shannon diversity under CA compared to CT (Table 1). Therefore, these results suggest that CA tends to support a more complex and stable soil trophic network compared to CT. In contrast, CT was closely associated with a less structured community and a greater dominance of opportunistic and plant-parasitic nematodes. These patterns are consistent with previous studies attributing positive effects of CA on soil nematode communities to improvements in soil structure, organic matter content and microhabitat stability resulting from reduced soil disturbance and the maintenance of permanent soil cover (Henneron et al., 2015; Puissant et al., 2021; Cárceles Rodríguez et al., 2022). Reduced tillage may favor the persistence of large-bodied nematodes and disturbance-sensitive nematodes by limiting direct mechanical damage and by reducing indirect effects associated with soil disturbance. Tillage can induce rapid nutrient mineralization and resource pulses that preferentially favor opportunistic taxa with high fecundity, while larger-bodied omnivores and predators respond more slowly and decline in abundance (Neher et al., 2019; Betancur-Corredor et al., 2022). In contrast, the diverse intercrop cover used in CA likely contributed to greater plant diversity compared to bare soil under CT, providing continuous habitat and organic inputs that sustain soil biota and favor the persistence of higher trophic-level nematodes (Neher, 2010; Sauvadet et al., 2025).

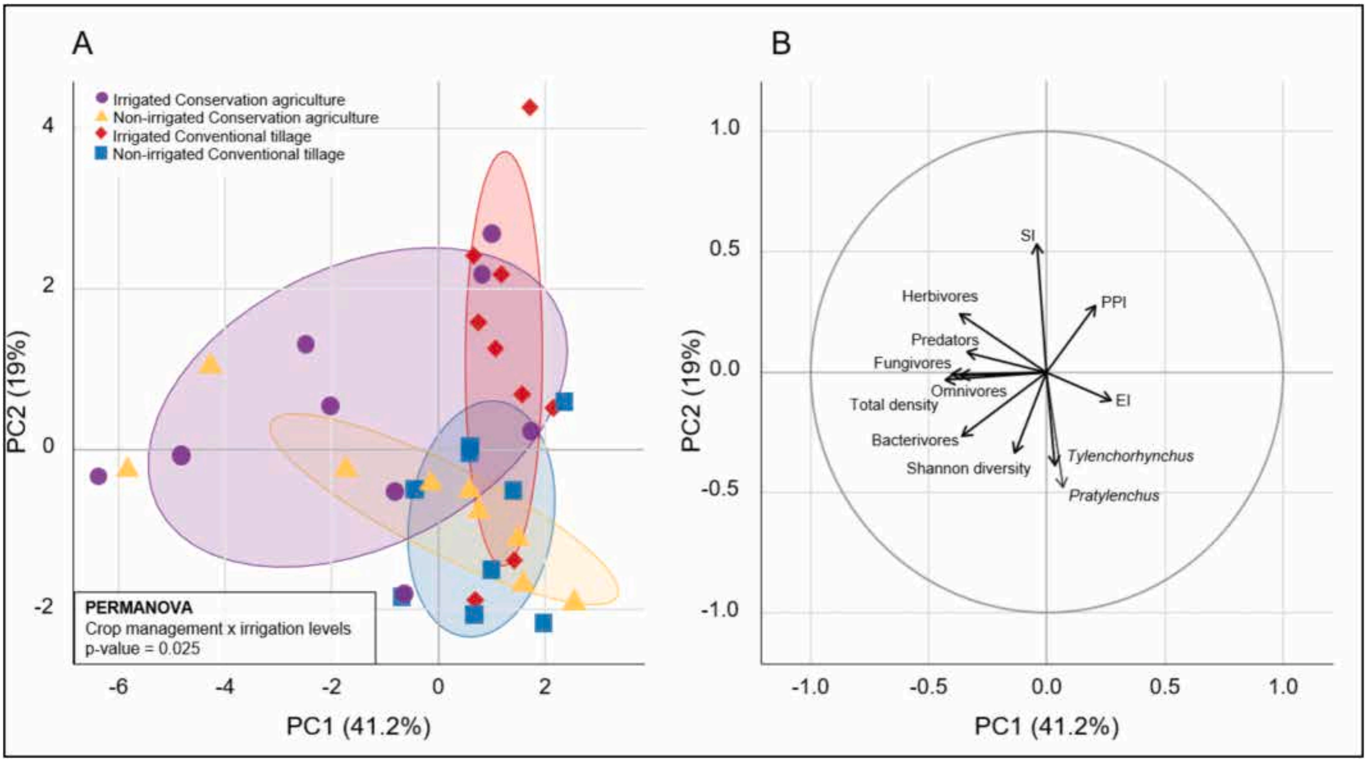

**Fig. 1.** Principal component analysis biplot (PCA) showing A) projection of the samples arranged by crop managements and irrigation levels and B) correlation circle based on the density of different nematode trophic groups, the two most frequent herbivore nematodes (*Pratylenchus* and *Tylenchorhynchus*), Shannon diversity and nematofaunal indices. PPI = Plant parasite index, EI = enrichment index and SI = structure index.

**Table 1**
Average density of total nematode, trophic groups (bacterivores, fungivores, predators, omnivores and herbivores; expressed as individuals per kg of dry soil) and nematofaunal indices according to crop managements and irrigation levels. Values are mean ± SE; $n = 36$. Different letter denotes significant differences between treatments according to post-doc Tuckey HSD test or Kruskal-Wallis (see Text).

| | Non-irrigated Conservation agriculture | Irrigated Conservation agriculture | Non-irrigated Conventional tillage | Irrigated Conventional tillage |
|---|---|---|---|---|
| **Total density** | 13,920.7 ± 8764.3<br>a | 18,116.2 ± 10,175.4<br>a | 10,338.4 ± 3248.8<br>a | 8543.6 ± 3412.9<br>a |
| **Bacterivores** | 5690.5 ± 2570.8<br>b | 6407.6 ± 5466.0<br>ab | 4704.2 ± 1985.2<br>ab | 2655.1 ± 2100.0<br>a |
| **Fungivores** | 2519.8 ± 2077.8<br>ab | 3454.7 ± 2488.4<br>b | 1446.3 ± 684.8<br>ab | 1159.0 ± 579.8<br>a |
| **Predators** | 757.4 ± 673.8<br>b | 483.1 ± 455.6<br>ab | 127.3 ± 143.2<br>a | 105.4 ± 115.3<br>a |
| **Omnivores** | 431.9 ± 483.9<br>a | 591.6 ± 507.5<br>a | 312.9 ± 383.3<br>a | 199.2 ± 164.1<br>a |
| **Herbivores** | 4521.0 ± 3428.4<br>ab | 7179.2 ± 2956.8<br>b | 3747.2 ± 1388.5<br>a | 4424.9 ± 1991.1<br>ab |
| **- Root-associated** | 2089.9 ± 660.1<br>ab | 3694.7 ± 1084.6<br>b | 1157.7 ± 200.3<br>a | 1127.2 ± 126.8<br>ab |
| **- Ectoparasites** | 870.6 ± 316.0<br>a | 864.1 ± 251.2<br>a | 556.6 ± 129.8<br>a | 228.0 ± 100.3<br>a |
| **- Semi-endoparasites** | 4.4 ± 4.4<br>a | 11.0 ± 11.0<br>a | 4.7 ± 4.7<br>a | 346.5 ± 117.1<br>b |
| **- Migratory Endoparasites** | 1556.1 ± 336.8<br>a | 2602.4 ± 647.8<br>a | 2029.7 ± 491.5<br>a | 2549.0 ± 491.5<br>a |
| **- Sedentary Endoparasites** | 0<br>a | 7.0 ± 7.0<br>a | 0<br>a | 174.1 ± 115.2<br>a |
| **Shannon diversity** | 12.2 ± 2.2<br>b | 11.6 ± 2.1<br>ab | 11.2 ± 1.3<br>ab | 9.2 ± 1.9<br>a |
| **Structure Index** | 42.8 ± 9.1<br>a | 51.8 ± 16.0<br>a | 35.3 ± 16.2<br>a | 48.3 ± 18.0<br>a |
| **Enrichment Index** | 61.4 ± 15.0<br>a | 57.7 ± 15.6<br>a | 62.5 ± 11.5<br>a | 60.5 ± 12.5<br>a |
| **Plant Parasitic Index** | 2.6 ± 0.2<br>a | 2.5 ± 0.3<br>a | 2.6 ± 0.3<br>a | 2.7 ± 0.2<br>a |

**Table 2**
Soil nematode taxa significantly associated to the treatments, *i.e.* crop managements and irrigation levels, as revealed by the indicator species analysis. Taxa were classified according to their trophic groups and c-*p* value (Bongers, 1990; Bongers and Bongers, 1998).

| Crop managements (conservation agriculture or conventional tillage) | Irrigation level (irrigated or non-irrigated) | Taxa | Trophic groups | c-p ou p-p value | Specificity | Fidelity | *p*-values |
|---|---|---|---|---|---|---|---|
| Conventional | Irrigated | *Helicotylenchus* | Herbivore | 3 | 0.69 | 0.67 | *** |
| | | *Aulolaimus* | Bacterivore | 3 | 0.83 | 0.44 | ** |
| | | *Acrobeloides* | Bacterivore | 2 | 0.29 | 1.00 | ** |
| | | *Eucephalobus* | Bacterivore | 2 | 0.28 | 1.00 | ** |
| | | *Aphelenchoides* | Fungivore | 2 | 0.27 | 1.00 | *** |
| Conventional | Non-irrigated | *Chiloplacus* | Bacterivore | 2 | 0.36 | 1.00 | * |
| Conservation | Irrigated | *Xiphinema* | Herbivore | 5 | 1.00 | 0.33 | * |
| Conservation | Non-irrigated | *Anaplectus* | Bacterivore | 2 | 0.50 | 0.78 | * |
| | | *Aporcelaimus* | Omnivore | 5 | 0.50 | 0.53 | * |

P-values with the respective symbols * for $p < 0.05$, ** for 0.01 and *** for $p < 0.001$, 1000 permutations.

Our results also suggest that irrigation may disrupt the balance of the soil nematode community. In CA, the ratio of non-parasitic nematodes (bacterivores, fungivores, omnivores and predators) to herbivores remained positive under both irrigation levels, although it decreased when soils were irrigated (Fig. 2). In contrast, this ratio became negative under CT, indicating an imbalance in nematode community and a dominance of herbivores under irrigation. Moreover, while CA supported higher herbivore densities than CT, most of these nematodes were non-damaging roots-associated taxa while CT was characterized by a higher proportion of plant-damaging herbivores (sedentary endoparasites and semi-endoparasites taxa; Table 1). In particular, the genus *Helicotylenchus*, a plant ectoparasitic nematode, was significantly associated to CT under irrigation (Table 2). This genus is common but can induce severe crop damages at high density (Uzma et al., 2015; Lopes-Caitar et al., 2019). By contrast, the genus *Aporcelaimus,* a sensitive omnivore taxon, was significantly associated with CA without irrigation (Table 2). We suppose that the maintenance of a diverse cover crop in CA contributed to this balanced nematode community response even under water limitation, as it has been identified as essential to promote beneficial free-living nematodes while limiting herbivores (Sauvadet et al., 2025). The observed effects of irrigation on nematode communities structure likely reflect legacy effects rather than short-term responses as the nematode sampling was conducted several months after the last irrigation event. The persistence of these patterns suggest that irrigation may have induced changes in soil structure, organic matter distribution, and microbial dynamics over time (Qi et al., 2022). Such modifications could continue to shape nematode communities beyond the immediate irrigation period, particularly under CT, where opportunistic and PPN appear favored. In CA, the presence of a diverse cover crop and reduced disturbance may buffer such long-term effects by stabilizing soil microhabitats and resource availability, thereby helping to maintain a more regulated nematode food-web. Comprehensive repeated sampling across seasons and years are needed to confirm the observed pattern and disentangle short *vs* long-term irrigation effects. Overall, our findings indicate that CT supports a soil nematode community sensitive to irrigation, by promoting the proliferation of plant-

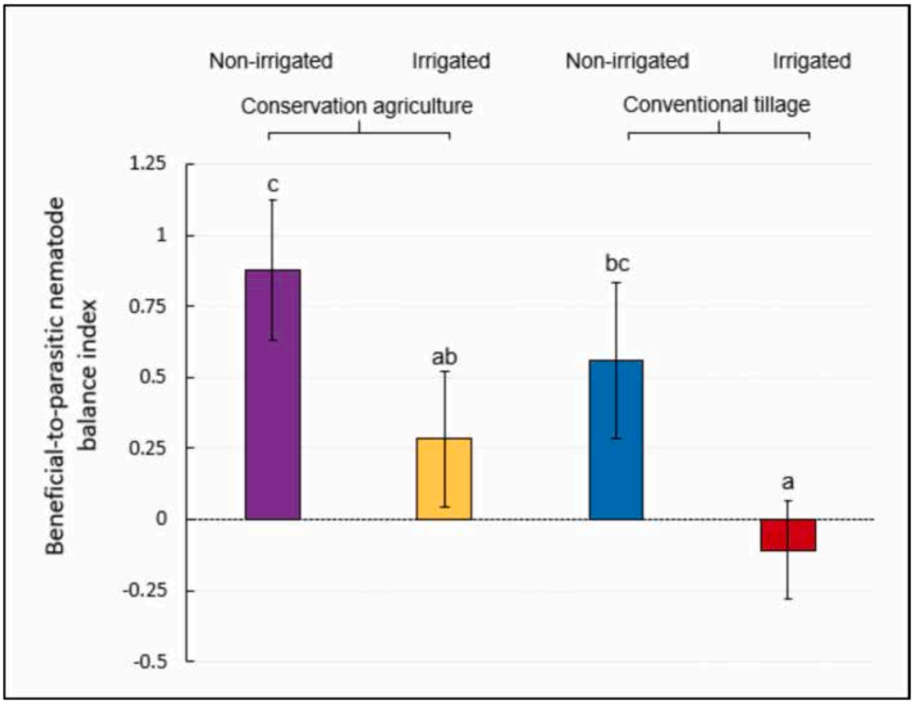

**Fig. 2.** Beneficial-to-parasitic nematode balance index according to crop managements and irrigation levels. Values are mean ± SE. Different letters denote significant difference between treatments (Tukey's post-hoc comparisons) with a < b < c.

parasitic and opportunistic nematodes, thereby increasing the risk of trophic imbalance. Conversely, CA sustains a more structured and regulated nematode food-web, with higher predator densities that help buffer the community against the destabilizing effects of irrigation. However, as quoted earlier, regarding the sample size of our dataset, our findings should be interpreted as exploratory insights into nematode responses to crop management and irrigation. Expanding the dataset is thus an important perspective for future research.

## CRediT authorship contribution statement

**Charlotte Biryol:** Writing – original draft, Investigation. **Claire Wittling:** Writing – review & editing. **Juan David Dominguez-Bohorquez:** Writing – review & editing. **Sidy Diakhate:** Writing – review & editing. **Stephan Hättenschwiler:** Writing – review & editing, Funding acquisition. **Grégoire T. Freschet:** Writing – review & editing, Funding acquisition. **Jean Trap:** Writing – original draft, Supervision, Resources.

## 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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## Data availability

Data will be made available on request.

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