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Evaluating the delayed, causal effects of summer irrigation on winter earthworm communities in a Mediterranean agroforestry trial

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ABSTRACT

Mediterranean agroecosystems increasingly face prolonged summer drought, extended bare-soil periods and heat extremes, all of which constrain soil biota and threaten long-term soil functioning. Management practices maintaining plant cover during summer, such as cover crops, may alleviate these constraints but generally require irrigation in dry regions. However, the ecological consequences of combining summer cover crops with irrigation remain poorly quantified for soil fauna, particularly in heterogeneous agroforestry systems. We monitored earthworm communities for six years (2019–2024) at the DIAMS experimental platform, a replicated Mediterranean alley-cropping agroforestry trial where an irrigated summer cover crop was implemented factorially. Earthworms were surveyed each winter across contrasted habitat types to assess delayed (legacy) effects of summer management. To isolate irrigation effects from spatial heterogeneity and interannual climatic variability, we applied a Difference-in-Differences framework complemented by event-study analyses. Summer crop irrigation did not affect earthworm biomass or species richness but induced habitat-specific changes in abundance. Abundance increased in irrigated agroforestry crop alleys (×3.5 in AF_C and ×2.5 in AF_C1m), while no detectable effects occurred in monoculture or tree-dominated habitats. Communities were largely dominated by *Microscolex dubius*, suggesting that irrigation primarily enhanced the survival or recruitment of this disturbance-tolerant species. Irrigation effects were stronger following dry autumns, indicating climate-dependent legacy responses. Overall, our results show that irrigation benefits for soil fauna are strongly context-dependent, emerging primarily in exposed crop habitats and shaped by habitat heterogeneity, seasonal legacy effects and interannual climatic variability.

1. Introduction

Mediterranean agroecosystems are increasingly exposed to recurrent summer droughts, heat extremes and prolonged periods of bare soil, which together threaten long-term soil functioning and sustainability (Iglesias et al., 2011; Molénat et al., 2023). These conditions intensify soil degradation by reducing organic matter inputs, enhancing erosion and imposing strong constraints on soil biota (Aupic-Samain et al., 2021; Homet et al., 2023; Leal Filho et al., 2023). In this context, irrigation has become a key management option to buffer summer soil stress. Summer irrigation facilitates the establishment of cover crops, which limit bare soil exposure and provide additional organic inputs compared to bare-soil management. Through root development, rhizodeposition and aboveground biomass production, summer crops can modify soil structure and produce organic substrates that decompose during autumn and early winter (Angers and Caron, 1998; Qu et al., 2025; Valckx et al., 2011).

While it is well-documented that these processes may indirectly improve habitat and food quality for earthworms several months after irrigation has ceased (Bruyn, de, Kingston, 1997; Euteneuer et al., 2020), the broader ecological consequences of summer irrigation are rarely assessed beyond the vegetation growing season itself. This is a

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significant oversight, as many soil organisms are likely to respond to these management legacy effects only after soils are rewetted in the following season (Blankinship et al., 2011; Eggleton et al., 2009).

Earthworms therefore provide a biologically and functionally meaningful indicator of legacy effects of summer soil management (Bruyn, de, Kingston, 1997). As key ecosystem engineers, they play a central role in soil structure formation, nutrient cycling and carbon dynamics (Blouin et al., 2013; Vidal et al., 2023). Their activity, survival and vertical distribution are tightly controlled by soil moisture and temperature (Johnston et al., 2018). In Mediterranean climates, earthworm communities are largely inactive during summer and resume activity in late autumn and winter. They thus integrate the cumulative effects of summer stress and management practices, responding to summer conditions with a substantial time lag (Capowiez and Sanchez-Hernandez, 2024).

Interannual variability in post-summer climate, particularly autumn precipitation, could therefore modulate irrigation legacy effects, with dry autumns amplifying and wet autumns alleviating the relative benefits of summer irrigation. Furthermore, the effects may be embedded within complex spatial mosaics, such as in alley cropping agroforestry systems. These systems, composed of cropped alleys and tree lines planted on herbaceous vegetation strips, are characterised by strong gradients in shading, rooting depth, litter inputs and disturbance regimes (Nungula et al., 2024). Trees can buffer summer soil conditions through shading, hydraulic redistribution and continuous litter supply, potentially reducing the marginal benefits of irrigation for soil fauna (Cardinael et al., 2020).

Capturing such delayed and context-dependent responses requires analytical approaches that explicitly contrast temporal trajectories rather than relying on static comparisons (Schrodt et al., 2025; Siegel and Dee, 2025). Difference-in-Differences (DiD) designs are particularly well suited to this purpose, as they estimate how changes through time in treated plots differ from simultaneous changes in comparable control plots, while accounting for unobserved, time-invariant site characteristics (Siegel and Dee, 2025). When combined with habitat-specific contrasts, event-study analyses and multivariate community trajectory approaches, DiD frameworks allow the investigation of both the magnitude and direction of community change through time.

Here, we investigate how the introduction of an irrigated summer cover crop influences earthworm communities in winter in a Mediterranean agroforestry system composed of crop alleys and tree lines, and compare these effects with those observed in control systems, i.e., crop monoculture and tree plantation systems. Specifically, we aim to (i) quantify the delayed causal effect of summer irrigation on winter earthworm abundance, biomass and species richness; (ii) assess how these effects vary across habitats within agroforestry mosaics and control systems; (iii) examine how interannual climatic variability, particularly autumn precipitation variability, modulates irrigation effects; and (iv) determine whether summer irrigation alters compositional trajectories through time. Our causal assumptions are formalised in a directed acyclic graph (Figure S1), which underpins the statistical analyses and hypothesis testing.

Based on current ecological understanding, we formulated five hypotheses regarding the delayed effects of summer irrigation on winter earthworm communities. First, irrigation may alleviate summer desiccation stress and enhance survival, leading to increased winter abundance, biomass and species richness (H1 – moisture pathway). Second, irrigated summer crops may increase plant-derived inputs (roots and residues), generating resource-mediated carry-over effects for soil fauna (H2 – resource pathway). Third, tree cover may buffer summer microclimatic stress through shading, litter inputs and hydraulic redistribution, reducing the marginal benefits of irrigation (H3 – tree-modulated microclimate). Fourth, irrigation benefits may depend on post-summer climatic conditions, with stronger effects following dry autumns (H4 – climate contingency). Finally, irrigation may alter not only community magnitude but also compositional trajectories over time, particularly in crop habitats (H5 – community trajectory shift). Detailed mechanistic expectations are provided in Appendix S1.

2. Material and methods

2.1. Study site

2.1.1. Location

The study was carried out at the DIAMS experimental agroforestry site, located in Mauguio, Hérault, in southern France (43.612°N, 3.976°E). The climatic series shows a well-defined seasonal pattern, with low winter temperatures, a spring warming phase, and peak temperature values in summer. Precipitations exhibit intra-annual variation, typical of a Mediterranean climate (Appendix S2), corresponding to a temperate climate with a hot and dry summer (Csa) in the Koppen classification (Beck et al., 2023). The soil is classified as a skeletic rhodic Luvisol (IUSS, 2024), characterised by a decarbonated surface horizon and a high, spatially variable stone content that can reach 60%. Details on soil are given in Table S3-1.

2.1.2. Agricultural trial design

The 5-ha site is organised into three blocks that serve as spatial replicates (Martin-Blangy et al., 2025; Siegwart et al., 2023; Vion-Guibert et al., 2026) (Figure S3-1). Each block contains three agrosystems representing contrasting management and vegetation structures: a monospecific crop (MC), a tree plantation (TP), and an agroforestry plot (AF). In the agroforestry plots, tree rows consisting of *Robinia pseudoacacia* L., a fast-growing, nitrogen-fixing species commonly used in Mediterranean agroforestry due to its drought tolerance (Mantovani et al., 2014), were established between 2017 and 2018. Tree rows in AF plots are spaced 17 m apart, while in the TP plots, also consisting of *R. pseudoacacia* trees, rows are 3 m apart. Within rows, trees were planted every 2 m.

Within the agroforestry system, we distinguished the centre of the cultivated alleys (AF_C) from the tree rows (AF_T) and the ecotone (1 m from tree row margin, AFC_1m). Tree-covered habitats are managed without tillage or herbicide application, maintaining a permanent understory. Agroforestry tree rows (AF_T) are 2 m wide and were initially sown in October 2019 with a grass-legume mixture. Understory composition has since evolved with tall fescue dominance in block 1 and higher floristic diversity in blocks 2 and 3 in 2024. The tree plantation understory has evolved spontaneously after the initial ploughing of an alfalfa crop in 2016, and is now dominated by grasses. Because this understory vegetation interacts strongly with tree effects, the two cannot be separated in practice. As a result, the habitat mosaic combines contrasting micro-environmental conditions, ranging from shaded, litter-rich areas beneath trees to more exposed to the sun, periodically tilled and fertilised crop zones. Details on trial spatial design are given in Appendix S3.

2.1.3. Agricultural management practices

Crop alleys and MC plots bore a 3-year rotation of cereal crops (durum wheat, spring barley) and legume crops (chickpea or field pea). The crops were conventionally managed, with fertilisation, residue retention, soil tillage and pesticides (mainly herbicides) according to common local practice.

The trial was designed to compare two alternative management strategies during the summer from 2022 to 2024 (Appendix S3). Within each block, each MC, AF and TP plot was split into a Control (C) plot and a Water (W) plot. Control plots received no irrigation and cropped control plots were left bare between crop harvest in June or early July and the sowing of the subsequent crop. All W plots were irrigated from July to September. In AF and MC plots, total summer irrigation with sprinklers reached approximately 190 mm in 2022, 155 mm in 2023, and 55–60 mm in 2024. In TP, irrigation was applied using a drip system in 2022–2023, resulting in lower inputs (approximately 80 mm in 2022 and 55 mm in 2023), whereas in 2024 all systems were irrigated using a sprinkler system, leading to more comparable water inputs (ca. 50–70 mm across systems). Cropped surfaces were sown with forage sorghum that was shredded and incorporated in the autumn before the sowing of the subsequent crop.

2.2. *Earthworm community assessment*

2.2.1. *Field sampling*

Earthworms were sampled annually for six consecutive years (2020–2025), always in late winter (from 20th of February to 10th of March depending on the year), a period when Mediterranean soils typically retain sufficient moisture for earthworm activity.

In each habitat type (AF_C, AF_T, AF_1m, TP and MC), and each control or irrigation treatment, five permanent sampling areas *sensu* Kapfer et al. (2017) were established within each block. Each permanent sampling area covered approximately 10 m^2. In total, 150 permanent sampling areas (5 permanent sampling areas × 5 habitats × 2 irrigation treatments × 3 blocks) were monitored annually from 2020 to 2025, yielding 900 hand-sorted soil monoliths over the entire survey.

Within each permanent sampling area, earthworms were sampled following the ISO (2361)1–1 (2018) standard for soil macrofauna. At each sampling event, a soil monolith (25 × 25 cm) was excavated to a depth of 20 cm. To avoid re-sampling the same soil volume and to limit local depletion or disturbance effects across years, the position of the monolith was shifted between consecutive years within each permanent sampling area, while remaining within its predefined boundaries to ensure spatial homogeneity. Monoliths were hand-sorted directly in the field, and all earthworms were collected. Individuals were killed, fixed, and stored in $>$ 96% ethanol.

2.2.2. *Earthworm identification and index computation*

In the laboratory, upon ethanol storing, adults and sub-adults were identified to species level. For this purpose, we used an Xper3 key developed by the Eco&Sols lab. This key is built using morpho-anatomical features employed to describe and identify earthworm species, and includes all accepted French species (Gérard et al., 2025). The morpho-anatomical features were extracted from Bouché (1972) and Qiu, Bouche (1998), and all species-description papers that followed describing species inhabiting France (e.g., Fernández Marchán et al., 2023; Marchán et al., 2023; Navarro et al., 2023); see Gérard et al. (2025) for the full list. Each ethanol-stored individual was weighed (pseudo-fresh body mass) to the nearest 0.001 g after blotting to remove excess ethanol. For each monolith, abundance represents the total count of individuals (including juveniles), biomass measures the sum of pseudo-fresh body masses of all specimens, and species richness corresponds to the total number of species identified.

2.3. *Causal effect of irrigated summer crop implementation on earthworms*

2.3.1. *Difference-in-difference*

To quantify the causal impact of the irrigated summer crop on earthworm communities, we implemented a Difference-in-Difference (DiD) approach (Angrist and Pischke, 2009), tailored to the multi-year, multi-habitat panel structure of the DIAMS experiment. Abundance, biomass and species richness data were log-transformed.

Prior to estimating causal effects, we assessed the validity of the DiD framework by examining pre-intervention trends. Specifically, we verified whether control and future-irrigated plots exhibited comparable year-to-year trajectories before summer 2022, when summer irrigation was set up. Visual inspection of abundance, biomass and species richness time series, along with their associated standard errors, did not reveal systematic divergence between groups in the pre-treatment period (Appendix S4). This supports the parallel-trend assumption required for causal identification.

Each response variable was fitted with a two-way fixed-effects model including block and plot identity (to control for unobserved spatial heterogeneity), year indicators (to account for system-wide temporal fluctuations), and habitat as a covariate. From a causal inference perspective, this specification is advantageous because plot fixed effects control for all time-invariant, unobserved heterogeneity across plots—factors that could otherwise bias treatment estimates (Dee et al., 2023). Year fixed effects likewise remove confounding effects from shared temporal dynamics, ensuring that estimated treatment effects reflect deviations specific to irrigated plots rather than system-wide trends.

The treatment variable identified plots assigned to cover crop irrigation from summer 2022 onward, and the post-treatment indicator coded sampling years 2023–2025. Because irrigation was introduced abruptly, uniformly, and independently of pre-existing earthworm trends or soil conditions, we considered it as an 'exogenous management shock'. This framework ensures that temporal changes observed in irrigated plots can be contrasted with simultaneous changes in control plots, allowing the isolation of irrigation-driven deviations from background temporal dynamics. The interaction between the treatment (identifying irrigated plots) and the post-treatment period (years 2023–2025) yielded the DiD estimator, quantifying how the temporal change in irrigated plots diverged from the counterfactual change expected in untreated plots.

To evaluate whether irrigation effects differed among habitats, we modelled a full three-way interaction between treatment status (summer irrigation or not), pre- vs post-irrigation period and habitat category (MC, AF_C, AF_C1m, AF_T and TP). Using monoculture crop (MC) as the reference level, the model estimated (i) a baseline DiD effect for MC (post-irrigation period × treatment status) and (ii) habitat-specific deviations (post-irrigation period × treatment status × habitat). Because these habitat-specific contrasts combine multiple coefficients, uncertainty was quantified using a cluster bootstrap that resampled entire sampling points (plot identity) with replacement. For each of 1000 bootstrap replicates, we re-estimated the full interaction model and recomputed the combined irrigation effect for each habitat. Percentile-based 95% confidence intervals from these bootstrap distributions provide robust inference under repeated-measures structure and potential departures from Gaussian residual assumptions. Causal effects were estimated with Difference-in-Difference models fitted using the 'fixest' R library (Bergé, 2018), with plot and block fixed effects and clustered standard errors. Temporal dynamics were examined using an event-study estimator, appropriate here because summer irrigation was introduced synchronously in all treated plots in 2022, and then applied every subsequent summer. The event-study contrasts each year with the final pre-treatment year (2022; year 0), providing estimates for two pre-treatment years (2020–2021; year -2 and -1) and three post-treatment years (2023–2025; year $+1$, $+2$ and $+3$). This single-onset design allows a clear test of the parallel-trends assumption and a characterisation of year-specific lagged responses to irrigation.

2.3.2. *Explaining treatment-effect heterogeneity by climate variability*

We explored how treatment-effect estimates obtained through the DiD framework aligned with broad environmental and management gradients. Because the number of estimated values was limited, we did not employ structural equation modelling (SEM), machine-learning approaches (random forest), or other high-dimensional methods that require substantially larger sample sizes to produce stable and interpretable results. Instead, we adopted a parsimonious and statistically robust approach grounded in ecological reasoning.

Autumn precipitation variability was used as a mechanistic moderator because early-autumn rewetting controls the recovery of earthworm activity following summer desiccation stress and shapes the extent of population survival (Bouché, 2014). Years with high autumn rainfall can rapidly restore soil moisture across all plots, thereby alleviating the detectable legacy of summer irrigation, whereas dry autumns exacerbate moisture deficits and strengthen treatment contrasts. Precipitation data were obtained from the on-farm weather station installed in 2012; means for 2012–2019 served as reference values to calculate annual anomalies for the 2020–2025 study period.

Monthly variability was computed as observed monthly precipitation minus reference monthly precipitation (2012–2019). Autumn anomalies correspond to the sum of anomalies for October, November and December for each study year (2020–2025). To relate variation in summer crop irrigation effects to climate gradients, we fitted simple linear models using base R (lm) with treatment-effect estimates as the response variable.

2.4. *Ecological trajectories*

We examined temporal changes in community composition using a combination of ordination and trajectory-based metrics. Species–abundance matrices were binarized by year, habitat and treatment into a 0/1 (absence/presence) matrix. Then, Bray–Curtis dissimilarities were computed with the vegdist function from the vegan package. A Principal Coordinates Analysis (PCoA) was then performed on the community matrix. Multivariate differences in composition were evaluated with a PERMANOVA (vegan package, ref) using 9999 permutations.

To better quantify the magnitude of temporal change, we defined multiyear community trajectories at the plot level using the ecotraj package (Sturbois et al., 2021) and extracted segment and total path lengths. Trajectory lengths were then modelled using linear mixed-effects models from the nlme package (Pinheiro et al., 1999), with year interval, habitat and treatment (irrigated or not) as fixed effects and plot identity as a random intercept. Post hoc contrasts for treatment differences within each habitat × time interval were obtained with the emmeans package (Lenth and Piaskowski, 2025).

3. Results

3.1. *Overall results*

Over the six-year survey, a total of 4758 earthworm individuals were collected, 2686 of them being identifiable (sub-)adults. Assemblages of adults were strongly dominated by *Microscolex dubius* (Fletcher, 1887), which accounted for 64% of all individuals, followed by *Allolobophora chlorotica* Savigny, 1826 (24%), pink morph. The remaining seven species—*Aporrectodea caliginosa* (Savigny, 1826), *Aporrectodea rosea* (Savigny, 1826), *Aporrectodea trapezoides* (Dugès, 1828), *Lumbricus castaneus* (Savigny, 1826), *Microscolex phosphoreus* (Dugès, 1837), *Scherotheca gigas* (Dugès, 1828) and *Scherotheca mifuga* Bouché, (1972)— contributed marginally, each representing 3.7–0.1% of all individuals identified to species level. *M. dubius* and *M. phosphorus* are non native species, *A. trapezoides*, *A. caliginosa*, *A. rosea*, *All. chorotica* and *L. castaneus* are European, widespread species and *S. gigas* and *S. mifuga* are mediterranean endemics.

Across the six years of monitoring, earthworm metrics varied markedly among habitats and sampling dates, consistent with strong climatic constraints in Mediterranean agroecosystems. Mean earthworm density varied between 0 and 685 individuals m^{-2}, with the lowest values observed in cropped habitats and the highest under tree plantations. Species richness ranged from 0 to 3 species per sampling point; assemblages composed exclusively of juveniles were regularly recorded in cropped habitats, whereas the most diverse communities occurred in wooded habitats. Total biomass showed a broader gradient, spanning 0–61.7 g m^{-2}, with marked increases in wooded habitats (Appendix S4).

3.2. *Causal analyses of summer crop irrigation effects on earthworms*

3.2.1. *Difference-in-difference*

The clearest responses were observed for earthworm abundance, with marked differences among habitats (Table 1, Fig. 1). In the monoculture crop (MC; reference), the estimated irrigation effect was small and not statistically significant (β = 0.36 ± 0.47 SE, ×1.44; p-value = 0.443). In the middle of the agroforestry cropping zone (AF_C), abundance increased following irrigation (β = 1.25 ± 0.38 SE, ×3.48; p-value = 0.001). A positive and statistically significant effect was also detected in the cropped area located 1 m from the tree line (AF_C1m; β = 0.91 ± 0.38 SE, ×2.49; p-value = 0.015).

In the tree-row habitat (AF_T), the estimated effect was negative and significant at a 10% rejection threshold (β = –0.53 ± 0.32 SE, ×0.59; p-value = 0.099). No detectable effect was found in the adjacent plantation (TP; β = 0.00 ± 0.12 SE, ×1.00; p-value = 0.974). Cluster-robust bootstrap confidence intervals (Fig. 1) illustrated these model-based estimates, showing positive responses in AF_C and AF_C1m and overlapping zero in the remaining habitats.

In contrast to abundance, biomass did not show statistically significant changes in response to irrigation in any habitat (absolute β < 0.07; all p-values > 0.66), and multiplicative effects were consistently close to unity (×0.95–1.07). Species richness also exhibited no consistent response, with small effect sizes across habitats (absolute β < 0.08; all p-values > 0.59) and confidence intervals broadly overlapping zero (Table 1; Fig. 1).

3.2.2. *Temporal dynamics of irrigation effects: event-study assessment*

Event-study estimates revealed no evidence of divergent pre-treatment trajectories between plots assigned to summer crop irrigation and their controls (Fig. 2). For all three community metrics—abundance, biomass, and species richness—the DiD contrasts for years −2 and −1 clustered around zero, with confidence intervals generally spanning both positive and negative values (for example in year −2, abundance = −0.22 ± 0.22SE and −0.15 ± 0.21SE in control and subsequently irrigated plots). No statistical differences were recorded (all p-values > 0.10). These results support the parallel-trends assumption required for causal inference.

Following the onset of irrigation (years +1 to +3), temporal deviations from the baseline year varied in magnitude and direction among metrics. In the first year after irrigation (+1), deviations in abundance were small and non-significant for irrigated plots (estimate = 0.29 ± 0.20 SE) and negative and significant in control plots (-0.46 ± 0.21 SE). By year + 2, however, both groups exhibited a marked negative departure from baseline trajectories, with temporal deviations of −1.00 ± 0.17 SE for controls and −1.16 ± 0.20 SE for irrigated plots (p-value < 0.001). By year + 3, patterns diverged: the control plot estimate remained negative (−0.43 ± 0.15 SE), whereas irrigated plots showed a positive deviation (0.51 ± 0.18 SE), each being highly significant (p < 0.001).

Temporal deviations from the baseline year remained consistently close to zero for biomass across all years. Post-treatment estimates also exhibited limited deviation in either direction (e.g., +1 year: −0.05 ± 0.05 SE for controls, −0.03 ± 0.03 SE for irrigated) in years + 1 and + 2 after the onset of summer crop irrigation. Statistical significance was reached in year + 3 with 0.08 ± 0.04 SE for controls, 0.08 ± 0.03 SE for irrigated plots (p-value < 0.05).

Species richness showed very limited temporal variation, with effect sizes centred around zero throughout the time series. Post-treatment responses remained weak and not significant in year + 1 and + 2 (year +1: 0.01 ± 0.04 SE for controls, −0.01 ± 0.04SE for irrigated; year +3: −0.05 ± 0.03SE for controls, 0.04 ± 0.04 SE for irrigated), and reached significance (p-value < 0.05) in year + 2 (-0.08 ± 0.03 SE for controls, −0.09 ± 0.03 SE for irrigated).

3.2.3. *Exploring soil and climate modulation of causal effects*

Inter-annual variation in irrigation effects was partly associated with autumn precipitation anomalies. For earthworm abundance, years with drier-than-average autumn conditions (negative anomalies) tended to show more positive DiD estimates, whereas wetter years were associated

Table 1

Habitat-specific irrigation effects on earthworm abundance, biomass and species richness estimated from Difference-in-Difference models. Log effects (β) represent the estimated change in irrigated plots relative to the temporal trajectory of control plots after the introduction of summer irrigation (post-2022). Effects are expressed on both the log scale (β ± SE) and the multiplicative scale (exp(β)), where values > 1 indicate a positive irrigation effect and values < 1 indicate a negative effect. Habitats include monoculture crop (MC), agroforestry crop alley centre (AF_C), agroforestry ecotone 1 m from tree rows (AF_C1m), agroforestry tree rows (AF_T) and tree plantation (TP). Models include plot and block fixed effects and year adjustments, with standard errors clustered at the plot level. $ indicates p-value < 0.1, * indicates p-value < 0.05, and *** indicates p-value < 0.001.

Habitat	Abundance β (log)	SE	Abundance (x effect)	Biomass β (log)	SE	Biomass (x effect)	Richness β (log)	SE	Species richness (x effect)
MC (ref)	0.363	0.473	1.44	0.155	0.473	1.17	0.077	0.473	1.08
AF_C	1.246 *** (ref + 0.833)	0.383	3.48	0.047 (ref - 0.108)	0.383	1.05	0.000 (ref- 0.077)	0.383	1.00
AF_C1m	0.912 * (ref + 0.549)	0.375	2.49	0.067 (ref - 0.089)	0.375	1.07	0.077 (ref + 0.000)	0.375	1.08
AF_T	-0.530 $ (ref - 0.892)	0.321	0.59	0.009 (ref - 0.146)	0.321	1.01	-0.037 (ref - 0.114)	0.321	0.96
TP	0.004 (ref - 0.359)	0.12	1.00	-0.052 (ref - 0.207)	0.120	0.95	-0.064 (ref - 0.141)	0.120	0.94

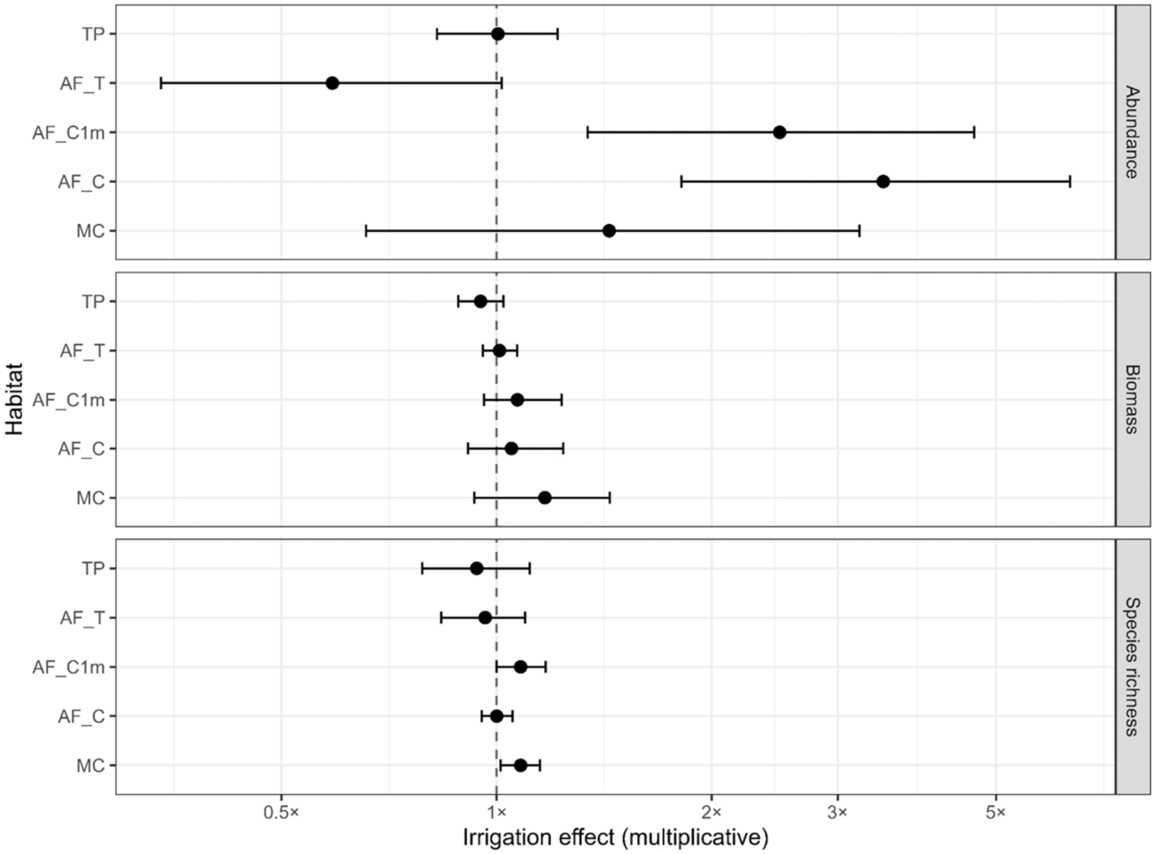

Fig. 1. Habitat-specific summer crop irrigation effects on earthworm community parameters (log-transformed values), estimated using a Difference-in-Difference (DiD) framework. Points represent multiplicative irrigation effects (exp(β)), and horizontal bars denote cluster bootstrap 95% confidence intervals (resampling at the sampling point level). Values > 1 indicate a positive effect of summer crop irrigation relative to the counterfactual trajectory of control plots; values < 1 indicate a negative effect. The five habitats correspond to the control monoculture crop (MC), the agroforestry cultivated alley centre (AF_C), the agroforestry ecotone crop 1 m from tree row margins (AF_C1m), the agroforestry tree row (AF_T), and the control tree plantation (TP). Panels show effects for earthworm abundance, total biomass, and species richness analysed separately with habitat-specific DiD models including block and plot fixed effects and year adjustments.

with weaker or even negative irrigation effects (Appendix S5). The meta-regression between yearly DiD and precipitation anomaly suggested a negative slope ($\beta = -0.37 \pm 0.15$ SE, $R^2 = 0.68$, p-value = 0.084). In contrast, biomass and species richness did not exhibit clear trends with autumn rainfall anomalies, and regression slopes for these metrics were close to zero.

3.3. Ecological trajectories

3.3.1. Community composition dynamics

The PCoA reveals pronounced habitat-specific changes in community composition over the study period (Fig. 3). In the monoculture habitat (MC), annual positions remain relatively close to each other, indicating limited temporal reorganisation. The agroforestry habitats show more contrasted patterns. In the crop area (AF_C), the trajectory describes a wide loop, with substantial year-to-year movements that

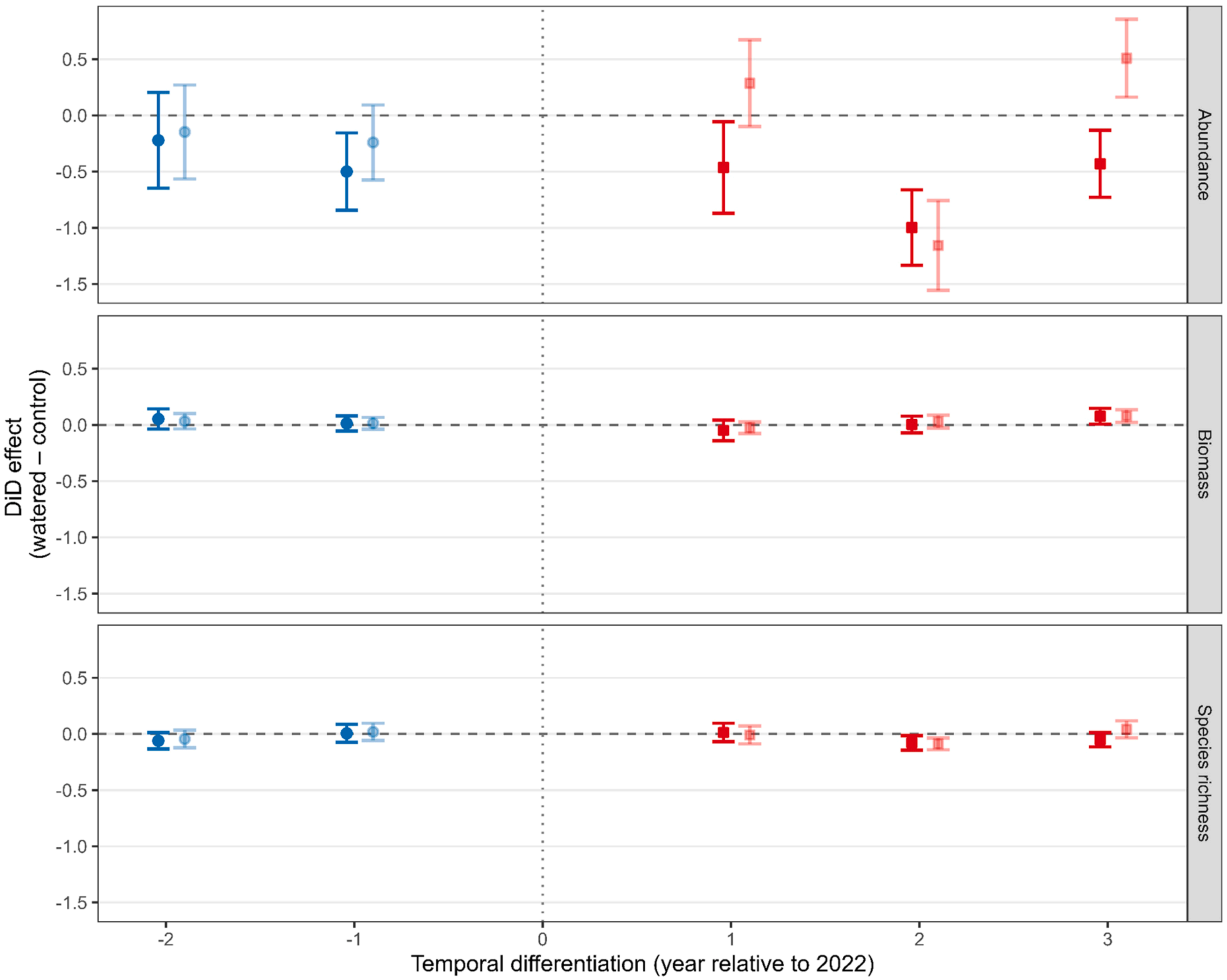

Fig. 2. Event-study estimates of temporal deviations in earthworm abundance (log-transformed), biomass and species richness relative to the last pre-irrigation year (2022). Points represent yearly coefficients estimated from the Difference-in-Differences model for control (light colour) and irrigated plots (dark colour), expressed as deviations from the baseline year (2022; year 0 on the temporal axis). Vertical bars indicate 95% confidence intervals clustered at the sampling point level. Negative temporal values correspond to pre-treatment years (blue symbols) and positive values to post-treatment years (red symbols). In the temporal differentiation axis, year −2 corresponds to 2020, year −1–2021, year 0–2022, year + 1–2023, year + 2–2024 and year + 3–2025. The horizontal dashed line marks a null effect, and the vertical dotted line indicates the timing of irrigation onset.

reflect strong species presence turnover. The ecotone between crop and tree row (AF_C1m) exhibits a restricted temporal reorganisation. In the tree row habitat (AF_T), changes follow a more constrained, primarily vertical direction, suggesting consistent but moderate adjustments in composition. The tree plantation (TP) habitat displays the most elongated trajectory, with little overlap among years and a steady progression across the ordination.

In all habitats, the blue segments of the trajectories in Fig. 3, corresponding to the period following the onset of summer irrigation, provide insight into how communities responded to this management change. In AF_C and AF_C1m, these blue segments show a noticeable shift in direction compared with the pre-irrigation years, suggesting that summer crop irrigation may have altered the trajectory rather than simply prolonging its previous trend. This shift in direction points toward the factorial space characteristic of woody habitats. In AF_T, the trajectory shows a pronounced shift after the onset of irrigation, followed by a partial return towards its earlier position in ordination space. By contrast, in TP, the post-irrigation trajectory continues along the same axis as earlier years but at a slightly reduced amplitude.

The PERMANOVA revealed that habitat was the main driver of community composition ($R^2 = 0.30$, $F = 5.77$, p-value < 0.001), explaining roughly 30% of the variation in Bray–Curtis dissimilarities. Differentiation duration also had a significant, although much weaker, effect ($R^2 = 0.035$, $F = 2.68$, p-value $= 0.022$). By contrast, the onset of the summer crop irrigation had no significant influence on community structure ($R^2 < 0.01$, $F = 0.60$, p-value $= 0.71$).

3.3.2. *Ecological trajectory*

Linear mixed-effects models revealed strong temporal and habitat effects on community trajectory length (Year: $F = 292.6$, p-value < 0.0001; habitat: $F = 27.7$, p-value < 0.0001) and a marked year × habitat interaction ($F = 16.6$, p-value < 0.0001). The main effect of summer crop irrigation (i.e., treatment) was weak and non-significant ($F = 0.44$, p-value $= 0.51$), but a significant year × habitat × treatment interaction ($F = 1.70$, p-value $= 0.030$) indicated that treatment differences depended on both habitat and time interval. Pairwise contrasts showed that irrigated plots displayed longer cumulative trajectories than controls in agroforestry crop alleys: + 0.10 in AF_C (p-value = 0.019) and + 0.13 in AF_C1m (p-value = 0.0006). A transient difference was also detected in AF_C during the 3rd-to-4th year interval (+0.087, p-

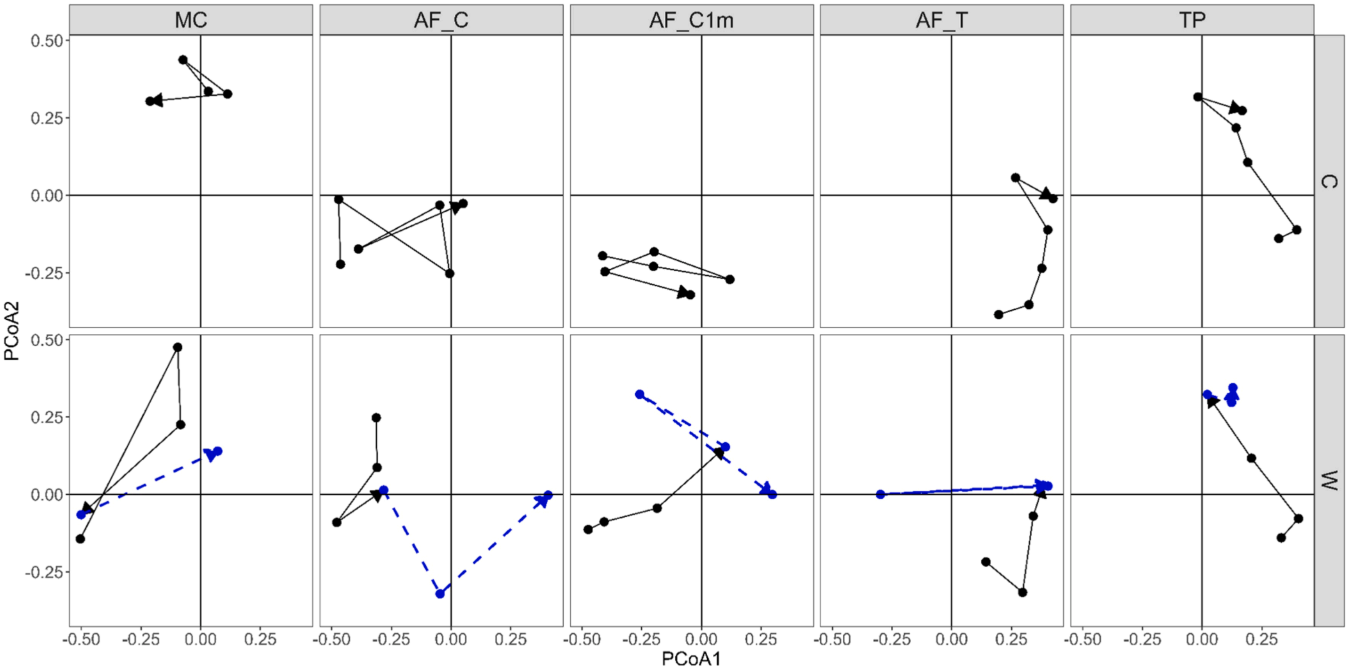

Fig. 3. Temporal trajectories of soil macroinvertebrate community composition across habitats from year −2 (2020) to year + 3 (2025). Trajectories are computed on a Principal Coordinates Analysis (PCoA) of Bray–Curtis dissimilarities. Each panel represents one habitat type in column (control monoculture crop – MC, middle of the crop alley in AF – AF_C, ecotone crop 1 m from tree row – AF_C1m, tree row in AF – AF_T, and control tree plantation – TP), and one treatment type in row (no irrigation – C, and summer irrigation implemented in summer 2022 – W). Within each habitat and each treatment, points indicate annual community positions in ordination space, and arrows show the direction of temporal change. Dashed blue arrows highlight the shift in treatment regime from no irrigation to summer irrigation implemented in summer 2022 (considered as year 0).In AF_T W, the blue line appears to be full rather than dashed, because it actually corresponds to two opposite changes, i.e., two arrows on top of each other.

value = 0.038). In contrast, cumulative trajectories were shorter under irrigation in monocrop plots (MC: −0.097, p-value = 0.011), while no significant treatment effects were detected in tree-line habitats (AF_T, all p-value > 0.16) or in the plantation (TP, all p-value > 0.35). Graphs displaying community trajectory lengths are presented in Figure S6.

4. Discussion

4.1. *A causal and lag-aware perspective on irrigation effects*

Our study demonstrates that assessing irrigation as an agroecological strategy in Mediterranean systems requires consideration of spatial heterogeneity, seasonal legacy effects, and probably interannual climatic variability. By combining a Difference-in-Differences (DiD) framework with habitat-specific contrasts, event-study analyses and community trajectory approaches, we disentangled irrigation-driven deviations from background temporal fluctuations and persistent plot-level differences. The absence of divergent pre-treatment trends supports the parallel-trends assumption and strengthens the credibility of causal inference. More broadly, our results illustrate a system in which a summer management intervention does not only translate into immediate biological responses, but instead materialises during the subsequent winter through slower pathways, potentially involving demographic processes, habitat quality and resource carry-over.

4.2. *Direct moisture pathway: benefits confined to exposed herbaceous habitats*

Partially consistent with Hypothesis 1, the clearest irrigation signal concerned earthworm abundance, with positive causal effects restricted to the cropped areas of the agroforestry plots (AF_C and AF_C1m). While this pattern is consistent with a moisture-related pathway, whereby summer irrigation alleviates desiccation stress and facilitates post-summer recovery (Singh et al., 2019), a purely moisture-driven mechanism would likely generate responses across habitats, including tree-dominated ones, although potentially with different magnitudes due to microclimatic buffering. Instead, irrigation effects were restricted to agroforestry crop alleys (AF_C and AF_C1m) and absent under tree cover (AF_T and TP). Our design does not allow a strict separation between direct effects of increased soil moisture and indirect effects mediated by irrigated crop cover and associated plant inputs. In the cropped alleys, irrigation was applied together with a sorghum cover crop, which may have altered both microclimatic conditions (e.g., shading, reduced evaporation) and the quantity of plant-derived resources entering the soil. These effects may be further influenced by the structurally heterogeneous vegetation context typical of agroforestry systems (Barrios et al., 2018).

By contrast, no detectable effect was observed in the monoculture crop, suggesting that the irrigated summer crop alone may not translate into sustained improvements in earthworm habitat under more exposed conditions. In the absence of structural buffering (e.g., shading) or nearby refuges, irrigation may be insufficient to offset extreme summer constraints, underscoring the role of the vegetation context in shaping irrigation outcomes (Mariotte et al., 2016; Plum and Filser, 2005).

Despite strong abundance responses, biomass remained unaffected across habitats. This decoupling is ecologically coherent, as irrigation may primarily enhance post-summer survival or autumn recruitment of juveniles, while changes in size structure and total biomass occur more slowly (Jimenez et al., 2000; Petersen and Luxton, 1982). Such patterns are typical of soil fauna responses to transient stress alleviation and reflect numerical rather than structural community responses (Bonato Asato et al., 2023).

The predominance of *M. dubius* may also contribute to the absence of detectable richness responses, as communities dominated by a single disturbance-tolerant species are more likely to exhibit numerical changes in abundance rather than shifts in species composition. This species is likely to rapidly exploit transient improvements in soil moisture or resource availability, leading to an increase in abundance without corresponding changes in diversity. Therefore, this pattern should be interpreted cautiously. While it reflects a response of a disturbance-tolerant species, it does not indicate the restoration of a diverse soil community. Meanwhile, *M. dubius* is increasingly reported in Mediterranean ecosystems (Decaëns et al., 2020; Gérard et al., 2025), suggesting that its dominance may also reflect broader processes of community reassembly in a context of global changs. In addition, conventional management, including moderate pesticide use, may act as a baseline filter favouring such species (Pelosi et al., 2014). The effects of an irrigated summer crop reported here should therefore be interpreted within this already filtered and context-dependent community.

The results suggest that although summer irrigation and the cover crop were also present in the monoculture, their ecological effects on earthworms depended on the surrounding vegetation context, with agroforestry providing additional buffering and refuge conditions not available in the open crop.

4.3. *Potential resource-mediated carry-over effects*

While our results do not allow a strict causal separation between moisture- and resource-mediated pathways (hypotheses 1 and 2, respectively), some of the observed patterns are compatible with resource effects acting as a secondary and context-dependent mechanism. Specifically, irrigation-induced increases in earthworm abundance were confined to agroforestry cropped habitats (AF_C and AF_C1m), despite the presence of irrigated summer crops in the monoculture, suggesting that resource-mediated carry-over effects are conditional on habitat context.

A complementary interpretation is that, in these agroforestry alleys, the irrigated summer crop enhanced plant-derived inputs—through root growth, rhizodeposition or residue production (Ngidi et al., 2024; Ruis et al., 2019; Yahaya and Shimelis, 2022)—that became available to earthworms during autumn decomposition and early winter (Curry and Schmidt, 2007; Kuzyakov and Domanski, 2000). Such carry-over effects would be expected where herbaceous biomass directly responds to watering and where micro-environmental conditions allow these inputs to be retained and exploited, as opposed to fully exposed or strongly buffered habitats.

From a mechanistic perspective, irrigation is expected to enhance soil faunal biomass through increased plant-derived carbon and nutrient inputs, fuelling microbial activity and consumer growth (McDermid et al., 2023; Yao et al., 2024). However, our results suggest that this metabolic pathway might be incomplete. Although irrigation was associated with slightly higher abundances, it did not translate into increased community biomass. This pattern probably indicates that additional resources are labile and primarily promoted transient demographic responses, such as juvenile recruitment, rather than sustained somatic growth or biomass accumulation (Yang et al., 2008). This pattern is consistent with short-lived resource pulses that increase turnover without long-term storage of biomass, likely due to elevated mortality or seasonal constraints (Ostfeld and Keesing, 2000).

4.4. *Tree-modulated microclimate: buffering and redundancy under woody cover*

As predicted by hypothesis H3, irrigation effects were weak or absent under tree rows and in the tree plantation. However, the absence of detectable responses in these habitats does not allow a direct test of the buffering mechanism proposed in H3. Instead, the observed pattern—-positive responses restricted to cropped habitats—appears more consistent with resource-mediated pathways (H2), whereby irrigation stimulates plant growth and residue inputs in herbaceous crop alleys, thereby increasing resource availability for earthworms. Such plant-derived inputs are known to enhance soil faunal activity and resource supply (Kemppinen et al., 2024; Rolo et al., 2023). Under tree rows and in the plantation, where vegetation structure and litter inputs are already largely controlled by woody plants, summer irrigation may therefore have a limited influence on resource availability for soil fauna. Taken together, these patterns suggest that irrigation effects in this system are more likely mediated by vegetation-driven resource inputs than by direct soil moisture alleviation alone.

This interpretation is, however, constrained by the fact that tree canopy effects and understory vegetation cannot be empirically disentangled in our design. The observed patterns likely reflect the combined effects of canopy-driven microclimatic buffering and understory-related resource inputs. The relatively stable trajectories observed under tree influence are therefore best understood as resulting from this combined vegetation effect, rather than a purely tree-driven mechanism.

4.5. *Climate-dependent modulation of irrigation legacy effects*

Interannual variability in irrigation effects was partly explained by autumn precipitation variability, supporting hypothesis 4 that irrigation benefits depend on post-summer climatic context (Bevacqua et al., 2024; Liu et al., 2024). In years with drier-than-average autumns, irrigation tended to yield more positive abundance responses, consistent with a scenario in which cumulative summer stress is amplified and irrigation provides a stronger relative advantage. Conversely, in wetter autumns, rapid soil rewetting may homogenise moisture conditions across treatments, favouring earthworm dispersal and thus reducing detectable contrasts. This climate dependency is ecologically plausible, as early autumn rewetting governs the timing and extent of earthworm reactivation (Capowiez and Sanchez-Hernandez, 2024). Nevertheless, inference is constrained by the limited number of years available. We therefore interpret this pattern as a preliminary observation, consistent with ecological expectations but requiring longer time series for confirmation.

4.6. *Community trajectories under strong assembly constraints: modulation of dynamics rather than reassembly*

Community composition was primarily structured by habitat type, confirming that vegetation context and associated disturbance regimes act as dominant filters on earthworm assemblages, even a few years after the onset of the trial (Hedde et al., 2024, 2019, 2013). Ordination and PERMANOVA results consistently showed that irrigation did not induce strong shifts in overall community structure, in line with the absence of detectable richness responses. Together, these results indicate that irrigation does not override the major compositional determinants imposed by woody versus herbaceous habitats, nor does it relax the strong environmental filtering characteristic of Mediterranean ecosystems (Si-Moussi et al., 2025).

Trajectory analyses however revealed subtle but consistent treatment-induced effects on the direction and pace of community change, particularly in agroforestry crop habitats. In AF_C and AF_C1m, post-irrigation trajectories deviated from pre-treatment paths, indicating that irrigation modulated temporal dynamics rather than amplifying existing trends, whereas trajectories under tree influence remained comparatively stable, consistent with microclimatic buffering by woody components (Betancur-Corredor et al., 2024). Mechanistically, this pattern is consistent with a seasonal decoupling between resource inputs and community assembly (Logue et al., 2011; Vellend, 2010). Herein, irrigation enhanced plant-derived resource availability during the summer, outside key windows for earthworm dispersal and establishment. Consequently, additional resources were likely exploited by resident taxa, generating transient demographic responses without sustained biomass accumulation or increases in diversity (Yang et al., 2008). Overall, under strong habitat- and climate-driven assembly constraints typical of Mediterranean agroecosystems, irrigation acted primarily as a temporal modulator of community dynamics rather than as a driver of community reassembly.

5. Conclusions

Together, our findings indicate that irrigated summer cover crops can generate measurable legacy benefits for soil fauna, but that these benefits are spatially restricted and context-dependent. In our agroforestry mosaics, irrigation appeared most effective in exposed herbaceous zones, while no detectable effects were observed under woody cover. This suggests that irrigation strategies aimed at supporting soil biodiversity may be more efficient when targeted to the most stress-prone habitats rather than applied uniformly. Because the community was largely dominated by *M. dubius*, a small-bodied, fast-reproducing and disturbance-tolerant species, caution is warranted when extrapolating our findings to less disturbed systems or communities dominated by native species.

More broadly, our results highlight the importance of evaluating management practices through the lens of seasonal carry-over effects, particularly in Mediterranean systems where biological activity is temporally decoupled from interventions. Combining vegetation-based buffering with context-aware water management may help maintain soil functioning under increasing drought pressure, even if biodiversity responses remain primarily quantitative and habitat-bounded.

Future work should therefore combine causal designs with high-frequency environmental monitoring, quantify cover crop biomass and litter inputs, and explicitly assess demographic structure to disentangle survival, recruitment and growth responses. More generally, agroforestry systems provide a powerful experimental setting to test how water, vegetation structure and climate interact to shape soil biodiversity over time—provided that both spatial and temporal dimensions are explicitly modelled.

CRediT authorship contribution statement

Orrière Solène: Methodology, Investigation. **Gérard Sylvain:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **HEDDE Mickael:** Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marsden Claire:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Goury Romain:** Writing – review & editing, Methodology, Formal analysis. **Masson Anne-Sophie:** Writing – review & editing, Investigation. **Belaud Emma:** Writing – review & editing, Investigation. **Biryol Charlotte:** Writing – review & editing. **Capowiez Yvan:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Forest Marion:** Writing – review & editing, Methodology, Investigation. **Ngao Jérôme:** Writing – review & editing, Project administration, Investigation. **Estopinan Joaquim:** Writing – review & editing, Methodology, Formal analysis. **Ferchaud Fabien:** Writing – review & editing, Project administration, Investigation.

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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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110455.

Data availability

Research Link Provided

Temporal monitoring of earthworm communities at the DIAMS experimental site (recherche.data.gouv)

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