

Management legacy effects drive soil food web resistance and resilience to climatic stress

Paula Lillo

paula.lillo@inia.csic.es

Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria

Tiaré Contreras-Hernández

Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria

María del Mar Delgado

Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria

Miguel Talavera

Andalusian Institute of Agricultural and Fisheries Research and Training

Sara Sánchez-Moreno

Museo Nacional de Ciencias Naturales

Research Article

Keywords: no-tillage, crop rotation, climate change, resilience, resistance, food-web

Posted Date: March 16th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9084156/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Biology and Fertility of Soils on August 27th, 2026. See the published version at <https://doi.org/10.1007/s00374-026-02044-1>.

Abstract

Soil organisms' response to climate change largely depends on soil management practices and resulting soil organic carbon levels. Conservation agriculture practices (e.g., no-tillage and crop diversification) have been shown to protect soil organisms, improve micro-food webs, maintain soil structure and enhance carbon sequestration compared to conventional practices, potentially improving soil resistance and resilience to climate change. In a greenhouse experiment, we assessed the legacy effects of contrasting long-term soil management practices (conventional tillage/no-tillage in monoculture/rotation systems) on resilience and resistance to warming and drought of soil microbial functions, microfaunal food webs, and crop performance in dryland soils. Our results demonstrate that under extreme weather conditions, no-till legacy and crop rotation enhances soil biota resistance and resilience to drought and warming by enhancing soil organic carbon and water-holding capacity. There is a trade-off between resistance and resilience, and while microbial functions, generalist bacterivores, and fungivores show resistance (and no resilience) to climatic stress, opportunistic bacterivores and upper soil micro-food web levels show resilience (but no resistance) instead. Increased soil organic carbon levels derived from no-tillage practices were only partially responsible for the observed soil responses, suggesting that other soil properties derived from management history determine soil organisms' resistance and resilience to climate change.

1. Introduction

The stability of ecosystems under stress is determined by their resistance and resilience to perturbation (Pimm 1984; Ingrisch and Bahn 2018). While resistance refers to the ability of a system to persist and maintain functioning during a disturbance, reflecting ecosystem capacity to withstand environmental changes, resilience describes ecosystem capacity to recover after a perturbation, reflecting the ability of ecosystems to return to equilibrium after perturbation (Bengtsson 2002). In soil systems subjected to climate change, emerging evidence suggests that agroecosystems with higher soil organic carbon (SOC) and subjected to sustainable management exhibit greater resistance to climate stressors than low SOC, conventional systems (Zhang et al., 2019). Indeed, management legacies appear to play a pivotal role in determining agroecosystem resilience (Brussaard et al. 2007; Teng et al. 2024). Soil organisms are keystone to ecosystem stability (Yang et al., 2018), but studies on the legacy effects of soil management in soils have primarily focused on the response of soil microbiota (Lavalley et al. 2024), while research on soil fauna has been limited to single climatic stressors (e.g., drought or heat) (de Vries et al., 2012a; de Vries et al., 2012b). Moreover, the enduring legacy effects of different agricultural practices on soil organisms and agroecosystem capacity to both withstand and recover from climatic disturbances remain insufficiently understood.

The inherent limitations of dryland agricultural soils—particularly their sandy textures, low soil organic matter (SOM) content, and limited water availability—create unique challenges for agricultural sustainability under climate change. Ploughing perturbs soil food webs by affecting higher trophic levels (Puissant et al. 2021), degrades soil structure—especially via macroaggregate breakdown—which accelerates SOM decomposition and ultimately reduces SOC stocks (Six et al., 2000; Six et al., 2002; Ye et al., 2020). Conversely, reducing tillage intensity enhances SOM accumulation (Martin-Rueda et al. 2007; López-Bellido et al. 2010; Sombrero and de Benito 2010; Fiorentini et al. 2024; Colunga et al. 2025)—particularly in low-SOC soils (Tadiello et al. 2023)—while promoting biological activity (Madejón et al. 2009; Farina et al. 2024), increasing soil diversity and food web stability (Bongiorno et al. 2019) and supporting soil fauna (Henneron et al. 2015; Betancur-Corredor et al. 2023). Additionally, reduced tillage boosts water retention in drylands (Lampurlanés et al. 2016; Castellini et al. 2019) and enhances soil aggregate stability (Hernanz et al. 2002; Pareja-Sánchez et al. 2017; Álvaro-Fuentes et al. 2025). The reduction of soil perturbation in no-till systems exacerbates such benefits (Six et al. 2000; Kan et al. 2022), and maintains crop yields under rain-fed conditions or water scarcity (Pittelkow et al. 2015), particularly in drylands (Adil et al. 2025; Álvaro-Fuentes et al. 2025).

Globally, crop rotation and cover crops promote basal soil food web levels and reduce soil pests (Puissant et al. 2021), and, under Mediterranean rainfed conditions, legume-cereal rotations enhance soil nutrient availability, promote microbial enzymatic activities (Holatko et al., 2024; Li et al., 2024a; Pareja-Sánchez et al., 2017), increase microbial diversity (Tiemann et al. 2015; Venter et al. 2016; Papp et al. 2018), and disrupt build-up of specialist pathogens, reducing pest pressure (Dias et al. 2014; Isbell et al. 2017; Peralta et al. 2018). For instance, cereals in rotation outperform continuous monocropping (Bonciarelli et al., 2016; Liu et al., 2023; Liu et al., 2022; McDaniel et al., 2014). In contrast, monocropping acts as a press perturbation, reducing ecosystem resilience and long-term productivity (de Oliveira et al. 2020; Gandía et al. 2021). Diversified rotations under no-tillage (NT) support soil food webs, increasing the resilience of soil faunal communities (Sánchez-Moreno et al. 2006; Zhong et al. 2016; Treonis et al. 2018).

Climate change intensifies extreme weather events (heatwaves, drought episodes), which alter microbial community composition (Kaisermann et al. 2013) and disrupt SOM decomposition and nutrient cycling (Sae-Tun et al., 2022; Zhou et al., 2023), posing a threat to wheat productivity (Asseng et al. 2014). These impacts are exacerbated by conventional tillage, which destabilizes C-N dynamics and reduces soil moisture retention (Santín-Montanyá et al., 2020; Six et al., 2000). In contrast, NT shifts microbial response to drought towards greater resistance (Kaisermann et al. 2013) and enhances resilience through improved soil health and structure (Blanco-Canqui and Ruis 2018; Teng et al. 2024), buffering against drought and extreme temperatures. Crop rotations, on the other hand, mitigate climate-driven yield losses (Costa et al. 2024; Kim et al. 2025) and increase resilience to heat stress (de Oliveira et al. 2020).

To experimentally assess soil biota and agroecosystem resilience and resistance against experimental climate change factors, we collected soils from a 28-year-old field experiment comparing CT and NT under both monoculture and a 4-year crop rotation management. In greenhouse microcosms, we examined the legacy effects of long-term tillage (CT vs NT) and cropping system (monoculture vs rotation) on soil properties, microfaunal food webs, microbial functions, and plant responses to climatic stress (i.e., warming and drought). We hypothesize that 1) legacy effects of no-till rotation mitigate the negative effects of climate change on microfaunal communities and soil functions and by enhancing SOC, 2) resistance and resilience of microfaunal food webs, enzymatic activities, soil respiration, and plants increase with decreasing soil perturbation, and 3) SOC contents resulting from long-term soil management drive soil resilience and resistance against climatic stress.

2. Material and methods

2.1 Study site and soil management

The soil used in this study was collected in a long-term field experiment established in 1994 at *La Canaleja* experimental farm (Alcalá de Henares, Madrid, central Spain, 40°30'57.0"N, 3°18'36.2"W). This site is characterized by a Mediterranean semi-arid climate, with a historical mean annual precipitation of 366.9 mm (1994–2022) and soil classified as sandy loam Calcic Haploxeralf. The long-term field trial comprises 2 tillage treatments and 2 cropping systems with a split-plot design. Tillage systems included: (1) conventional tillage (standard moldboard ploughing to a depth of 30 cm, CT) and (2) no-tillage, with herbicide applications as needed for weed control (NT). Cropping systems included (1) wheat monoculture (*mon*), and (2) a four-year rotation (*rot*) of winter wheat (*Triticum aestivum* L. 'Marius'), vetch (*Vicia sativa* L. 'Senda'), barley (*Hordeum vulgare* L. 'Vinagrosa'), and bare fallow. At the time of sampling, soil management practices had been applied in the experimental field for 28 years.

2.2 Experimental setup – warming and drought simulation

For the purpose of this study, four management legacy treatments were selected to represent a gradient of management intensification: CT-*mon* (winter wheat monoculture under conventional tillage), CT-*rot* (winter wheat in rotation under conventional tillage), NT-*mon* (winter wheat monoculture under no-tillage), and NT-*rot* (winter wheat under no-tillage). Initial soil properties are shown in supplementary material (Table S1). In the winter of 2022, soils were collected from the field site (CT-*mon*, CT-*rot*, NT-*mon*, and NT-*rot*) before sowing and after tillage operations, homogenized, and used to fill a total of 128 pots (1.5L volume, 32 pots with each soil type), and a microcosm experiment was established in a greenhouse to simulate warming and drought conditions.

Ten wheat (*Triticum aestivum* L. 'Marius') seeds were sown in each pot in December 2022. No further management practices were simulated and pots were left undisturbed along the experiment duration. Germination was assessed daily for the first 2 weeks, and pots were cleared to get a final density of 8 seedlings per pot. By mid-March, when seedlings were 40-day old, the climatic treatments (warming and drought periods) started. Heat waves were simulated by moving pots to a greenhouse section with an increased ambient temperature of $4.06 \pm 0.05^{\circ}\text{C}$ above ambient levels (Fig S1-S2; Table S2). Simulated drought was imposed by reducing watering to 20% water holding capacity (WHC), while control pots were maintained at 60% WHC. Climatic stress was imposed in 10-day periods, followed by another 10-day period of no stress (rewetting phase under ambient temperature conditions), and each cycle was repeated three times (Table S2). Four climatic treatments were established: 1) *Control*: ambient temperature + regular watering, 2) *Warming*: increased temperature + normal watering, 3) *Drought*: ambient temperature + reduced watering, and 4) *Warming + drought*, *DxW* (increased temperature + reduced watering). A total of 128 microcosms were established, following a full factorial design comprising 4 soil legacy treatments (CT-*mon*, CT-*rot*, NT-*mon*, NT-*rot*) x 4 climate treatments x 4 replications x 2 destructive samplings.

The first destructive sampling was performed at the end of the third climatic stress cycle to assess the acute impact (peak) of experimental drought and warming on microbial functions (enzymatic activities, microbial biomass carbon, and soil respiration), microfaunal food web structure (nematode trophic groups), and crop performance (root and shoot biomass). Following the final stress period, all microcosms were maintained at 60% of WHC and ambient temperature for a 4-week recovery period, after which a second destructive sampling was conducted to evaluate resilience of the same biological parameters. In such last sampling, soil properties were also analyzed (see section 3.1).

2.3 Soil properties and agroecosystem functions

Soil gravimetric content was determined by oven-drying samples at 105°C to constant weight. Soil pH and electrical conductivity were determined in an aqueous extract (1:2.5 and 1:5 w/v, respectively) using a pH meter and conductance meter (BASIC20, Crison, Barcelona, Spain). Soil organic carbon and available phosphorus were measured following Walkley (1935) and Olsen and Watanabe (1957), respectively. Soil mineral N ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) was determined by extraction with 2.0 mol/L KCl, followed by analysis in a flow injection autoanalyzer (SEAL-AA100, Seal Analytical, WI, USA). Microbial biomass carbon (MBC) was assessed using the chloroform fumigation method (Vance et al. 1987) and was calculated as the difference in dissolved organic carbon (DOC) between fumigated and non-fumigated samples and converted using k_{EC} correction factor of 0.45 (Joergensen 1996). Analyses were conducted at the Biogeochemical Instrumental Techniques Lab, MNCN-CSIC (Madrid, Spain). Extracellular enzyme activities and basal respiration were measured as indicators of soil biological activity: alkaline phosphatase (P mineralization; Tabatabai and Bremner, 1969), β -glucosidase (C cycling via cellulose degradation; Tabatabai, 1982), and urease (N mineralization; Nannipieri et al., 1980) and were determined using UV-VIS spectrophotometry. Extracellular enzyme activity analyses were performed at Nutrilab-URJC (Madrid, Spain). Soil basal respiration was measured by weighing 70 g of fresh soil into 125 cm³ airtight containers with silicone caps, adjusted to 60% water holding capacity, and incubated in the dark at 28°C for 21 days. After each 3-day incubation period, CO₂ accumulation in headspace was measured by gas infrared analyzer (Dansensor® CheckMate3, Ametek Mocon, MN, USA). Final basal respiration was expressed as the amount of carbon mineralized daily per unit mass of dry weight soil ($\text{mg C-CO}_2 \text{ kg}^{-1} \text{ d}^{-1}$). Dry shoot and root biomass were determined after each sampling. Plant height was recorded 4 times during the cropping cycle.

2.4 Microfaunal soil food webs

Nematodes were extracted from the soil following the modified Baermann funnel method (Barker et al. 1985). All nematodes in each sample were counted under a dissecting microscope, and approximately 100 nematodes were identified to trophic group level (bacterivores, fungivores, herbivores, omnivores, and predators) following Yeates et al. (1993) under a compound microscope at 400× magnification. Bacterial feeders were further divided into opportunistic bacterivores, which rapidly respond to increases in bacterial biomass from organic enrichment belonging to the colonizer-persister group c-

p1, and generalist bacterivores, which are ubiquitous nematodes generally resistant to soil disturbance and are classified into c-p groups 2–5 (Bongers 1990; Ferris et al. 2001).

2.5 Resistance and resilience indices

To evaluate how soil management legacies drive soil microbial and nematode responses to drought and warming, we used the Orwin and Wardle (2004) resistance (RS) and resilience (RL) indices. The RS index was calculated as $RS(t_0) = 1 - (2|D_0|)/(C_0 + |D_0|)$, in which D_0 represents the difference between the control (C_0 , i.e., the value of each functional variable under ambient climatic conditions) and the stress climatic condition (P_0) at the end of the disturbance (t_0). Positive RS values indicate minimal or no disturbance effect; negative values reflect stronger impacts. An index of +1 signifies full resistance (no change relative to control), 0 indicates a 100% change, and negative values represent changes exceeding 100%.

The RL index was calculated as $RL(t_{40}) = (2|D_0|)/(|D_0| + |D_2|) - 1$, in which D_2 represents the absolute difference between the control and the climate treatment at t_{40} (after the 40-day recovery period). Similarly to RS, positive RL values indicate partial or full recovery. Complete resilience occurs when the response returns to control levels under stress ($RL = +1$), while an RL index between 0 and -1 denotes the occurrence of a pulse in which post-disturbance deviation (D_2) exceeds the initial impact (D_0), reaching higher values relative to control than those at the initial state. Resilience and resistance indices were applied to indicators of soil functioning (DOC, MBC, basal respirations, and enzymatic activities) and nematode functional groups.

2.6 Statistical analysis

All statistics and indices calculation were performed in R version 4.4.0 (R Core Team 2024). To test the impacts of legacy and climate effects on soil properties, microbial functions, soil nematodes and crop performance, we ran a 'glmmTMB' model in the glmmTMB package (generalised linear mixed models using Template Model Builder) (v1.1.9, Brooks et al., 2017), including an extension for zero-inflation and a negative binomial distribution for nematode abundance. The interactions of tillage legacy (*conventional* vs. *no-till*), rotation legacy (*rotation* vs. *monoculture*), drought treatment, and warming treatment were used as fixed effects in the models. For crop performance, we include *Sampling* as random effect. Analysis of variance were determined using the *Anova()* function in the car package (v3.1.2, Fox and Weisberg, 2018). We checked models' residuals for normality and variance homogeneity using DHARMA package (v0.4.6, Hartig, 2021) and pairwise contrasts were calculated using *emmeans()* in the emmeans package (v1.10.1, Lenth, 2024). To assess model fit, we calculated the coefficients of determination (R^2) for each model using *r.squaredGLMM()* function from MuMIn package (v1.47.5, Bartoń, 2023). Principal component analyses (PCA) were performed with all soil parameters, nematode trophic group abundances, and crop variables for each sampling time by standardizing variables with z-score transformation and running the *prcomp()* function in the R core package. Permutational multivariate analysis of variance (PERMANOVA) was used to test the effects of soil legacy and climate treatments, as well as their interaction, on the combined dataset using *adonis2()* in vegan package (v2.6.4, Oksanen et al., 2022) based on Euclidean distances and using 999 permutations. In a second step, we tested whether agricultural management legacy (i.e., tillage and crop rotation) modulated the resistance and resilience of microbial activity and soil nematodes to climate stress (*Warming*, *Drought*, and their combined effect, $D \times W$). Correlation and linear regression analyses were performed using soil parameters and climate legacy treatment to explore the relationships between soil organic carbon and indicators of soil biological resistance and resilience. Regression models were calculated using *lmer()* function of lme4 package (v1.1.35.3, Bates et al., 2015) and correlation analysis were conducted using *cor()* function. All figures and ordination results were visualized using the ggplot2 package (Wickham 2016).

3. Results

3.1 Soil management and climatic effects on soil properties

Drought and the combination of drought and warming significantly reduced gravimetric soil moisture at the first sampling (-73.0% on average; $P_{\text{drought}} < .0001$), and NT-rot buffered the impact of climate stress by retaining more soil water than conventional tillage under single-factor climatic treatments ($P_{\text{tillage} \times \text{drought} \times \text{warming}} < .01$) (Fig. 1A). After the second sampling, no differences in soil moisture were observed among treatments (Fig. 1A).

At the second sampling, the effects of climate and management legacies on soil properties were evaluated (Fig. 1; Table S3). NT increased electrical conductivity ($+14.29\%$; $P_{\text{tillage}} = .0223$; Fig. 1-B), nitrate ($+64.93\%$; $P_{\text{tillage}} = .007$; Fig. 1-C), SOC ($+54.41\%$; $P_{\text{tillage} \times \text{rotation}} < .0001$; Fig. 1-E) and available phosphorus ($+78.72\%$ $P_{\text{tillage}} < .0001$; Fig. 1-F). In contrast, soil pH decreased under no-till $P_{\text{tillage}} < .05$; Fig. 1-G).

The analysis of the effects of climatic stress on soil properties showed that $D \times W$ generally raised nitrate concentrations across all management practices ($P_{\text{drought}} < .001$; Fig. 1C; Table S3) and electrical conductivity under NT-mon ($P_{\text{tillage} \times \text{rotation} \times \text{drought}} < .1$, Fig. 1B; Table S3). Warming had a detrimental effect on ammonium levels ($P_{\text{tillage} \times \text{rotation} \times \text{drought} \times \text{warming}} < .05$, Fig. 1E; Table S3), and drought increased soil pH under CT-rot ($P_{\text{tillage} \times \text{drought}} < .001$; Fig. 1G; Table S3). SOC was reduced by drought under CT-rot ($P_{\text{tillage} \times \text{drought}} < .0013$; Fig. 1G; Table S3), while available phosphorus was sensitive to drought under rot and increased under NT-mon ($P_{\text{rotation} \times \text{drought}} < .001$, Fig. 1F; Table S3).

3.2 Soil management and climatic effects on soil functioning and soil food webs

No-tillage significantly enhanced all parameters measured: microbial biomass carbon, dissolved organic carbon, β -glucosidase, phosphatase, and urease enzymatic activities, and soil basal respiration ($P_{\text{tillage}} < .05$, Table S4; Fig S3). In contrast, drought had a detrimental effect on MBC, β -glucosidase and phosphatase ($P_{\text{drought}} < .0001$, Table S4; Fig S3B-D).

Nematode communities responded variably to management legacies. Conventional tillage favored fungal-feeding nematodes, especially under CT-*rot* (+ 50.5%; $P_{\text{till}} = .018$, Fig. S4C; Table S6), whereas root-associated nematodes (i.e., Tylenchidae) were more abundant under no-till (+ 33.6%; $P_{\text{till}} = .035$, Fig. S4D; Table S5) and monoculture systems (+ 34.9%; $P_{\text{rotation}} = .008$). Omnivores and predators were also more prevalent under no-till conditions (+ 31.2%; $P_{\text{till}} = .035$, Fig. S4F; Table S5).

A principal component analysis (PCA) of soil biological functions, nematode community structure, and crop performance at the first sampling, revealed a clear separation of samples with different tillage practices (Fig. 2A). In addition, soils subjected to double stress (DxW) clustered separately from control conditions (Fig. 2A, PERMANOVA: $P_{\text{till}} < .001$; $P_{\text{drought}} < .001$). While fungal-feeding nematodes were predominantly associated with conventionally tilled soils, omnivores–predators and most indicators of biological activity (e.g., enzymatic activity, microbial biomass) were associated with no-tillage systems. Plant variables, including aboveground biomass and height, were more closely aligned with control conditions under no-tilled soils. The second sampling PCA (recovery; Fig. 2B) also revealed a distinction between tillage management, with no-till soils again associated with higher biological activity. However, the effects of the climate treatments were less pronounced.

3.3 Soil functional responses: resistance, resilience, and legacy effects under climate stress

In general, MBC ($P_{\text{climate}} < .05$), soil respiration ($P_{\text{climate}} < .01$), B-glucosidase ($P_{\text{climate}} < .001$), and phosphatase ($P_{\text{till} \times \text{climate}} < .05$) activities, were more resistant to warming than to drought or the combination drought x warming (Fig. 3A-E; Table S6). Significant pulses of phosphatase and urease activities occurred under warming (Fig. 3E-F). Legacy effects on soil resistance and resilience to climate stress were evident across multiple biological parameters. DOC revealed legacy effects on resistance ($P_{\text{till} \times \text{climate}} = .029$; Fig. 3A), with ST-*rot* performing better under *Warming*, and NT-*mon* under *Drought* ($P_{\text{till} \times \text{climate}} = .029$; Fig. 3A). Under such legacies, negative resilience index values indicate significant pulses of DOC concentrations at the second sampling that surpass the levels detected immediately after stress ($P_{\text{till} \times \text{climate}} = .01$). Respiration resistance was generally stronger under monoculture systems ($P_{\text{rotation}} < .0001$), while NT-*rot* showed higher resilience ($P_{\text{till} \times \text{rotation}} < .05$; Fig. 3C). MBC showed the lowest resistance under NT-*mon* in the double stress treatment ($P_{\text{till} \times \text{rotation} \times \text{climate}} < .05$; Fig. 3B).

Extracellular enzyme activities, including β -glucosidase and phosphatase presented lowest resistance to DxW under CT-*rot* ($P_{\text{till} \times \text{climate}} < .05$, $P_{\text{till} \times \text{climate}} < .05$, respectively; Fig. 3D-E) and urease under NT-*rot* ($P_{\text{rotation} \times \text{climate}} < .05$). β -glucosidase showed greater resilience under NT-*mon* and double stress while suffered a significant pulse under NT-*rot* ($P_{\text{till} \times \text{rotation}} < .05$; Fig. 3D). Urease exhibited pulses with warming and drought under all legacies except for NT-*rot* ($P_{\text{till}} < .01$; Fig. 3F).

3.4 Soil nematode responses: resistance, resilience, and legacy effects under climate stress

Opportunistic bacterial feeders were, overall, sensitive to climate stress ($RS < 0.5$) but resilient to warming and DxW ($RL > 0$; Fig. 4A). In contrast, generalist bacterial feeders and fungal feeders displayed the opposite trend, with higher resistance (< 0.5) than resilience (Fig. 4B-C). Plant-parasites were more resistant to warming conditions ($P_{\text{climate}} = .034$; Fig. 4E).

Opportunistic bacterial feeders presented low resistance to drought under CT ($P_{\text{climate}} = .031$, Fig. 4A; Table S7), while generalist bacterivores showed higher resilience to drought under NT-*rot* and a pulse under CT-*mon* ($P_{\text{climate}} = .077$; Fig. 4B). Fungal feeders showed low resistance to drought and DxW under CT-*mon* ($P_{\text{climate}} = .07$; Fig. 4C). Root-associated nematodes demonstrated higher resilience in NT-*mon* ($P_{\text{till} \times \text{rotation}} = .002$; Fig. 4D) under drought and drought x warming, while omnivores and predators also exhibited also highest resilience to such legacy ($P_{\text{till} \times \text{rotation}} = .002$; Fig. 4F).

3.5 Wheat performance responses: resistance, resilience, and legacy effects under climate stress

Aboveground biomass did not differ between the first and second samplings ($P_{\text{sampling}} = 0.4$), indicating that crop aboveground biomass had reached its maximum growth already in the first sampling, but belowground biomass decreased in June compared to May ($P_{\text{sampling}} < .0001$), resulting in lowest values under CT-*mon* ($P_{\text{till} \times \text{rotation}} < .0001$; Fig. 5A). Below and above-ground plant biomass progressively decreased from warming to drought x warming (Fig. 5A and 5C).

Aboveground biomass exhibited higher resistance to drought and DxW in NT-*rot* and lowest in CT-*mon* ($P_{\text{till}} < .001$; Fig. 5B), the latter showing lowest resilience to warming ($P_{\text{till} \times \text{climate}} < .0001$; Fig. 5B). Root biomass showed lower resistance and highest resilience in NT-*rot* ($P_{\text{till} \times \text{climate}} < .0001$; Fig. 5D). Overall, plant height was clearly influenced by both tillage and rotation, being consistently greater under no-till and rotation system ($P_{\text{rotation}} < .0001$). In contrast, CT systems exhibited a negative response to climate stress ($P_{\text{till} \times \text{drought}} = .02$; $P_{\text{till} \times \text{warming}} < .001$; Fig. 5E), with reductions observed under both warming and drought treatments.

3.6. Relationship between resistance and resilience and SOC as influenced by tillage legacy

Since tillage legacy exerted a significant effect on SOC levels (section 3.1), we assessed the relationships between resistance, resilience, and SOC across tillage legacies. Our results show that SOC was in general poorly associated to resistance and resilience (Fig. 6D), and only a few RS and RL indices significantly correlated to carbon levels (Fig. 6). Plant-parasite nematode resilience increased significantly with SOC under no-till ($R^2 = 0.10$, $p = .0206$; Fig. 6A), but not under conventional tillage. Fungal-feeder resilience showed a marginally positive association with SOC under conventional tillage ($p = .093$; Fig. 6B), while β -glucosidase resistance was significantly correlated with SOC in conventionally tilled soils ($R^2 = 0.261$, $p = .0036$; Fig. 6C), but not under no-till.

4. Discussion

We found that historical soil management legacies, particularly tillage practices, significantly modulate agroecosystem responses to climate change—with cascading effects on soil communities and properties, and plant performance.

4.1 Management legacy drives microbial resistance and resilience

Our results confirm that no-till legacy promotes soil resistance to drought and warming in terms of moisture retention (Lampurlanés et al. 2016; Eeswaran et al. 2021; Madejón et al. 2023), enhancing SOC levels that increase water-holding capacity (Hudson 1994). In our experiment, soils under no-tillage also exhibited higher resource availability, such as mineral nitrogen and available phosphorus, which may enable microbial communities to better resist physiological stress (Malik and Bouskill, 2022; Schimel et al., 2007). Our results also show nitrate and dissolved organic carbon pulses after recovery from drought conditions. It's been previously demonstrated that nitrogen cycling processes and available carbon increase when the soil is rewetted after drought (Maxwell et al. 2022), surpassing initial values. During soil recovery after drought events, microbes recover from stress and resources bloom, which stimulates microbial activity (Schimel, 2018). Other changes, such as decreased pH values under no-till management (Chen et al., 2020; Zhu et al., 2024), may further influence microbial community dynamics and soil biochemical processes.

Our findings showed that legacy effects of long-term reduced tillage significantly enhance soil functioning, corroborating previous reports (Chen et al., 2020; Nunes et al., 2020). Specifically, we observed enhanced MBC and soil enzymatic activities, mirroring previous patterns reported in the same long-term trial (Martín-Lammerding et al. 2015; Waibel et al. 2024). This confirms that conservation agriculture (i.e., zero tillage with crop rotation) maintain particularly high biological activity, in agreement with previous findings (Wang et al., 2017, 2023; Zhang et al., 2021; Zhu et al., 2024; Zuber and Villamil, 2016). Indeed, microbial functioning was particularly reduced during peak drought conditions and seemed to be more adapted to warming than to drought. Soil microbial communities in arid soils might be adapted to severe drought periods (Hueso et al. 2011), but our observations support multiple studies reporting reduced microbial activity under water limitation (Amarasinghe et al., 2024; Asensio et al., 2024; Lazicki et al., 2023; Oram et al., 2025; Ren et al., 2018; Szejgis et al., 2024; Wang et al., 2021; Xu et al., 2020), which caused a decline in soil resistance and resilience to episodes of climatic stress. As shown in forest and arable sites (Guillot et al. 2019; Lazicki et al. 2025), the combination of drought and heat stress exacerbated these effects, likely through drought-induced shifts in microbial community composition (Kost et al., 2024; Ochoa-Hueso et al., 2018; Petermann et al., 2024; Wittwer et al., 2023; Zhou et al., 2020). Also as previously reported (Megan-Steinweg et al. 2013; Guillot et al. 2019), DOC was promoted under no-tillage and concomitant drought and warming, possibly due to enhanced SOM decomposition (Canarini et al. 2017).

In response to drying-rewetting cycles, Zhang et al. (2019) reported high resistance but low resilience of soil multifunctionality under no-till. A similar trade-off between resistance and resilience was evident in our findings: while microbial activity was often maintained under stress, showing high resistance, recovery capacity post-disturbance (resilience) remained limited, and transient activity pulses (e.g., of urease activity) were detected. Soil basal respiration reflected the Birch effect (Birch 1958), i.e., the pulse of CO_2 released upon rewetting dry soil, which initially exceeds basal respiration rates (Liang et al. 2014; Du et al. 2021), which was also evident in DOC levels in our experiment. However, under warm conditions, soil microbial activity was generally resistant—possibly due to high microbial turnover (Tian et al. 2023)—, while resilience remained low. Specific microbial functions (i.e., β -glucosidase activity) showed high resilience in NT-mon, which might be due to microbial selection towards resilient communities when subjected to chronic perturbations (Philippot et al. 2021). Nevertheless, it is important to note that heat stress was applied at constant soil watering in our experiment. Since natural heat waves are often concomitant with reduced rainfall, our experimental conditions may underestimate warming effects in natural systems.

4.2 Microfaunal response to climatic stress varies across functional guilds

Contrary to most indicators of microbial functioning, opportunistic bacterial feeders showed low resistance but high resilience to climate stress. This was probably due to the increase in resource availability after the stress and during the recovery period, which would have favored the recovery of fast-growing, r-strategist nematodes. Soil bacteria have been shown to be resilient to drought due to their rapid growth, fast reproduction, and capacity to produce cysts (de Vries et al., 2013; Lennon and Jones, 2011). Fast bacterial recovery after drought has been observed in ecosystems with low mean annual precipitation (Tang et al. 2023) and in croplands (Brangarí et al. 2022), although some empirical evidence suggested low bacterial resistance to drought (Dacal et al. 2022).

Opportunistic bacterivore nematodes have also been found to be resilient to other ecosystem perturbations such as forest dieback (Sánchez-Moreno and Curiel Yuste 2022). In our study, this functional group is mainly represented by *Panagrolaimus* spp., a nematode genus with high anhydrobiotic potential (Ricci and Pagani 1997; Evangelista et al. 2017), which could explain their notable resilience. In contrast, generalist bacterivores (e.g., Cephalobidae) possess intrinsic attributes that confer resistance to stress, such as low-resource availability (Mosdossy et al. 2024) and drought-tolerance (Landesman et al., 2011; Treonis et al., 1999). Similarly, our observations on fungal feeder resistance to drought under low soil perturbations—probably linked to the resistance of fungi to short-term drying stress (Yuste et al. 2011; Barnard et al. 2013; Canarini et al. 2017, 2024; Tang et al. 2023)—, support that

resistance in fungal-based food webs is typical in low-perturbance systems (de Vries et al., 2012a). However, despite their resistance, fungal-based systems and associated nematodes often display low resilience and slow recovery following stress events (Vandeghechuchte et al. 2015; Bristol et al. 2023; Zhao et al. 2024; Boyle et al. 2024). In particular, fungal-feeding nematodes such as *Aphelenchus* and *Aphelenchoides* are well adapted and tolerant to a wide range of soil conditions, and their dominance may reflect a shift toward stress-tolerant taxa (Brangarí et al. 2022), especially in systems with a history of tillage disturbance. Indeed, no-till practices have shown some negative effects in terms of fungivore abundances (Dong et al. 2013; Cozimegges et al. 2025), suggesting that although fungal feeders were more abundant under tillage disturbance, tillage legacy reduced their resistance to drought.

Conversely, root-associates (nematodes that feed in root hairs, i.e., Tylenchidae) under no-till monoculture legacy showed low resistance but some resilience to climatic stress. These root-associates tended to decrease under crop rotation and were more abundant under no-till management, as previously reported (Sánchez-Moreno et al. 2006). Overall, plant-parasitic nematodes (including ecto- and endo-parasitic nematodes that feed in plant roots) showed low resistance to climate stress. In accordance with previous reports (Bristol et al., 2023; Yang et al., 2022; Zhao et al., 2024), drought significantly reduced their abundances, suppressing their populations regardless of soil legacy. However, they have shown considerable resilience to climatic conditions, likely explained by the high anhydrobiotic abilities detected in herbivores (i.e., *Pratylenchus*, Ribeiro et al., 2020), which contribute to their better recovery from drought stress. Besides, low soil disturbance and high SOC tended to increase populations of omnivores and predators, in line with previous studies (Sánchez-Moreno et al. 2006; Puissant et al. 2021; Betancur-Corredor et al. 2022; Lori et al. 2025). Tillage inhibited such groups, likely because they are sensitive to physical disturbance (Huang et al. 2025). Although they showed low resistance, omnivores and predators exhibited recovery under no-tillage monoculture legacy, reflecting the role of soil management legacy in soil food web response to climate change. As shown in the PCA analysis, changes in soil food webs induced by no-till were mainly driven by the positive effects of enhanced soil microbial activity, which promoted high trophic levels (omnivores-predators) probably controlled by bottom-up cascades (Zhang et al., 2025) and plant productivity.

4.3 No-tillage legacy enhances crop performance under climatic stress

Contrary to previous studies (Waibel et al. 2025), no-tillage legacy in this trial increased crop biomass under rainfed conditions. While aboveground biomass showed no signs of post-stress recovery, indicating a persistent tillage legacy effect on crop performance, shoot biomass generally tended to benefit from no-till legacy. Our results confirm previous observations on the positive effects of no-tillage on wheat root development in Mediterranean conditions (Muñoz-Romero et al. 2010). Notably, plant height under no-till with rotation remained unaffected by drought, whereas it declined under conventional tillage as previously reported (Kost et al. 2024). Overall, our results highlight a net positive effect of no-tillage combined with crop rotation legacy on crop performance, enhancing both resilience and resistance to climate stress. Although conservation tillage is often reported to have limited capacity to buffer drought effects (Wittwer et al. 2023), our findings suggest that soils conditioned by conservation agriculture better support crop recovery under extreme weather.

4.4 Contribution of SOC to soil resistance and resilience to climate change

Soil organic carbon is the keystone of ecosystem resilience against climate change (Imran 2025), ensuring crop yields under adverse weather conditions (Droste et al. 2020; He et al. 2025). High SOC levels promote soil water storage (Li et al., 2024b) and foster resistant microbial communities (Qi et al. 2025), but the mechanisms that explain the link between soil carbon and soil response to climate change are not fully understood. In some cases, SOC does not explain the observed differences in soil resilience against climatic extremes (Kost et al. 2024). In accordance with such observations, our results only partially support the hypothesis on the key role of soil organic carbon in soil resistance and resilience. Although we observed generally positive associations between SOC levels and resistance and/or resistance of soil functions and the soil food web, significant associations were limited, which suggests that other soil properties and functions might be driving soil organisms' resilience and resistance to climatic stress.

5. Conclusion

In conclusion, our study showed that long-lasting soil management legacies based on minimizing soil disturbance and diversifying crops, exert a strong influence on soil biota and crop resistance and resilience against climate change. Management legacies determined soil moisture levels during peak climate stress, and no-tillage practices combined with crop rotation effectively buffered against negative impacts of dry and hot climatic conditions. Our hypothesis on the capacity of low-perturbance management practices to mitigate the negative effects of climate changes in crop soils proved true, as did our expectations on increasing soil resistance and resilience under reduced soil perturbation. Our results, however, are based on an experimental setup, and experimental limitations such as restricted soil volume in pots, the absence of fluctuating precipitation patterns and other biotic (e.g. pest) and abiotic (e.g. wind) interactions, prevent direct extrapolations to natural conditions, which have to be done with caution. In spite of such limitations, our results provide relevant insights into the effects of soil management legacy on soil functioning and ecosystem services in future climatic scenarios.

Declarations

Acknowledgments

This project was funded by MICIU/AEI/10.13039/501100011033 (PID2019-105373RB-I00). P.L. was supported by a MICIU/AEI/10.13039/501100011033 and "ESF Investing in your future" grant (PRE2020-093315). We are deeply grateful to Patricia Plaza and Miguel Ángel Porcel for their invaluable support during field and lab work, and Inés Santín for her hard work leading the long-term field experiment which provided experimental soils. T.C.H. wants to thank Claire Marsden for her kind support along her MSc research work.

Data availability

Datasets used for this study and R codes associated with this analysis can be accessed on Zenodo (<https://doi.org/10.5281/zenodo.16679856>).

Authors' contributions

P.L: data curation, formal analysis, investigation, visualization, writing- original draft, writing – review and editing. T.C-H: investigation, writing – review and editing. MdM.D: conceptualization, investigation, writing – review and editing. M.T: conceptualization, investigation, writing – review and editing. S.S-M: conceptualization, visualization, funding acquisition, writing – review and editing, writing – original draft, supervision, project administration.

Competing Interest declaration

The authors declare that they have no competing interests.

References

1. Adil M, Wang Z, Chen Y, et al (2025) Long-term impacts of agronomic practices on winter wheat yield, water use efficiency, and nitrogen use efficiency in global dryland regions: A meta-analysis. *Soil Tillage Res* 253:106653. <https://doi.org/10.1016/J.STILL.2025.106653>
2. Álvaro-Fuentes J, Cantero-Martínez C, Alonso-Ayuso M, et al (2025) Soil carbon, aggregation and crop residue dynamics under different tillage and nitrogen fertilization strategies in rainfed Mediterranean conditions. *Soil Tillage Res* 253:106650. <https://doi.org/10.1016/J.STILL.2025.106650>
3. Amarasinghe A, Chen C, Van Zwieten L, Rashti MR (2024) The role of edaphic variables and management practices in regulating soil microbial resilience to drought - A meta-analysis. *Sci Total Environ* 912:169544. <https://doi.org/10.1016/J.SCITOTENV.2023.169544>
4. Asensio D, Zuccarini P, Sardans J, et al (2024) Soil biomass-related enzyme activity indicates minimal functional changes after 16 years of persistent drought treatment in a Mediterranean holm oak forest. *Soil Biol Biochem* 189:109281. <https://doi.org/10.1016/J.SOILBIO.2023.109281>
5. Asseng S, Ewert F, Martre P, et al (2014) Rising temperatures reduce global wheat production. *Nat Clim Chang* 2014 52 5:143–147. <https://doi.org/10.1038/nclimate2470>
6. Barker K, Carter CC, Sasser J (1985) An advanced treatise on Meloidogyne. Volume II: Methodology.
7. Barnard RL, Osborne CA, Firestone MK (2013) Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME J* 7:2229–2241. <https://doi.org/10.1038/ISMEJ.2013.104>
8. Bartoń K (2023) MuMIn: Multi-Model Inference
9. Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/JSS.V067.I01>
10. Bengtsson J (2002) Disturbance and resilience in soil animal communities. *Eur J Soil Biol* 38:119–125. [https://doi.org/10.1016/S1164-5563\(02\)01133-0](https://doi.org/10.1016/S1164-5563(02)01133-0)
11. Betancur-Corredor B, Lang B, Russell DJ (2023) Organic nitrogen fertilization benefits selected soil fauna in global agroecosystems. *Biol Fertil Soils* 59:1–16. <https://doi.org/10.1007/S00374-022-01677-2/FIGURES/8>
12. Betancur-Corredor B, Lang B, Russell DJ (2022) Reducing tillage intensity benefits the soil micro- and mesofauna in a global meta-analysis. *Eur J Soil Sci* 73:e13321. <https://doi.org/10.1111/EJSS.13321>; WEBSITE: WEBSITE: BSSS JOURNALS; PAGE GROUP: STRING: PUBLICATION
13. Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10:9–31. <https://doi.org/10.1007/BF01343734/METRICS>
14. Blanco-Canqui H, Ruis SJ (2018) No-tillage and soil physical environment. *Geoderma* 326:164–200. <https://doi.org/10.1016/J.GEODERMA.2018.03.011>
15. Bonciarelli U, Onofri A, Benincasa P, et al (2016) Long-term evaluation of productivity, stability and sustainability for cropping systems in Mediterranean rainfed conditions. *Eur J Agron* 77:146–155. <https://doi.org/10.1016/J.EJA.2016.02.006>
16. Bongers T (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83:14–19. <https://doi.org/10.1007/BF00324627/METRICS>
17. Bongiorno G, Bodenhausen N, Bünemann EK, et al (2019) Reduced tillage, but not organic matter input, increased nematode diversity and food web stability in European long-term field experiments. *Mol Ecol* 28:4987–5005. <https://doi.org/10.1111/MEC.15270>
18. Boyle JA, Murphy BK, Ensminger I, et al (2024) Resistance and resilience of soil microbiomes under climate change. *Ecosphere* 15:e70077. <https://doi.org/10.1002/ECS2.70077>
19. Brangarí AC, Lyonnard B, Rousk J (2022) Soil depth and tillage can characterize the soil microbial responses to drying-rewetting. *Soil Biol Biochem* 173:108806. <https://doi.org/10.1016/J.SOILBIO.2022.108806>
20. Bristol D, Hassan I, Kamrul, Blankinship JC, et al (2023) Responses of nematode abundances to increased and reduced rainfall under field conditions: A meta-analysis. *Ecosphere* 14:e4364. <https://doi.org/10.1002/ECS2.4364>
21. Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. <https://doi.org/10.32614/RJ-2017-066>
22. Brussaard L, de Ruiter PC, Brown GG (2007) Soil biodiversity for agricultural sustainability. *Agric Ecosyst Environ* 121:233–244. <https://doi.org/10.1016/J.AGEE.2006.12.013>

23. Canarini A, Fuchslueger L, Schnecker J, et al (2024) Soil fungi remain active and invest in storage compounds during drought independent of future climate conditions. *Nat Commun* 2024 15:1–13. <https://doi.org/10.1038/s41467-024-54537-y>
24. Canarini A, Kiær LP, Dijkstra FA (2017) Soil carbon loss regulated by drought intensity and available substrate: A meta-analysis. *Soil Biol Biochem* 112:90–99. <https://doi.org/10.1016/J.SOILBIO.2017.04.020>
25. Castellini M, Fornaro F, Garofalo P, et al (2019) Effects of No-Tillage and Conventional Tillage on Physical and Hydraulic Properties of Fine Textured Soils under Winter Wheat. *Water* 2019, Vol 11, Page 484 11:484. <https://doi.org/10.3390/W11030484>
26. Chen H, Dai Z, Veach AM, et al (2020) Global meta-analyses show that conservation tillage practices promote soil fungal and bacterial biomass. *Agric Ecosyst Environ* 293:106841. <https://doi.org/10.1016/J.AGEE.2020.106841>
27. Colunga SL, Wahab L, Fierro Cabo A, Pereira E (2025) Carbon sequestration through conservation tillage in sandy soils of arid and semi-arid climates: A meta-analysis. *Soil Tillage Res* 245:106310. <https://doi.org/10.1016/j.still.2024.106310>
28. Costa A, Bommarco R, Smith ME, et al (2024) Crop rotational diversity can mitigate climate-induced grain yield losses. *Glob Chang Biol* 30:e17298. <https://doi.org/10.1111/GCB.17298;PAGE:STRING:ARTICLE/CHAPTER>
29. Cozim-Melges F, Ripoll-Bosch R, Oggiano P, et al (2025) The effect of alternative agricultural practices on soil biodiversity of bacteria, fungi, nematodes and earthworms: A review. *Agric Ecosyst Environ* 379:109329. <https://doi.org/10.1016/J.AGEE.2024.109329>
30. Dacal M, García-Palacios P, Asensio S, et al (2022) Climate change legacies contrastingly affect the resistance and resilience of soil microbial communities and multifunctionality to extreme drought. *Funct Ecol* 36:908–920. <https://doi.org/10.1111/1365-2435.14000/SUPPINFO>
31. de Oliveira AB, Cantarel AAM, Seiller M, et al (2020) Short-term plant legacy alters the resistance and resilience of soil microbial communities exposed to heat disturbance in a Mediterranean calcareous soil. *Ecol Indic* 108:105740. <https://doi.org/10.1016/j.ecolind.2019.105740>
32. de Vries FT, Liiri ME, Bjørnlund L, et al (2012) Legacy effects of drought on plant growth and the soil food web. *Oecologia* 170:821–833. <https://doi.org/10.1007/S00442-012-2331-Y/FIGURES/5>
33. De Vries FT, Liiri ME, Bjørnlund L, et al (2012) Land use alters the resistance and resilience of soil food webs to drought. *Nat Clim Chang* 2012 24 2:276–280. <https://doi.org/10.1038/nclimate1368>
34. De Vries FT, Thébault E, Liiri M, et al (2013) Soil food web properties explain ecosystem services across European land use systems. *Proc Natl Acad Sci U S A* 110:14296–14301. https://doi.org/10.1073/PNAS.1305198110/SUPPL_FILE/SAPP.PDF
35. Dias T, Dukes A, Antunes PM (2014) Accounting for soil biotic effects on soil health and crop productivity in the design of crop rotations. *J Sci Food Agric* 95:447–454. <https://doi.org/10.1002/JSFA.6565;REQUESTEDJOURNAL:JOURNAL:10970010;WGROUPE:STRING:PUBLICATION>
36. Dong Z, Hou R, Chen Q, et al (2013) Response of soil nematodes to elevated temperature in conventional and no-tillage cropland systems. *Plant Soil* 373:907–918. <https://doi.org/10.1007/S11104-013-1846-2/FIGURES/3>
37. Droste N, May W, Clough Y, et al (2020) Soil carbon insures arable crop production against increasing adverse weather due to climate change. *Environ Res Lett* 15:124034. <https://doi.org/10.1088/1748-9326/ABC5E3>
38. Du K, Li F, Qiao Y, et al (2021) Influence of no-tillage and precipitation pulse on continuous soil respiration of summer maize affected by soil water in the North China Plain. *Sci Total Environ* 766:144384. <https://doi.org/10.1016/J.SCITOTENV.2020.144384>
39. Eeswaran R, Nejadhashemi AP, Alves FC, Saravi B (2021) Evaluating the applicability of soil moisture-based metrics for gauging the resiliency of rainfed agricultural systems in the midwestern United States. *Soil Tillage Res* 205:104818. <https://doi.org/10.1016/J.STILL.2020.104818>
40. Evangelista CCS, Guidelli GV, Borges G, et al (2017) Multiple genes contribute to anhydrobiosis (tolerance to extreme desiccation) in the nematode *Panagrolaimus superbus*. *Genet Mol Biol* 40:790–802. <https://doi.org/10.1590/1678-4685-GMB-2017-0030>
41. Farina R, Piccini C, Bene C Di, et al (2024) No tillage and leguminous cover crop improve soil quality in a typical rainfed Mediterranean system. *Can J Soil Sci* 104:257–272. https://doi.org/10.1139/CJSS-2023-0106/ASSET/IMAGES/CJSS-2023-0106_F6.JPG
42. Ferris H, Bongers T, de Goede RGM (2001) A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Appl Soil Ecol* 18:13–29. [https://doi.org/10.1016/S0929-1393\(01\)00152-4](https://doi.org/10.1016/S0929-1393(01)00152-4)
43. Fiorentini M, Orsini R, Zenobi S, et al (2024) Soil tillage reduction as a climate change mitigation strategy in Mediterranean cereal-based cropping systems. *Soil Use Manag* 40:e13050. <https://doi.org/10.1111/SUM.13050>
44. Fox J, Weisberg S (2018) *An R companion to applied regression*. Sage publications
45. Gandía ML, Del Monte JP, Tenorio JL, Santín-Montanyá MI (2021) The influence of rainfall and tillage on wheat yield parameters and weed population in monoculture versus rotation systems. *Sci Reports* 2021 11:1–12. <https://doi.org/10.1038/s41598-021-00934-y>
46. Guillot E, Hinsinger P, Dufour L, et al (2019) With or without trees: Resistance and resilience of soil microbial communities to drought and heat stress in a Mediterranean agroforestry system. *Soil Biol Biochem* 129:122–135. <https://doi.org/10.1016/J.SOILBIO.2018.11.011>
47. Hartig F (2021) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models
48. He Q, Li L, Shi Y, et al (2025) Soil organic carbon improvement for mitigating crop yield losses under global warming. *Eur J Agron* 170:127739. <https://doi.org/10.1016/J.EJA.2025.127739>
49. Henneron L, Bernard L, Hedde M, et al (2015) Fourteen years of evidence for positive effects of conservation agriculture and organic farming on soil life. *Agron Sustain Dev* 35:169–181. <https://doi.org/10.1007/S13593-014-0215-8/FIGURES/5>
50. Hernanz JL, López R, Navarrete L, Sánchez-Girón V (2002) Long-term effects of tillage systems and rotations on soil structural stability and organic carbon stratification in semiarid central Spain. *Soil Tillage Res* 66:129–141. [https://doi.org/10.1016/S0167-1987\(02\)00021-1](https://doi.org/10.1016/S0167-1987(02)00021-1)

51. Holatko J, Brtnicky M, Baltazar T, et al (2024) Long-term effects of wheat continuous cropping vs wheat in crop rotation on carbon content and mineralisation, aggregate stability, biological activity, and crop yield. *Eur J Agron* 158:127218. <https://doi.org/10.1016/J.EJA.2024.127218>
52. Huang Y, Xu W, Xiao F, et al (2025) Anthropogenic disturbances shape soil nematode communities in urban green spaces. *CATENA* 250:108790. <https://doi.org/10.1016/J.CATENA.2025.108790>
53. Hudson BD (1994) Soil organic matter and available water capacity. *J Soil Water Conserv* 49:189–194. <https://doi.org/10.1080/00224561.1994.12456850>
54. Hueso S, Hernández T, García C (2011) Resistance and resilience of the soil microbial biomass to severe drought in semiarid soils: The importance of organic amendments. *Appl Soil Ecol* 50:27–36. <https://doi.org/10.1016/J.APSOIL.2011.07.014>
55. Imran (2025) Carbon Cultivation for Sustainable Agriculture, Ecosystem Resilience, and Climate Change Mitigation. *Commun Soil Sci Plant Anal* 56:1430–1456. <https://doi.org/10.1080/00103624.2025.2453996>
56. Ingrisch J, Bahn M (2018) Towards a Comparable Quantification of Resilience. *Trends Ecol Evol* 33:251–259. <https://doi.org/10.1016/j.tree.2018.01.013>
57. Isbell F, Adler PR, Eisenhauer N, et al (2017) Benefits of increasing plant diversity in sustainable agroecosystems. *J Ecol* 105:871–879. <https://doi.org/10.1111/1365-2745.12789>
58. Joergensen RG (1996) The fumigation-extraction method to estimate soil microbial biomass: Calibration of the kEC value. *Soil Biol Biochem* 28:25–31. [https://doi.org/10.1016/0038-0717\(95\)00102-6](https://doi.org/10.1016/0038-0717(95)00102-6)
59. Kaisermann A, Roguet A, Nunan N, et al (2013) Agricultural management affects the response of soil bacterial community structure and respiration to water-stress. *Soil Biol Biochem* 66:69–77. <https://doi.org/10.1016/J.SOILBIO.2013.07.001>
60. Kan ZR, Liu WX, Liu WS, et al (2022) Mechanisms of soil organic carbon stability and its response to no-till: A global synthesis and perspective. *Glob Chang Biol* 28:693–710. <https://doi.org/10.1111/GCB.15968>;REQUESTEDJOURNAL:JOURNAL:13652486;JOURNAL:JOURNAL:13652486;WGROU:STRING:PUBLICATION
61. Kim DH, Wade T, Brym Z, et al (2025) Assessing the agricultural, environmental, and economic effects of crop diversity management: A comprehensive review on crop rotation and cover crop practices. *J Environ Manage* 387:125833. <https://doi.org/10.1016/J.JENVMAN.2025.125833>
62. Kost E, Kundel D, Conz RF, et al (2024) Soil microbial resistance and resilience to drought under organic and conventional farming. *Eur J Soil Biol* 123:103690. <https://doi.org/10.1016/J.EJSOBI.2024.103690>
63. Lampurlanés J, Plaza-Bonilla D, Álvaro-Fuentes J, Cantero-Martínez C (2016) Long-term analysis of soil water conservation and crop yield under different tillage systems in Mediterranean rainfed conditions. *F Crop Res* 189:59–67. <https://doi.org/10.1016/J.FCR.2016.02.010>
64. Landesman WJ, Treonis AM, Dighton J (2011) Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. *Pedobiologia (Jena)* 54:87–91. <https://doi.org/10.1016/J.PEDOBI.2010.10.002>
65. Lavalée JM, Chomel M, Alvarez Segura N, et al (2024) Land management shapes drought responses of dominant soil microbial taxa across grasslands. *Nat Commun* 15:1–11. <https://doi.org/10.1038/S41467-023-43864-1>;TECHMETA=23,45;SUBJMETA=158,2445,2453,704,855;KWRD=ECOSYSTEM+ECOLOGY,GRASSLAND+ECOLOGY,MICROBIAL+ECOLOGY
66. Lazicki P, Lee J, Mengistu A, Jagadamma S (2023) Drought, heat, and management interact to affect soil carbon and nitrogen losses in a temperate, humid climate. *Appl Soil Ecol* 189:104947. <https://doi.org/10.1016/J.APSOIL.2023.104947>
67. Lazicki P, Lee J, Mengistu A, Jagadamma S (2025) Do soil health indicators predict carbon and nitrogen functional stability under drought and heat? *PLoS One* 20:e0325128. <https://doi.org/10.1371/JOURNAL.PONE.0325128>
68. Lennon JT, Jones SE (2011) Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat Rev Microbiol* 2011 9:119–130. <https://doi.org/10.1038/nrmicro2504>
69. Lenth R V (2024) emmeans: Estimated Marginal Means, Aka Least-Squares Means
70. Li T, Li G, Lu Z, et al (2024a) Crop diversification increases soil extracellular enzyme activities under no tillage: A global meta-analysis. *Soil Tillage Res* 235:105870. <https://doi.org/10.1016/J.STILL.2023.105870>
71. Li Y, Feng X, Huai Y, et al (2024b) Enhancing crop productivity and resilience by promoting soil organic carbon and moisture in wheat and maize rotation. *Agric Ecosyst Environ* 368:109021. <https://doi.org/10.1016/J.AGEE.2024.109021>
72. Liang C, Zhu X, Fu S, et al (2014) Biochar alters the resistance and resilience to drought in a tropical soil. *Environ Res Lett* 9:064013. <https://doi.org/10.1088/1748-9326/9/6/064013>
73. Liu C, Feng X, Xu Y, et al (2023) Legume-based rotation enhances subsequent wheat yield and maintains soil carbon storage. *Agron Sustain Dev* 43:1–13. <https://doi.org/10.1007/S13593-023-00918-4>;METRICS
74. Liu X, Tan S, Song X, et al (2022) Response of soil organic carbon content to crop rotation and its controls: A global synthesis. *Agric Ecosyst Environ* 335:108017. <https://doi.org/10.1016/J.AGEE.2022.108017>
75. López-Bellido RJ, Fontán JM, López-Bellido FJ, López-Bellido L (2010) Carbon Sequestration by Tillage, Rotation, and Nitrogen Fertilization in a Mediterranean Vertisol. *Agron J* 102:310–318. <https://doi.org/10.2134/AGRONJ2009.0165>
76. Lori M, Leitaó R, Felix D, et al (2025) Response of soil biota to agricultural management practices: A systematic quantitative meta-data-analysis and method selection framework. *Soil Biol Biochem* 207:109815. <https://doi.org/10.1016/J.SOILBIO.2025.109815>
77. Madejón E, Murillo JM, Moreno F, et al (2009) Effect of long-term conservation tillage on soil biochemical properties in Mediterranean Spanish areas. *Soil Tillage Res* 105:55–62. <https://doi.org/10.1016/J.STILL.2009.05.007>

78. Madejón P, Fernández-Boy E, Morales-Salmerón L, et al (2023) Could conservation tillage increase the resistance to drought in Mediterranean faba bean crops? *Agric Ecosyst Environ* 349:108449. <https://doi.org/10.1016/J.AGEE.2023.108449>
79. Malik AA, Bouskill NJ (2022) Drought impacts on microbial trait distribution and feedback to soil carbon cycling. *Funct Ecol* 36:1442–1456. <https://doi.org/10.1111/1365-2435.14010>
80. Martín-Lammerding D, Navas M, Albarrán M del M, et al (2015) LONG term management systems under semiarid conditions: Influence on labile organic matter, β -glucosidase activity and microbial efficiency. *Appl Soil Ecol* 96:296–305. <https://doi.org/10.1016/J.APSOIL.2015.08.021>
81. Martín-Lammerding D, Tenorio JL, Albarrán M, et al (2013) Influence of tillage practices on soil biologically active organic matter content over a growing season under semiarid Mediterranean climate. *Spanish J Agric Res* 11:232–243. <https://doi.org/10.5424/SJAR/2013111-3455>
82. Martín-Rueda I, Muñoz-Guerra LM, Yunta F, et al (2007) Tillage and crop rotation effects on barley yield and soil nutrients on a Calciortidic Haploxeralf. *Soil Tillage Res* 92:1–9. <https://doi.org/10.1016/J.STILL.2005.10.006>
83. Maxwell TL, Canarini A, Bogdanovic I, et al (2022) Contrasting drivers of belowground nitrogen cycling in a montane grassland exposed to a multifactorial global change experiment with elevated CO₂, warming, and drought. *Glob Chang Biol* 28:2425–2441. <https://doi.org/10.1111/GCB.16035>;PAGEGROUP:STRING:PUBLICATION
84. McDaniel MD, Tiemann LK, Grandy AS (2014) Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecol Appl* 24:560–570. <https://doi.org/10.1890/13-0616.1>
85. Megan-Steinweg J, Dukes JS, Paul EA, et al (2013) Microbial responses to multi-factor climate change: effects on soil enzymes. *Front Microbiol* 4:146. <https://doi.org/10.3389/FMICB.2013.00146/BIBTEX>
86. Mosdossy K, Kallenbach CM, Mimee B (2024) Adding ligneous litter to cultivated organic soil changes the soil micro-food web and alters soil nitrogen availability. *Appl Soil Ecol* 196:105271. <https://doi.org/https://doi.org/10.1016/j.apsoil.2024.105271>
87. Muñoz-Romero V, Benítez-Vega J, López-Bellido L, López-Bellido RJ (2010) Monitoring wheat root development in a rainfed vertisol: Tillage effect. *Eur J Agron* 33:182–187. <https://doi.org/10.1016/J.EJA.2010.05.004>
88. Nannipieri P, Ceccanti B, Cervelli S, Matarese E (1980) Extraction of Phosphatase, Urease, Proteases, Organic Carbon, and Nitrogen from Soil. *Soil Sci Soc Am J* 44:1011–1016. <https://doi.org/10.2136/SSSAJ1980.03615995004400050028X>
89. Nunes MR, Karlen DL, Veum KS, et al (2020) Biological soil health indicators respond to tillage intensity: A US meta-analysis. *Geoderma* 369:114335. <https://doi.org/10.1016/J.GEODERMA.2020.114335>
90. Ochoa-Hueso R, Collins SL, Delgado-Baquerizo M, et al (2018) Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Glob Chang Biol* 24:2818–2827. <https://doi.org/10.1111/GCB.14113>
91. Oksanen, Jari, Gavin L. Simpson, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin RBO (2022) *vegan: Community Ecology Package*
92. Olsen SR, Watanabe FS (1957) A Method to Determine a Phosphorus Adsorption Maximum of Soils as Measured by the Langmuir Isotherm. *Soil Sci Soc Am J* 21:144–149. <https://doi.org/10.2136/SSSAJ1957.03615995002100020004X>
93. Oram NJ, Brennan F, Praeg N, et al (2025) Plant community composition and traits modulate the impacts of drought intensity on soil microbial community composition and function. *Soil Biol Biochem* 200:109644. <https://doi.org/10.1016/j.soilbio.2024.109644>
94. Orwin KH, Wardle DA (2004) New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. *Soil Biol Biochem* 36:1907–1912. <https://doi.org/10.1016/J.SOILBIO.2004.04.036>
95. Papp R, Marinari S, Moscatelli MC, et al (2018) Short-term changes in soil biochemical properties as affected by subsidiary crop cultivation in four European pedo-climatic zones. *Soil Tillage Res* 180:126–136. <https://doi.org/10.1016/J.STILL.2018.02.019>
96. Pareja-Sánchez E, Plaza-Bonilla D, Ramos MC, et al (2017) Long-term no-till as a means to maintain soil surface structure in an agroecosystem transformed into irrigation. *Soil Tillage Res* 174:221–230. <https://doi.org/10.1016/J.STILL.2017.07.012>
97. Peralta AL, Sun Y, McDaniel MD, Lennon JT (2018) Crop rotational diversity increases disease suppressive capacity of soil microbiomes. *Ecosphere* 9:e02235. <https://doi.org/10.1002/ECS2.2235>;WEBSITE:WEBSITE:ESAJOURNALS;REQUESTEDJOURNAL:JOURNAL:21508925;WGROU:STRING:PUBLICATION
98. Petermann BJ, Lewis K, Acosta-Martinez V, et al (2024) Soil health influenced more by conservation tillage and cropping practice than irrigation level in a sandy semiarid cotton system. *Soil Sci Soc Am J* 204:105711. <https://doi.org/10.1002/SAJ2.20737>
99. Philippot L, Griffiths BS, Langenheder S (2021) Microbial Community Resilience across Ecosystems and Multiple Disturbances. *Microbiol Mol Biol Rev* 85:. <https://doi.org/10.1128/MMBR.00026-20/ASSET/857C84E6-4F1B-423E-832E-F0396D8E8F71/ASSETS/IMAGES/LARGE/MMBR.00026-20-F0006.JPG>
100. Pimm SL (1984) The complexity and stability of ecosystems. *Nat* 1984 3075949 307:321–326. <https://doi.org/10.1038/307321a0>
101. Pittelkow CM, Linquist BA, Lundy ME, et al (2015) When does no-till yield more? A global meta-analysis. *F Crop Res* 183:156–168. <https://doi.org/10.1016/J.FCR.2015.07.020>
102. Puissant J, Villenave C, Chauvin C, et al (2021) Quantification of the global impact of agricultural practices on soil nematodes: A meta-analysis. *Soil Biol Biochem* 161:108383. <https://doi.org/10.1016/J.SOILBIO.2021.108383>
103. Qi J, Gao M, Peng Z, et al (2025) Microbial community resistance is associated with soil carbon degradation under warming condition in dryland agroecosystems. *Appl Soil Ecol* 212:106168. <https://doi.org/10.1016/J.APSOIL.2025.106168>
104. R Core Team (2024) *R: A Language and Environment for Statistical Computing* Title

105. Ren C, Chen J, Lu X, et al (2018) Responses of soil total microbial biomass and community compositions to rainfall reductions. *Soil Biol Biochem* 116:4–10. <https://doi.org/10.1016/j.soilbio.2017.09.028>
106. Ribeiro LM, Campos HD, Neves DL, Dias-Arieira CR (2020) Survival of *Pratylenchus brachyurus* under dry soil conditions. *Heliyon* 6:e05075. <https://doi.org/10.1016/J.HELIYON.2020.E05075>
107. Ricci C, Pagani M (1997) Desiccation of *Panagrolaimus rigidus* (Nematoda): Survival, reproduction and the influence on the internal clock. *Hydrobiologia* 347:1–13. <https://doi.org/10.1023/A:1002979522816/METRICS>
108. Sae-Tun O, Bodner G, Rosinger C, et al (2022) Fungal biomass and microbial necromass facilitate soil carbon sequestration and aggregate stability under different soil tillage intensities. *Appl Soil Ecol* 179:104599. <https://doi.org/10.1016/J.APSOIL.2022.104599>
109. Sánchez-Moreno S, Curiel Yuste J (2022) Forest dieback switches the relationships between microfaunal bacterivore guilds and soil nutrients. *Soil Biol Biochem* 172:108763. <https://doi.org/10.1016/j.soilbio.2022.108763>
110. Sánchez-Moreno S, Minoshima H, Ferris H, Jackson LE (2006) Linking soil properties and nematode community composition: effects of soil management on soil food webs. *Nematology* 8:703–715. <https://doi.org/10.1163/156854106778877857>
111. Santín-Montanyá MI, Gandía-Toledano ML, Zambrana E, Tenorio JL (2020) Effects of tillage systems on wheat and weed water relationships over time when growing together, in semiarid conditions. *Ann Appl Biol* 177:256–265. <https://doi.org/10.1111/AAB.12620;PAGEGROUP:STRING:PUBLICATION>
112. Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88:1386–1394. <https://doi.org/10.1890/06-0219;WEBSITE:WEBSITE:ESAJOURNALS;REQUESTEDJOURNAL:JOURNAL:19399170;JOURNAL:JOURNAL:19399170;WGROUP:STRING:PUBLICATION>
113. Schimel JP (2018) Life in dry soils: Effects of drought on soil microbial communities and processes. *Annu Rev Ecol Evol Syst* 49:409–432. <https://doi.org/10.1146/ANNUREV-ECOLSYS-110617-062614/CITE/REFWORKS>
114. Six J, Elliott ET, Paustian K (2000) Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. *Soil Biol Biochem* 32:2099–2103. [https://doi.org/10.1016/S0038-0717\(00\)00179-6](https://doi.org/10.1016/S0038-0717(00)00179-6)
115. Six J, Feller C, Denef K, et al (2002) Soil organic matter, biota and aggregation in temperate and tropical soils - Effects of no-tillage. *Agronomie* 22:755–775. <https://doi.org/10.1051/AGRO:2002043>
116. Sombrero A, de Benito A (2010) Carbon accumulation in soil. Ten-year study of conservation tillage and crop rotation in a semi-arid area of Castile-Leon, Spain. *Soil Tillage Res* 107:64–70. <https://doi.org/10.1016/J.STILL.2010.02.009>
117. Szejgis J, Carrillo Y, Jeffries TC, et al (2024) Altered rainfall greatly affects enzyme activity but has limited effect on microbial biomass in Australian dryland soils. *Soil Biol Biochem* 189:109277. <https://doi.org/10.1016/j.soilbio.2023.109277>
118. Tabatabai MA (1982) Soil Enzymes. 903–947. <https://doi.org/10.2134/AGRONMONOGR9.2.2ED.C43>
119. Tabatabai MA, Bremner JM (1969) Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. *Soil Biol Biochem* 1:301–307. [https://doi.org/10.1016/0038-0717\(69\)90012-1](https://doi.org/10.1016/0038-0717(69)90012-1)
120. Tadiello T, Acutis M, Perego A, et al (2023) Soil organic carbon under conservation agriculture in Mediterranean and humid subtropical climates: Global meta-analysis. *Eur J Soil Sci* 74:e13338. <https://doi.org/10.1111/EJSS.13338>
121. Tang Y, Winterfeldt S, Brangarí AC, et al (2023) Higher resistance and resilience of bacterial growth to drought in grasslands with historically lower precipitation. *Soil Biol Biochem* 177:108889. <https://doi.org/10.1016/J.SOILBIO.2022.108889>
122. Teng J, Hou R, Dungait JAJ, et al (2024) Conservation agriculture improves soil health and sustains crop yields after long-term warming. *Nat Commun* 2024 151 15:1–12. <https://doi.org/10.1038/s41467-024-53169-6>
123. Tian Y, Schindlbacher A, Malo CU, et al (2023) Long-term warming of a forest soil reduces microbial biomass and its carbon and nitrogen use efficiencies. *Soil Biol Biochem* 184:109109. <https://doi.org/10.1016/J.SOILBIO.2023.109109>
124. Tiemann LK, Grandy AS, Atkinson EE, et al (2015) Crop rotational diversity enhances belowground communities and functions in an agroecosystem. *Ecol Lett* 18:761–771. <https://doi.org/10.1111/ELE.12453>
125. Treonis AM, Unangst SK, Kepler RM, et al (2018) Characterization of soil nematode communities in three cropping systems through morphological and DNA metabarcoding approaches. *Sci Reports* 2018 81 8:1–12. <https://doi.org/10.1038/s41598-018-20366-5>
126. Treonis AM, Wall DH, Virginia RA (1999) Invertebrate biodiversity in Antarctic Dry Valley soils and sediments. *Ecosystems* 2:482–492. <https://doi.org/10.1007/S100219900096/METRICS>
127. Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. *Soil Biol Biochem* 19:703–707. [https://doi.org/10.1016/0038-0717\(87\)90052-6](https://doi.org/10.1016/0038-0717(87)90052-6)
128. Vandegehuchte ML, Sylvain ZA, Reichmann LG, et al (2015) Responses of a desert nematode community to changes in water availability. *Ecosphere* 6:1–15. <https://doi.org/10.1890/ES14-00319.1>
129. Venter ZS, Jacobs K, Hawkins HJ (2016) The impact of crop rotation on soil microbial diversity: A meta-analysis. *Pedobiologia (Jena)* 59:215–223. <https://doi.org/10.1016/J.PEDOBI.2016.04.001>
130. Waibel M, Michel J, Antoine M, et al (2025) Tensions in tillage: Reduction in tillage intensity associates with lower wheat growth and nutritional grain quality despite enhanced soil biological indicators. *Agric Ecosyst Environ* 389:109675. <https://doi.org/10.1016/J.AGEE.2025.109675>
131. Waibel M, Michel J, Antoine M, et al (2024) Tensions in tillage: Reduction in tillage intensity associates with lower wheat growth and nutritional grain quality despite enhanced soil biological indicators. *bioRxiv* 2024.12.09.627503. <https://doi.org/10.1101/2024.12.09.627503>

132. Walkley A (1935) An Examination of Methods for Determining Organic Carbon and Nitrogen in Soils¹. (With One Text-figure.). *J Agric Sci* 25:598–609. <https://doi.org/10.1017/S0021859600019687>
133. Wang C, Sun Y, Chen HYH, et al (2021) Meta-analysis shows non-uniform responses of above- and belowground productivity to drought. *Sci Total Environ* 782:146901. <https://doi.org/10.1016/J.SCITOTENV.2021.146901>
134. Wang Y, Ji H, Chen Y, et al (2023) Thirty-year dryland crop rotation improves soil multifunctionality and shifts soil fungal community. *Plant Soil* 507:11–24. <https://doi.org/10.1007/S11104-023-06412-W/FIGURES/4>
135. Wang Y, Ji H, Wang R, et al (2017) Impact of root diversity upon coupling between soil C and N accumulation and bacterial community dynamics and activity: Result of a 30 year rotation experiment. *Geoderma* 292:87–95. <https://doi.org/10.1016/j.geoderma.2017.01.014>
136. Wickham H (2016) ggplot2. <https://doi.org/10.1007/978-3-319-24277-4>
137. Wittwer RA, Klaus VH, Miranda Oliveira E, et al (2023) Limited capability of organic farming and conservation tillage to enhance agroecosystem resilience to severe drought. *Agric Syst* 211:103721. <https://doi.org/10.1016/J.AGSY.2023.103721>
138. Xu S, Geng W, Sayer EJ, et al (2020) Soil microbial biomass and community responses to experimental precipitation change: A meta-analysis. *Soil Ecol Lett* 2:93–103. <https://doi.org/10.1007/S42832-020-0033-7/METRICS>
139. Yang G, Wagg C, Veresoglou SD, et al (2018) How Soil Biota Drive Ecosystem Stability. *Trends Plant Sci* 23:1057–1067. <https://doi.org/10.1016/J.TPLANTS.2018.09.007>
140. Yang Q, Veen GF, Wagenaar R, et al (2022) Temporal dynamics of range expander and congeneric native plant responses during and after extreme drought events. *Ecol Monogr* 92:e1529. <https://doi.org/10.1002/ECM.1529>
141. Ye Y, Xiao S, Liu S, et al (2020) Tillage induces rapid loss of organic carbon in large macroaggregates of calcareous soils. *Soil Tillage Res* 199:104549. <https://doi.org/10.1016/J.STILL.2019.104549>
142. Yeates GW, Bongers T, De Goede RGM, et al (1993) Feeding Habits in Soil Nematode Families and Genera—An Outline for Soil Ecologists. *J Nematol* 25:315
143. Yuste JC, Peñuelas J, Estiarte M, et al (2011) Drought-resistant fungi control soil organic matter decomposition and its response to temperature. *Glob Chang Biol* 17:1475–1486. <https://doi.org/10.1111/J.1365-2486.2010.02300.X>
144. Zhang B, Liang A, Wei Z, Ding X (2019) No-tillage leads to a higher resistance but a lower resilience of soil multifunctionality than ridge tillage in response to dry-wet disturbances. *Soil Tillage Res* 195:104376. <https://doi.org/10.1016/J.STILL.2019.104376>
145. Zhang B, Wei Z, Schaeffer SM, et al (2021) Recovery of bacterial communities and functions of soils under ridge tillage and no-tillage after different intensities and frequencies of drying-wetting disturbances in agroecosystems of northeastern China. *CATENA* 203:105367. <https://doi.org/10.1016/J.CATENA.2021.105367>
146. Zhang S, Kuzyakov Y, Jia Z, et al (2025) Cascading Effects Within Soil Food Web Amplify Fungal Biomass and Necromass Production. *Glob Chang Biol* 31:e70235. <https://doi.org/10.1111/GCB.70235>
147. Zhao C, Shao Y, Lu H, et al (2024) Drought shifts soil nematode trophic groups and mediates the heterotrophic respiration. *J Plant Ecol* 17:. <https://doi.org/10.1093/JPE/RTAE012>
148. Zhong S, Zeng H cai, Jin Z qiang (2016) Response of soil nematode community composition and diversity to different crop rotations and tillage in the tropics. *Appl Soil Ecol* 107:134–143. <https://doi.org/10.1016/J.APSOIL.2016.05.013>
149. Zhou R, Liu Y, Dungait JAJ, et al (2023) Microbial necromass in cropland soils: A global meta-analysis of management effects. *Glob Chang Biol* 29:1998–2014. <https://doi.org/10.1111/GCB.16613>
150. Zhou Z, Wang C, Luo Y (2020) Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nat Commun* 2020 11:11:1–10. <https://doi.org/10.1038/s41467-020-16881-7>
151. Zhu Y, Zhang H, Wang Q, et al (2024a) Soil extracellular enzyme activity linkage with soil organic carbon under conservation tillage: A global meta-analysis. *Eur J Agron* 155:127135. <https://doi.org/10.1016/J.EJA.2024.127135>
152. Zhu Y, Zhang H, Wang Q, et al (2024b) Soil extracellular enzyme activity linkage with soil organic carbon under conservation tillage: A global meta-analysis. *Eur J Agron* 155:127135. <https://doi.org/10.1016/J.EJA.2024.127135>
153. Zuber SM, Villamil MB (2016) Meta-analysis approach to assess effect of tillage on microbial biomass and enzyme activities. *Soil Biol Biochem* 97:176–187. <https://doi.org/10.1016/J.SOILBIO.2016.03.011>

Figures

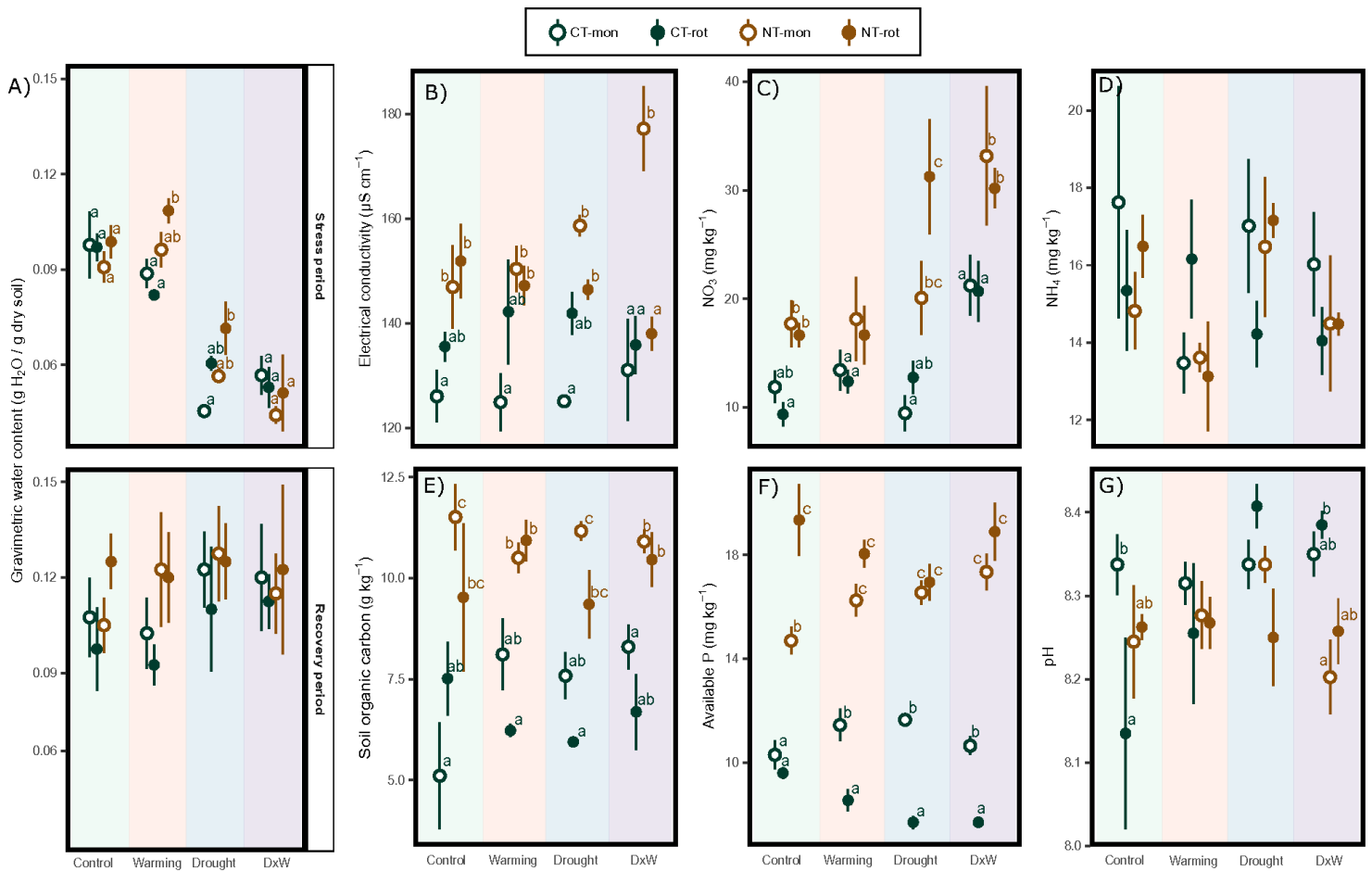


Figure 1

Responses of soil variables to simulated warming, drought and drought x warming (DxW) under different soil management legacies (CT = conventional tillage, NT= no-tillage, mon = monoculture, rot= rotation): (A) Soil gravimetric water content at maximum climatic stress (first sampling) and after the recovery period (second sampling); (B-G) Soil properties at the second sampling after the recovery period. Points represent mean log-response ratio and lines indicate 95% confidence intervals. Letters indicate significant differences between legacies ($p < 0.05$).

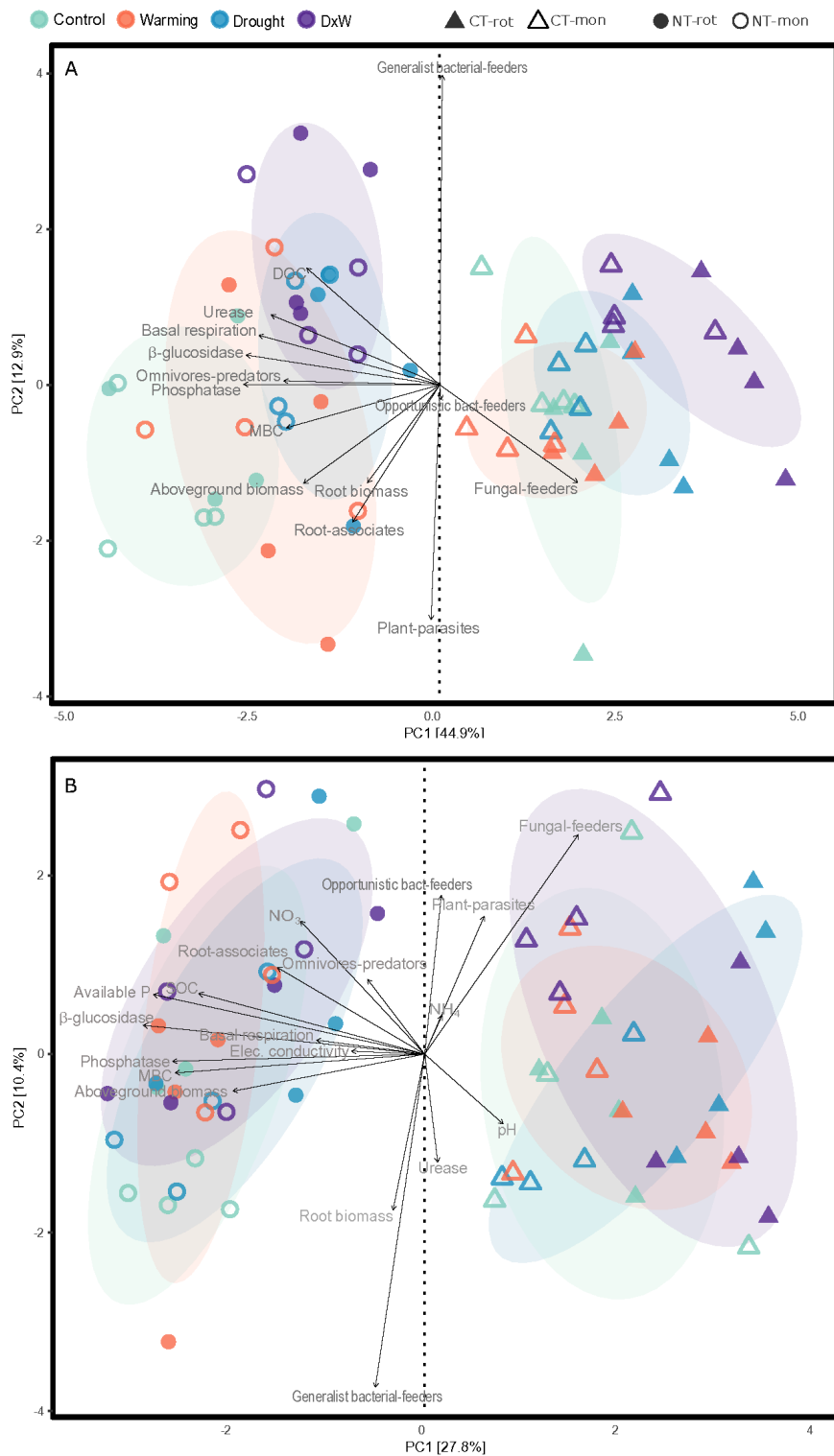


Figure 2

Result of the Principal Component Analysis of soil, nematode, and crop traits in response to simulated warming, drought, and drought x warming (DxW), and ambient control under different soil management legacies (CT = conventional tillage, NT = no-tillage, mon= monoculture, rot= rotation). DOC = dissolved organic carbon, MBC = Microbial biomass carbon, SOC = Soil organic carbon.

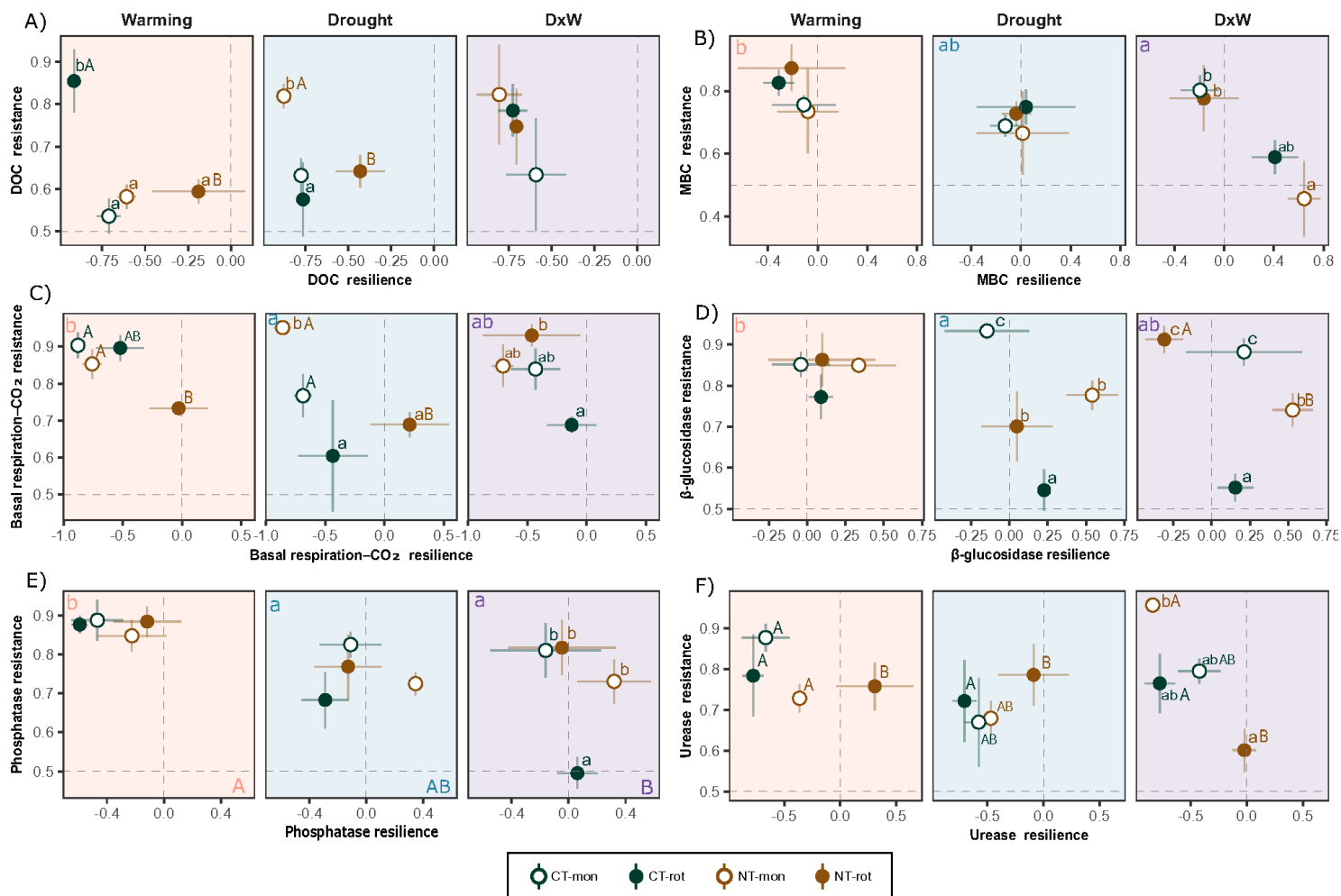


Figure 3

Resistance and resilience index values of indicators of microbial functions (DOC = dissolved organic carbon; MBC = microbial biomass carbon) to simulated warming, drought, and drought x warming (DxW) under different soil management legacies (CT= conventional tillage, NT = no-tillage, mon = monoculture, rot= rotation). Points represent mean index values and lines indicate $\pm$ standard errors. Lower and upper letters indicate significant differences ($p < 0.05$) in resistance and resilience between legacy treatments respectively. Different lowercase letters in the bottom right corner indicate significant differences ($p < 0.05$) in resilience among climatic treatments, while uppercase letters in upper left corners indicate significant differences ($p < 0.05$) in resistance.

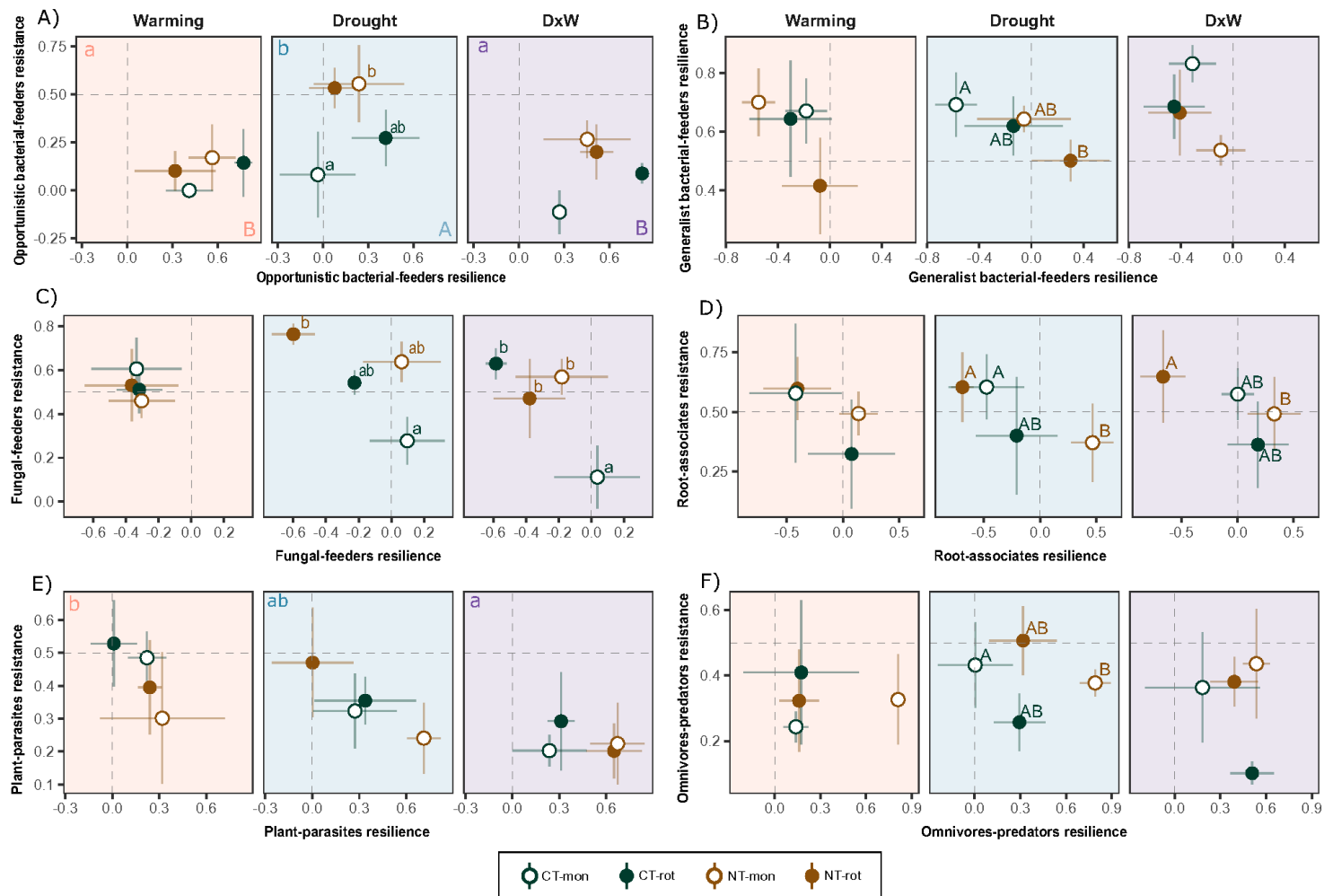


Figure 4

Resistance and resilience index values of nematodes trophic groups to simulated warming, drought, and drought x warming (DxW) under different soil management legacies (CT= conventional tillage, NT = no-tillage, mon = monoculture, rot= rotation). Points represent mean index values and lines indicate standard errors. Lower and upper letters indicate significant differences ($p<0.05$) in resistance and resilience between legacy treatments respectively. Different lowercase letters in the bottom right corner indicate significant differences ($p<0.05$) in resilience among climatic treatments, while uppercase letters in upper left corners indicate significant differences ($p<0.05$) in resistance.

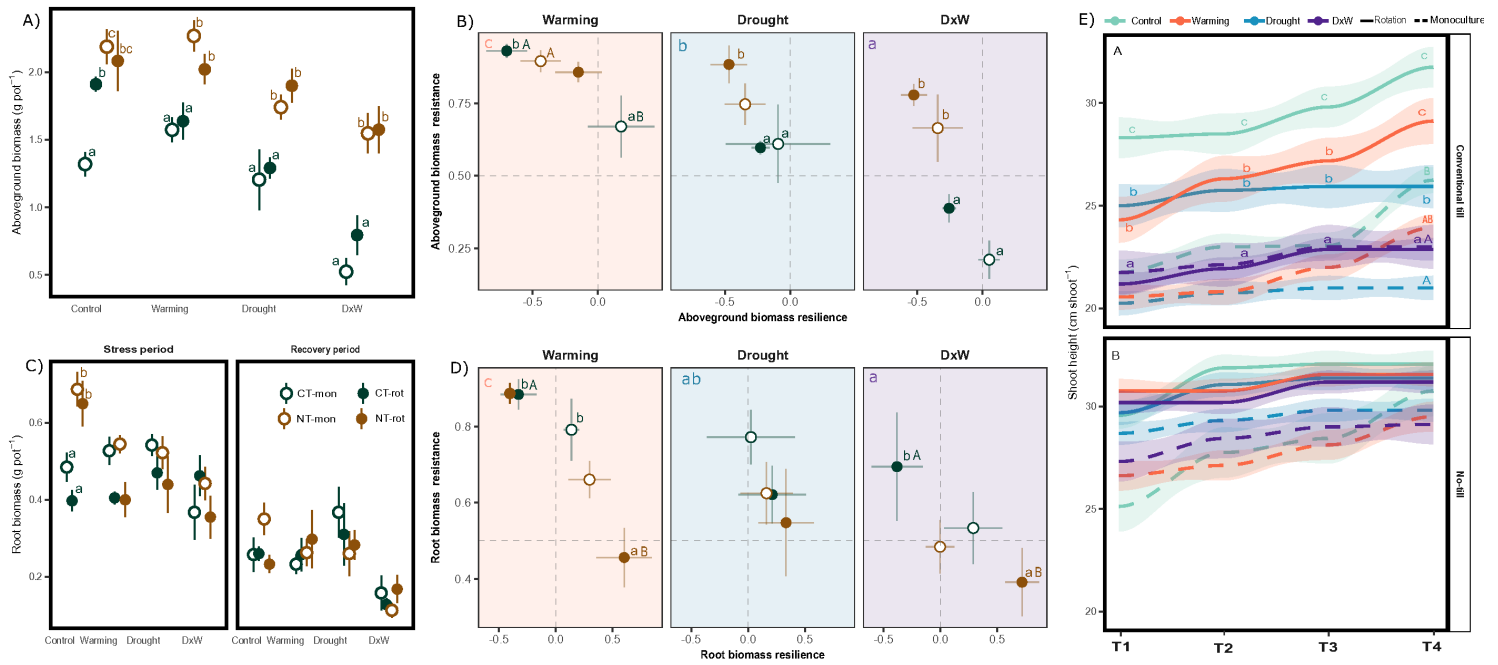


Figure 5

Crop response (A-B: aboveground biomass; C-D: belowground biomass; E: shoot height along the cropping cycle (T1 = pre-disturbance; T2 = after first climatic stress cycle; T3 = after first re-wetting/ambient temperature cycle; T4 = after second climatic stress cycle) to simulated warming, drought, and drought x warming (DxW) under different soil management legacies (CT = conventional tillage, NT = no-tillage, mon = monoculture, rot = rotation). See Figs 1-4 for label and graph interpretations. Points represent mean $\pm$ standard errors. Shaded areas represent the 95% confidence interval for the linear fits.

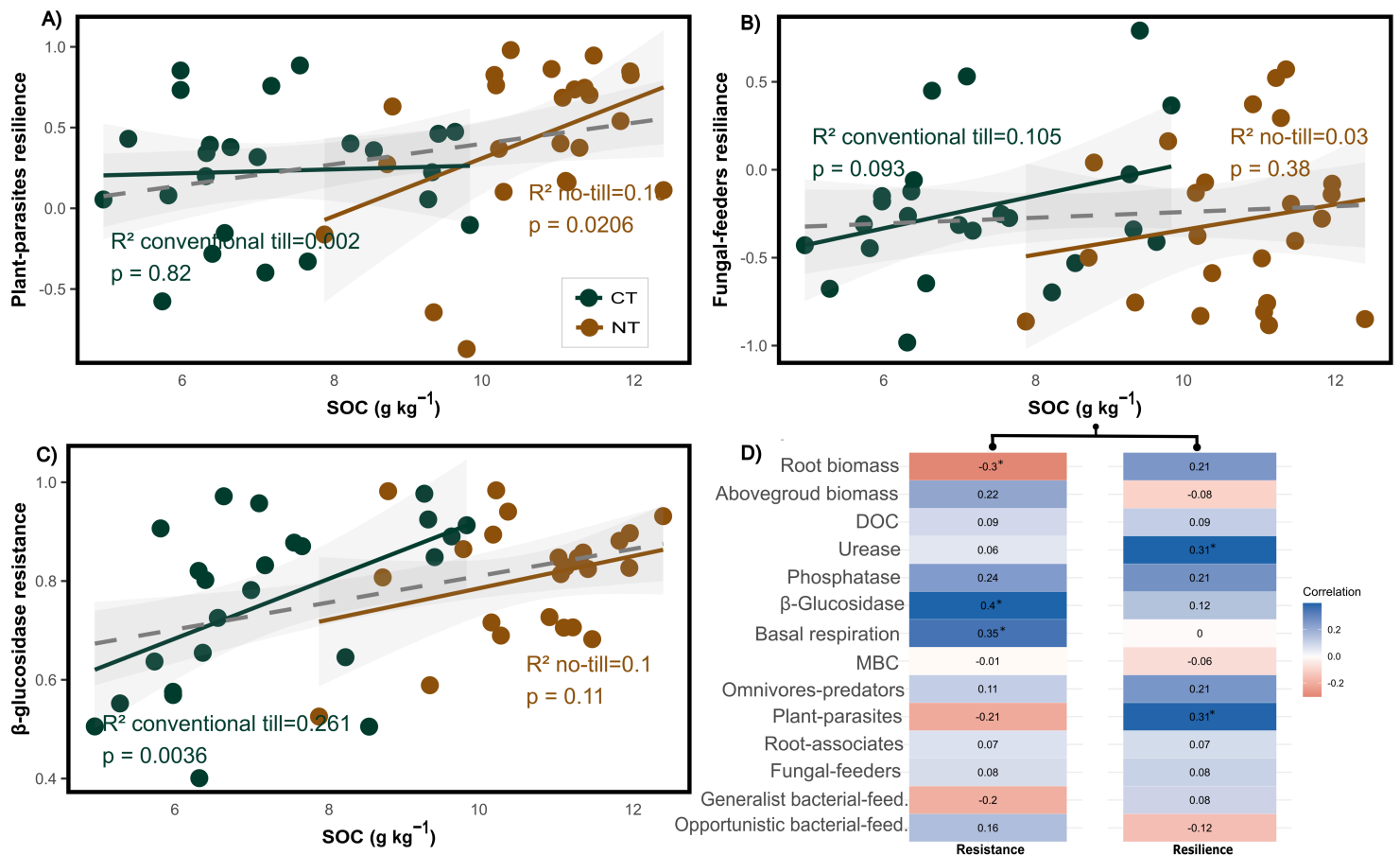


Figure 6

Linear regression analyses between soil organic carbon (SOC) and measures of resilience and resistance of soil nematode groups and functional activity. Regressions between SOC and resilience and resistance indices were performed using all replicates (grey line) and separately for each tillage treatment: (A) Relationship between SOC and plant-parasite resilience under conventional tillage (CT, green) and no-till (NT, brown); (B) Relationship between SOC and fungal-feeder resilience under CT and NT; (C) Relationship between SOC and β -glucosidase resistance under CT and NT. Shaded areas represent the 95% confidence interval for the linear fits. (D) Heatmap showing correlation coefficients between SOC and multiple indicators of resistance and resilience, with significant correlations indicated by asterisks (*).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Legacymatsup.pdf](#)