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OPEN Temporal response of belowground and aboveground organisms to microclimate changes in irrigated mediterranean vineyards

Emile Melloul^{1,2}✉, Marine Nicolas³, Léo Rocher¹, Armin Bischoff¹, Raphaël Gros⁴ & Olivier Blight¹

As a major adaptation to climate change in European crop production, irrigation is constantly increasing, particularly in Mediterranean agroecosystems. However, changes in microclimatic conditions due to irrigation may affect agroecosystem components, including soil organisms, ground-dwelling arthropods and their associated ecological functions. This study analyses the short-term effects of irrigation on Mediterranean vineyard ecosystems during the summer drought period. Soil microorganisms (phospholipid fatty acid analysis), enzymatic activity, soil respiration, organic matter decomposition, mesofauna and ground-dwelling arthropods were analysed in South-eastern French vineyards. We set up a randomised block design in two vineyards, each comprising 12 blocks with one irrigated and one non-irrigated plot per block. All response variables were measured four times: before irrigation, during irrigation, two days after irrigation, and one month later following the first rainfall. Effects of irrigation were analysed using mixed models. Irrigation exclusion reduced the abundance and activity of microorganisms, the abundance of mites and springtails, and soil respiration. It also affected the decomposition of organic matter, as evaluated using the tea bag method. The duration of these effects varied from a few hours for microorganism abundance to one month for mesofauna abundance. No differences remained after the drought period, when late summer precipitations compensated for differences in soil moisture. As drought periods may become more frequent and severe, the effects of irrigation are likely to increase. This may lead to long-term changes in soil community composition and associated functions. Our study highlighted the need for long-term monitoring of irrigation effects, as irrigation will likely become standard practice in future.

Keywords Irrigation, Vineyard, Microclimate, Soil microorganisms, Mesofauna, Arthropods

Irrigation has been a common practice in agriculture since the Neolithic period¹. Its primary purpose is to increase the stability of water supply, thereby improving crop yields and the economic value of agricultural products^{1,2}. Irrigation is rapidly expanding in agroecosystems around the world. Between 1980 and 2012, the total irrigated agricultural area grew from 182 million hectares to 324 million hectares³. This expansion is mainly driven by climate change⁴, that is expected to further increase temperature and to change precipitation patterns^{5,6}. Current climate models predict particularly pronounced changes in the Mediterranean region resulting in a higher frequency and intensity of summer droughts^{7,8}.

In the Mediterranean, viticulture is one of the most widespread cropping systems with more than half of the global wine production being concentrated in Italy, France and Spain⁹. In France, viticulture occupies 16% of the total arable land, and in several French Mediterranean departments it is the dominant crop¹⁰. Rising temperatures are expected to alter vineyard phenology, leading to higher alcohol content in wine, severe yield reduction^{11,12} and a decrease in the number of wine-producing regions¹³. For example, over the next fifty years, grapevine yields in Portugal may decrease by 60%, underlining the need to irrigate¹⁴. In the French Mediterranean, the proportion of irrigated vineyards has increased from 6 to 20% between 2010 and 2020¹⁰. Vineyard irrigation compensates for the increased duration and intensity of drought and the rise of summer temperatures. However, irrigation effects are not limited to the crop but potentially affect the entire agroecosystem. Irrigation related

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changes in soil moisture may change community assembly¹⁵ and ecological functions¹⁶. Indeed, microclimate is known to influence populations, communities, and ecosystems, including ecological functions and services¹⁷.

An increase in soil moisture impacts the biodiversity of agroecosystems by enhancing vegetation biomass production, as well as by affecting both below and above-ground organisms. As highly diverse and complex groups^{18,19}, soil biota in vineyards may be affected by irrigation. An increase of microbial biomass and changes in microbial community composition are expected^{20–22}, as irrigation favours bacterial and fungal biomass production as well as microbial activity^{23–25}. Moreover, irrigation may indirectly influence microbial communities by enhancing plant productivity, which leads to increased litter production^{23,26,27}.

Similarly to bacteria and fungi, irrigation also affects larger soil organisms^{28,29}. The major mesofauna groups of mites and springtails respond sensitively to soil moisture^{29,30}. Irrigation may alter mesofauna community composition and increase mite and springtail abundances which has been shown for forest^{29,31,32} and agroecosystems^{33,34}. While the effects on ground-dwelling arthropods such as ants, spiders, and beetles are less consistent, several studies found changes in arthropod communities in response to irrigation (wheat³⁵ and soybean fields³⁶). For example, irrigated wheat fields showed higher arthropod abundance (Aphididae and Coccinellidae), species richness (Aphididae, Aphidiinae and Coccinellidae) and diversity (Aphidiinae, Coccinellidae and Syrphidae)³⁵. Apart from direct effects, soil arthropods may also benefit from increased plant productivity increasing organic matter content and prey abundance^{37–39}.

In affecting both below- and above-ground arthropods, irrigation may change key ecosystem functions that are related to plant nutrition^{40–42}. Soil organisms provide key ecological functions and services that may be altered by irrigation, such as litter decomposition⁴³ and carbon sequestration³². Positive effects on carbon and nutrient cycling result in increased nutrient availability^{21,44}. These organisms may also contribute to pest control and natural disease regulation. Mesofauna groups, particularly predatory mites and springtails, are involved in the control of pest arthropods and pathogenic fungi^{40,45,46}. Predatory mites, such as Mesostigmata^{47–49} and Prostigmata^{50,51}, are already used as biocontrol agents in agroecosystems, showing strong potential for pest management. Springtails, that feed on fungi^{40,42}, reduce infestations of *Fusarium* spp. (e.g., *F. graminearum*) in winter wheat fields⁵², potentially mitigating mycotoxin risks. Springtails may also enhance mycorrhizal functioning by feeding on non-mycorrhizal fungi⁵³. Ground-dwelling arthropods such as ants, predatory beetles, and spiders act as generalist biocontrol agents, preying on a variety of crop pests^{54–56}.

The magnitude and the temporal response of soil organisms to irrigation may depend on their sensitivity to soil moisture and their movement capacity. Microbial biomass and activity changed within hours to a few days in studies using re-wetting cycles^{21,57}. Mites and springtails may show fast responses, moving from deeper soil layers in response to changes in soil moisture^{58,59}. However, activity and abundance of ground-dwelling arthropods may decrease due to changes in vegetation cover and soil structure caused by irrigation⁶⁰. Although the effects of irrigation have already been analysed for grapevine microbial communities^{25,61}, grapevine performance, yield^{14,24}, and pest insects^{37,38,62}, studies integrating communities of different soil organisms, their ecological functions and interactions are lacking. Our study aims to characterize the response of soil organisms and ground-dwelling arthropods on related functions to short-term irrigation in Mediterranean vineyard ecosystems. We hypothesize that irrigation (1) increases bacteria and fungi biomass resulting in higher enzymatic activity, soil respiration, and organic matter decomposition. We also expect (2) a positive effect on soil mesofauna groups sensitive to soil moisture such as springtails and mites. We finally hypothesize (3) that the effects of irrigation vanish after the drought period.

Methods

Site study area

The study was carried out in the southern Luberon mountain range in Southeastern France. The study area is characterized by Mediterranean climate with hot and dry summers, and mild winters. Rainfalls occur mainly in spring and autumn. The average annual temperatures and precipitations are 13.9 °C and 701 mm, respectively (Pertuis weather station, 1991–2020). In the study year 2023, the mean temperature was 14.4 °C with an annual precipitation of 570 mm. Due to sufficient rainfall in May and June, irrigation started only late July. During the authorized irrigation period between May 1st and August 15th, precipitation was approximately 200 mm with only 5 mm from July 1st to 15th August). The mean temperature during this drought period was 24 °C. Two weeks after the irrigation period, on 28th August, a rainfall event with 39 mm of precipitation occurred.

The irrigation experiment was set up in 24 blocks of 4.8m² (4.8 m long x 1 m large), randomly distributed across two similar organic vineyards (12 blocks each) and belonging to the same winegrower. Each block consisted of six consecutive grapevine plants in the same row, of which three were irrigated and three non-irrigated. Sampling and measurements were consistently performed at the basis of the second grapevine trunk within each treatment replicate.

To avoid a potential border effect, the first 5 m from the vineyard border were excluded. In both vineyards, surface drip irrigation was used, with one dripper per grapevine plant. The dripper flow rate was 1.6 L per hour. The vineyards were more than 20 years old and had been irrigated for five years before the experiment started in 2023. Both vineyards have been managed organically since planting with the grapevine variety Grenache. The inter-rows were dominated by spontaneous vegetation that was mown two to three times per year. The soil in both vineyards is classified as calcareous clay loam, and the planting density is 4,000 grapevine plants per hectare.

Treatment and sampling

Plots were irrigated twice, 13 mm late July and 15 mm mid-August. Water addition of each irrigation corresponded to 13 mm of rainfall. The plots were sampled four times: one week before irrigation in July (S1),

during the first irrigation in late July (S2), two days after the end of the first irrigation (S3) and three weeks later, at the end of the irrigation period and following the first rainfall event (S4).

Soil moisture and temperature measurements

Soil moisture was measured in each sampling session using ML3 ThetaProbe soil moisture sensors to a depth of 10 cm under the drippers and in the non-irrigated plots. Three measurements were taken in each plot for both irrigated and non-irrigated plots. Soil temperature was measured simultaneously in each plot using a STP-1 Soil Temperature Probe to 10 cm depth.

Phospholipid fatty acid analysis of microbial communities

The first 7 cm of soil were sampled using cylinders of 5 cm diameter to study the microbial community structure, biomass, and enzymatic activity. Samples were taken at the same locations as the moisture and temperature measurements.

The soil microbial community structure and biomass were studied using phospholipid fatty acid analysis (PLFA)^{63–65}. Lipids were extracted following a standard method⁶⁶. The lipid fraction was decomposed into fatty acid methyl ester (FAME), that was then analysed using gas chromatography-mass spectrometry (GC-MS), configured and maintained for lipid analysis according to MIDI recommendations (MIDI Inc., Newark DE). The quantities of FAME were measured using a known concentration standard (C19:0). Identified fatty acids extracted from the soil were assigned using Sherlock software^{67,68}. We distinguished the following taxonomic groups: actinobacteria (10Me17:0, 10Me18:0), arbuscular-mycorrhizal fungi (AMF) (16:1 ω 5c), fungi (without arbuscular-mycorrhizal fungi) (18:1 ω 9c, 18:2 ω 6,9c, 18:3 ω 6,9,12c, 20:1 ω 9c), total FAME (sum of markers) used as a proxy of total soil microbial biomass, gram-negative bacteria (14:0-3OH, 14:1 ω 5c, 15:1 ω 5c, 16:1 ω 7c, 16:1 ω 9c, 17:0cy, 17:1 ω 8c, 18:1 ω 5c, 18:1 ω 7c, 19:0cy(ω 9), 19:1 ω 9c), gram-positive bacteria (14:0i, 15:0a, 15:0i, 16:0i, 17:0a, 17:0i, 18:0i), sum of microbial eukaryotes (total fungi, protozoa, and other polyunsaturated fatty acids (PUFA) biomarkers). The total microbial biomass was measured as the total amount of phospholipid fatty acids.

Soil enzymatic activity

Total microbial activity was measured by monitoring the hydrolysis of fluorescein diacetate (FDA)⁶⁹. The hydrolysis of FDA is the result of enzymatic activity including esterases, proteases and lipases produced by bacteria, fungi, and protists^{70,71}. The measurements were taken without FDA substrate (control) twice with FDA to obtain FDAse activity.

Soil respiration

Soil CO₂ effluxes were analysed using a portable respirometer (EGM 4) at the same location as the moisture and temperature measurements. Soil respiration was calculated as carbon dioxide release over 124 s. The obtained values were standardized for 10 °C temperature using the following formula:

$$R_{\text{standardized}} = R_{\text{measured}} \times 6.312 \times Q_{10}^{(10-T)/10}$$

“ $R_{\text{standardized}}$ ” is the soil respiration ($\mu\text{mol}/\text{m}^2/\text{s}$) for 10 °C temperature, “ R_{measured} ” the measured respiration ($\text{gCO}_2/\text{m}^2/\text{h}$), “ Q_{10} ” represents the increase in respiration for a rise of 10 °C: in our case, $Q_{10} = 2$; “6.312” is a constant to convert $\text{gCO}_2/\text{m}^2/\text{h}$ into $\mu\text{mol}/\text{m}^2/\text{s}$, and “ T ” the soil temperature.

Organic matter decomposition

To analyse the organic matter decomposition by soil microorganisms, we used the tea bag index method (TBI)⁷². The method involves the decomposition of green tea EAN: 87 22700 05552 5) that is characterized by rapid decomposition, and Rooibos red tea (EAN: 87 22700 18843 8) that shows slower decomposition. Tea bags were weighed and buried at 8 cm depth from 22 June to 8 September 2023. After burial, tea bags were dried at 70 °C for 48 h and weighed again. Two indicators were calculated: the stabilisation factor (S) (Eq. 1) and the decomposition rate (k) (Eq. 2).

$$S = 1 - \frac{a_g}{H_g} \quad (1)$$

With “ a_g ” being the decomposable green tea fraction and “ H_g ” being the hydrolysable green tea fraction (= 0.552).

$$k = \frac{(\ln(a_r) - \ln(a_r - M_{\text{loss}_r}))}{t} \quad (2)$$

With “ a_r ” being the decomposable rooibos tea fraction ($a_r = H_r(1 - S)$), “ H_r ” being the hydrolysable rooibos tea fraction (= 0.842), “ t ” being the time buried and M_{loss_r} being the rooibos mass loss ratio during “ t ”.

Mesofauna

We analysed the soil mesofauna using Berlese - Tullgren funnels. Mesofauna organisms were collected in 5 × 7 cm cylinders at the same location as the moisture and temperature measurements, and were extracted for seven days. We focused on mites (Acari) and springtails (Collembola) as the most abundant mesofauna groups. Mites were categorized according to their feeding guilds (detritivores and predators) and all individuals were counted.

Ground dwelling arthropods

We sampled ground dwelling arthropods using pitfall traps. Plastic pots of 8 cm diameter and 15 cm height were buried close to the grapevine trunk, at a distance of 30 cm from the next dripper. Pitfall traps were filled with a mixture of salt-saturated water with two drops of liquid soap and left for 48 h. Arthropods were identified to the taxonomic groups of spiders (Aranea), beetles (Coleoptera), ants (Formicidae), woodlice (isopoda), mites (Acari), myriapods (Myriapoda), net-winged insect larvae (Neuroptera), harvestmen (Opiliones), pseudoscorpions (Pseudoscorpionida), springtails (Collembola), caddisfly larvae (Trichoptera), silverfish (Zygentoma) and classified according to their trophic habits (predators vs. detritivores). The predator group includes spiders, harvestmen, net-winged larvae, predator beetles, predator mites, predator myriapods and pseudoscorpions. The detritivore group includes detritivore beetles, isopods, detritivore myriapods, springtails, caddisfly larvae, silverfish. Ants were identified to species⁷³.

Data analysis

Data were analysed using R software⁷⁴. The effect of irrigation on soil moisture, microorganisms, respiration, enzymatic activity, and tea bag decomposition was analysed using linear mixed models, whereas its effect on temperature, mesofauna, and ground-dwelling arthropods was analysed using generalized linear mixed models (GLMM, R packages Lme4 or glmmTMB). We fitted irrigation and the sampling period as fixed factors using an interaction term, and block as a random effect nested in vineyards. Soil moisture, microorganism biomass, respiration, enzymatic activity and tea bag decomposition were analysed using linear mixed models (LMM) with gaussian error distribution. When model residuals were not normally distributed, data were transformed using the bestNormalize package⁷⁵. Soil temperature was analysed using GLMMs with gamma error distribution. For arthropod and mesofauna abundance, we used GLMMs with Poisson error distribution. In case of overdispersion, negative binomial error distribution was fitted. Ground-dwelling arthropods and mesofauna that occurred less than ten times per sampling period were excluded from the data analysis. We performed post-hoc Tukey tests when the interaction between irrigation and the sampling period was significant. All model distributions were analysed using the DHARMA package. Due to the low springtail number in non-irrigated plots, guilds could not be separately analysed.

To analyse changes in structure or composition of microbial, ant and ground-dwelling arthropod communities, non-metric multidimensional scaling (NMDS) was performed for each sampling period using the vegan package⁷⁶. For the microbial community, analyses were based on Hellinger index. Abundances were transformed into presence/absence data for ant species richness since abundance is biased by the distance to ant nests. Jaccard dissimilarity instead of Hellinger index was used. For ground-dwelling arthropods, a Bray-Curtis dissimilarity index was used. The effects of irrigation were tested using permutational analysis (PERMANOVA) with adonis function⁷⁶.

We calculated the effect size for each sampling session (S1 to S4) using the Cohen index⁷⁷ (Eq. 3):

$$d = \frac{X_I - X_{NI}}{\sqrt{\frac{\sigma_I^2 + \sigma_{NI}^2}{2}}} \quad (3)$$

With “ X_I ” being the average value for irrigated plots, and “ X_{NI} ” the average value for non-irrigated plots. “ σ_I ” is the standard deviation for irrigated values and “ σ_{NI} ” the standard deviation for non-irrigated values. The Cohen index (d) provides information on the size of the effect using the following scale: $|d| < 0.2$: very small effect, $0.2 < |d| < 0.5$: small effect, $0.5 < |d| < 0.8$: medium effect, $|d| > 0.8$: large effect. A positive index represents a positive irrigation effect due to higher values in irrigated plots whereas a negative index represents a negative effect of irrigation.

Results

Soil moisture and temperature

Before irrigation started, we did not find significant differences in soil moisture between the two treatments (Table B.1). During irrigation (S2), soil moisture was four times higher in irrigated (17%) than in non-irrigated plots (4%). Two days after irrigation (S3), moisture dropped to 12% being three times higher than in non-irrigated plots. These differences disappeared three weeks after irrigation (S4) when first rainfalls occurred, increasing soil moisture levels of non-irrigated plots to 11% (Fig. A.1).

Soil temperature was lower in irrigated plots in general (Fig. A.1) (Chisq = 13.436; $p < 0.001$). Mean soil temperature during and two days after irrigation (S2 & S3) was 22 °C in irrigated plots and 22.8 °C in non-irrigated plots. Three weeks after irrigation and first rainfall, no significant differences were observed between the irrigated and non-irrigated conditions (S4: Chisq = 1.922; $p = 0.166$).

Microbial community

We recorded a significant effect of the sampling period on all soil microbiota groups (Table 1). Total microbial (total FAME) and bacterial biomass (Gram-Positive and -Negative) responded positively to irrigation with a medium effect size for total FAME and Gram-negative during irrigation (S2), and a weak effect for Gram-positive bacteria (Figs. 1a and 2, Table B.1). In contrast, fungi, actinobacteria, microbial eukaryotes did not show any changes, while AM fungi showed a negative response to irrigation during S4 (Table 1, Table B.1). There was no evidence for an effect on the ratio of fungi to bacteria (Table 1). Three weeks after irrigation (S4), the effect of irrigation did not persist, as no differences between treatments were found, except for AM Fungi that showed a decrease in irrigated plots (Fig. 2). The microbial community structure was not affected by irrigation (Fig C.2). FDA hydrolase activity was significantly increased by irrigation, being higher in irrigated plots (Table 1).

	Sampling period		Irrigation		Interaction Sampling/Irrigation	
	Chisq	P	Chisq	P	Chisq	P
Soil moisture	113.190	< 0.001	73.851	< 0.001	152.889	< 0.001
Soil temperature	210.747	< 0.001	5.217	0.022	3.237	0.356
Soil microorganisms						
Microorganism biomass	47.122	< 0.001	2.148	0.143	16.669	< 0.001
Bacteria	41.845	< 0.001	2.707	0.100	15.104	0.002
Gram +	16.603	< 0.001	1.362	0.243	10.192	0.017
Gram -	46.857	< 0.001	1.601	0.206	13.672	0.003
Actinobacteria	69.089	< 0.001	0.232	0.630	1.383	0.710
Fungi	26.322	< 0.001	0.506	0.477	4.829	0.185
AM Fungi	37.692	< 0.001	0.169	0.681	12.610	0.006
Fungi/Bacteria	11.104	0.011	0.320	0.571	2.096	0.552
Microbial eukaryote	24.295	< 0.001	0.289	0.590	6.279	0.099
Enzymatic activity	9.162	0.027	5.605	0.018	1.827	0.609
Soil respiration	160.243	< 0.001	10.266	0.001	19.439	< 0.001
Mesofauna						
Total mites	75.874	< 0.001	38.307	< 0.001	55.301	< 0.001
Predator mites	21.823	< 0.001	23.724	< 0.001	34.690	< 0.001
Decomposer mites	72.952	< 0.001	38.549	< 0.001	48.398	< 0.001
Total springtails	51.796	< 0.001	37.206	< 0.001	36.385	< 0.001
Ground-dwelling arthropods						
Total arthropods	58.597	< 0.001	3.835	<i>0.050</i>	9.710	0.021
Detritivores	43.881	< 0.001	5.359	0.021	7.214	<i>0.065</i>
Predators	138.706	< 0.001	0.038	0.844	10.284	0.016
Harvestmen	16.733	< 0.001	0.021	0.884	3.567	0.312
Spiders	40.933	< 0.001	1.776	0.183	1.153	0.764
Beetles	19.101	< 0.001	0.170	0.680	9.096	0.028
Springtails	43.985	< 0.001	4.339	0.037	7.810	<i>0.050</i>
Mites	157.046	< 0.001	0.421	0.516	8.774	0.032
Ant species richness	77.082	< 0.001	0.274	0.601	2.993	0.392

Table 1. Effect of irrigation and sampling period on microorganism biomass, biological soil activity, mesofauna abundance, ground-dwelling arthropod abundance and ant species richness. Chisq represents Chi-squared of generalized linear mixed models. Values in bold indicate significant differences at $p < 0.05$, values in italics marginally significant differences at $p < 0.1 - p > 0.05$.

Additionally, a strong effect of the period was measured with greater activity in S3 and S4 than in S1 (Table 1, Table D.2).

Biological activity

Soil respiration increased with irrigation during (S2) and two days after irrigation (S3) but the effect did not persist in S4 (Fig. 1b, Table B.1). Global respiration was higher during irrigation (S2) and three weeks after irrigation (S4) than before the irrigation period (S1) (Fig. 1b, Table D.2).

The mass loss of green tea was significantly higher in irrigated (65%) than in non-irrigated plots (58%) (Chisq = 19.117, $p < 0.001$), but there was no effect on red tea mass loss (23% for both treatments) (Chisq = 0.328, $p = 0.567$). The stabilisation factor was higher in non-irrigated plots (0.33) than in irrigated plots (0.23), indicating a higher proportion of stabilised organic matter in non-irrigated plots and a more effective decomposition in irrigated plots (Fig. 3). No difference was found in the decomposition coefficient (Fig. 3).

Mesofauna

In total, 3,710 mites and 319 springtails were found. The mite number included 3,070 detritivores and 640 predators. Irrigation showed a strong positive effect on mites (total, detritivores, predators) and springtails, that was apparent during irrigation (S2) and two days after (S3) (Fig. 1c, d; Table 1, Table B.1). In September, after the first rainfall (S4), mite abundances were similar in both treatments (Fig. 1c, Table B.1). In non-irrigated plots, springtail abundance was very low and increased after the drought period (S4), being even higher than in irrigated plots (Figs. 1d and 2, Table B.1). The size of the irrigation effect was strongly positive for mites (S2, S3) and strongly (S2) to moderately (S3) positive for springtails (Fig. 2).

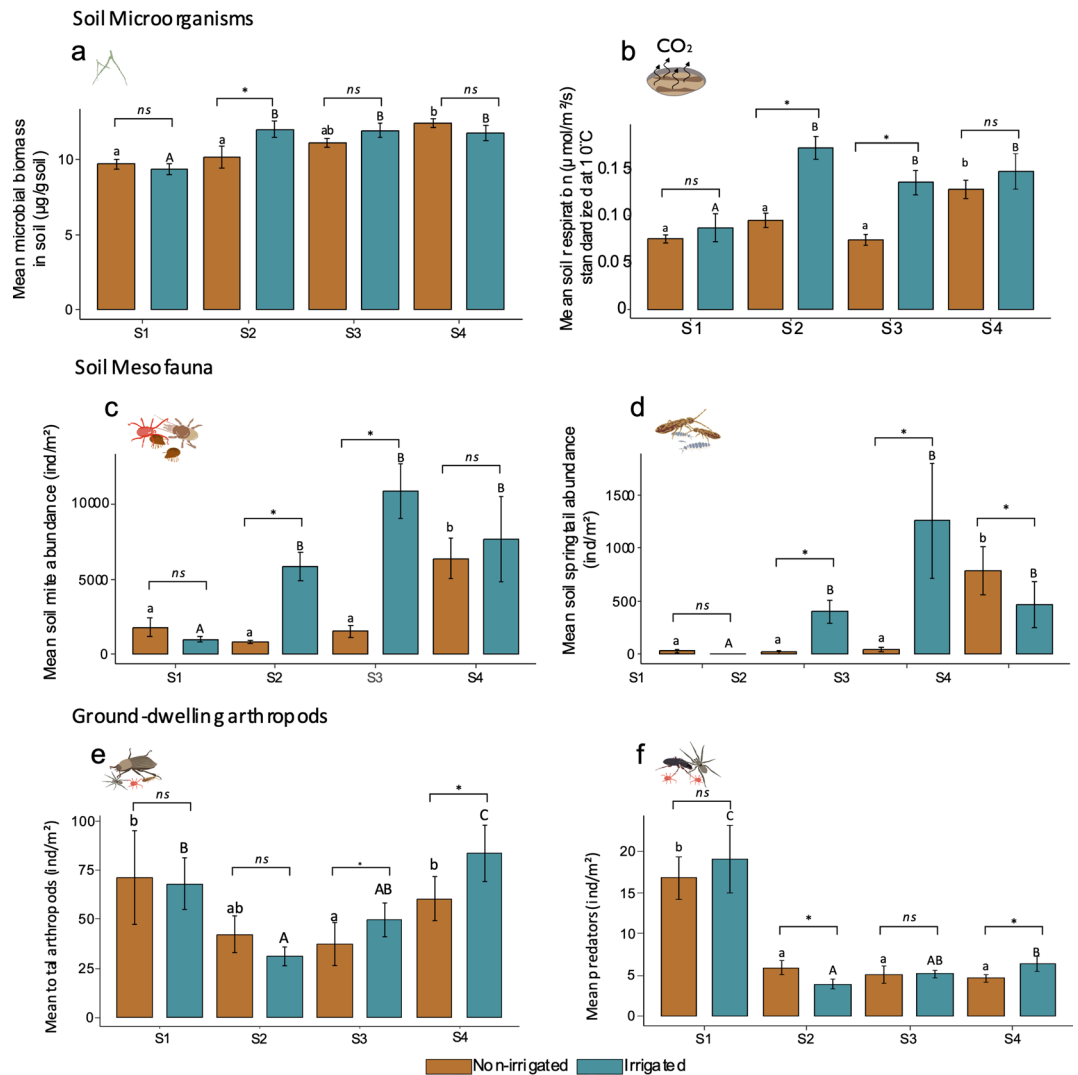


Fig. 1. Effect of irrigation and sampling period (mean \pm SE) on (a) total soil microbial biomass; (b) soil respiration (c) total soil mites; (d) mean total soil springtails; (e) mean ground-dwelling arthropods; (f) ground-dwelling predators. Different lower-case and capital letters indicate significant differences ($p < 0.05$) between sampling dates for non-irrigated and irrigated plots, respectively. Braces “*” show significant differences between the two irrigation treatments in the same sampling period while “ns” indicates no difference.

Ground-dwelling arthropods

In total, 22,644 individuals were collected belonging to 20 taxonomic groups. Samples were mainly dominated by ants (12,500) and springtails (8,475), followed by spiders (672), mites (580), harvestmen (216), beetles (74), isopods (39), myriapods (36), pseudoscorpions (21), net-winged insect larvae (15), caddisfly larvae (12), earwigs (5), silverfish (4). The remaining taxonomic groups were represented by only one individual. Seventeen ant species were identified. The most common species were *Cataglyphis cursor* (Formicinae), *Pheidole pallidula* (Myrmicinae), and *Messor structor* (Myrmicinae), occurring in 98%, 97%, and 92% of the plots, respectively.

The different arthropod groups did not show a consistent response to irrigation. Detritivores and springtails were generally more abundant in irrigated plots (Table 1). Two days (S3) and even three weeks after irrigation (S4), total ground-dwelling arthropod abundance was higher in irrigated than in non-irrigated plots (Fig. 1e, Table B.1) but the effect size was low (Fig. 2). Ground-dwelling predators and mites showed a negative effect of irrigation in S2 but a positive effect in S4 (Fig. 1f, Table B.2) with a medium effect size (Fig. 2). Surprisingly, beetle abundance was lower in irrigated plots before irrigation S1 (Table B.2) showing a medium effect size (Fig. 2). Spiders and harvestmen were not affected by irrigation (Table 1).

Ground-dwelling arthropods were affected by the sampling period (Table 1). Total ground-dwelling arthropod abundance decreased from early (S1) to late July (S2) and increased to the S1 level in early September (S4, Table D.2). The decomposer dynamics showed the same pattern as the total arthropod abundance. Predator abundance decreased after S1, and stayed significantly lower in the other sampling periods (S2, S3, S4) (Table D.2). The same dynamics was observed for mites and spiders (Table D.2). Harvestmen abundance decreased

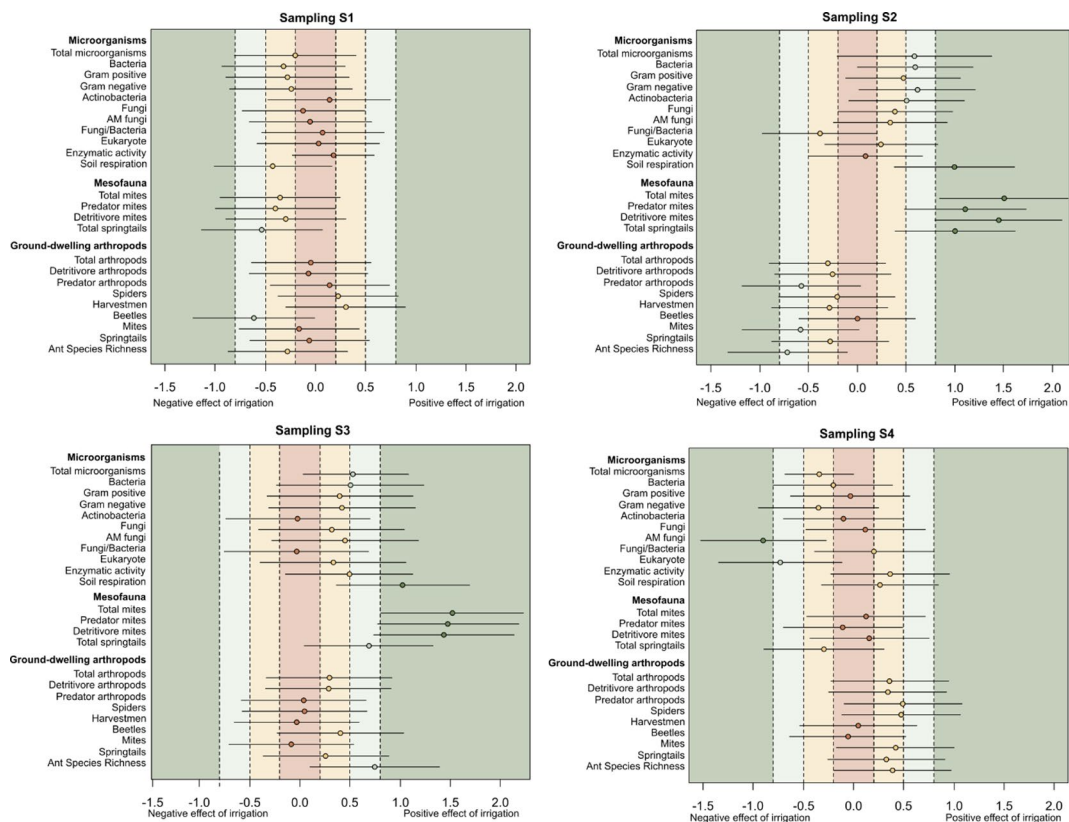


Fig. 2f. Cohen's index (effect size) with standard-error intervals for the effect of irrigation on soil microorganisms, biological soil activity, mesofauna and ground-dwelling arthropod abundances for each sampling session. A positive Cohen's index indicates a higher value in non-irrigated vineyards. Effect size classes are indicated by different colours $|d| < 0.2$: very small effect (brown), $0.2 < |d| < 0.5$: small effect (yellow), $0.5 < |d| < 0.8$: medium effect (blue), $|d| > 0.8$: large effect (green).

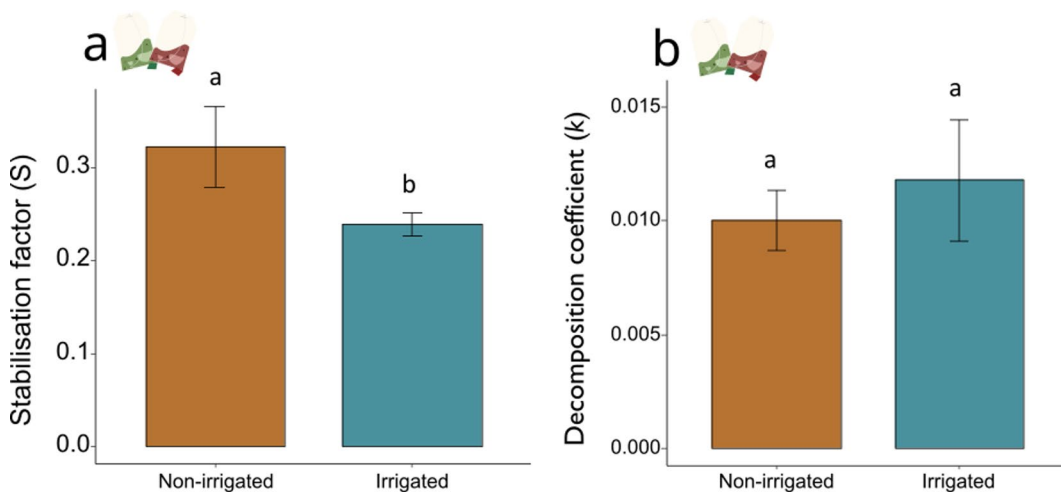


Fig. 3. Effect of irrigation on tea bag decomposition (\pm SE) after 78 days. Stabilisation factor (a) and decomposition rate (b). Different letters indicate significant differences ($p < 0.05$).

after S3 (Table D.2) and beetle abundance was higher in S4 than S1 (Table D.2). The ground-dwelling arthropod composition was not affected by irrigation in any sampling (Fig. E.3).

The ant species richness responded to sampling period with a decrease between S1, S2/S3, and S4 (Table D.2) but not to irrigation (Table 1). Ant community composition was not affected by irrigation in any sampling period (Fig. F.4).

Discussion

In this study, we analysed the effect of irrigation during summer drought on soil organisms, ground-dwelling arthropods and soil biological activity. Irrigation changed microclimatic conditions by largely increasing soil moisture and reducing soil temperature. Most of the analysed organism groups and related functions responded positively to these microclimatic changes, showing an increase during and shortly after irrigation. However, most positive effects disappeared three weeks after the irrigation period when late-summer rainfall increased soil moisture of non-irrigated controls. After the drought period, in early September, a persistent effect was only observed for some ground-dwelling arthropod groups. PLFA of soil fungi, actinobacteria, microbial eukaryotes and several ground-dwelling arthropods such as spiders, harvestmen, beetles and ants were not affected by irrigation.

Soil moisture and temperature are known to affect the survival of soil organisms and thus change the structure of their communities^{78,79}. Although it is difficult to disentangle both factors, soil moisture was most likely the main structuring factor⁸⁰. However, effects may vary depending on the analyzed groups. For example, in a laboratory experiment, springtails depended more on temperature than on moisture⁸¹, while soil temperature was a major driver of microbial community and activity in subtropical forests⁸².

Soil organisms may have benefited indirectly from irrigation through plant biomass. Irrigation increases plant growth if water-limited but also facilitates nutrient uptake^{83,84} leading to a higher plant biomass and litter production^{85–87}. Previous studies have shown the positive effect of irrigation on soil microorganisms and soil fauna mediated by plant biomass^{24,27,88}. The short-term character of positive irrigation effects on most organisms and soil functions suggests, however, that direct effects of irrigation and increased soil moisture prevailed in our study. Effects on plant biomass may rapidly occur but organic matter as major resource of soil organisms would only be available after the death of plants or plant organs.

In agreement with our first two hypotheses, irrigation had a significant positive effect on soil microbial biomass and enzymatic activity. Soil moisture is recognized as a key abiotic factor influencing soil microorganisms and their activity^{20,89,90}. The irrigation-mediated increase in soil moisture has a generally positive effect on microbial activity^{25,61}. Under favourable other abiotic conditions, dormant bacteria become active, and biomass may also increase in abundance due to the accumulation of organic carbon (plant litter, dead organisms) during the drought period^{91,92}. Bacteria may also benefit from the assimilable organic carbon released by the death of bacterial cells. A sudden increase in soil moisture may result in an osmotic shock, since the strong increase in water uptake may destroy the membranes^{57,93}. The death of bacterial cells provides rapidly available organic carbon for the remaining bacterial population⁵⁷. An increase in bacteria biomass and the associated enzymatic activity can in turn lead to the decomposition of stabilised soil organic matter^{94,95}. This phenomenon, known as the 'priming effect'⁹⁶, was confirmed in our study by the significant reduction of the stabilisation factor (S) in irrigated plots. The stabilisation factor (S) reflects the proportion of the initial organic matter that transforms into recalcitrant (stabilized) compounds⁷². A reduction in (S) leads to a decrease in recalcitrant litter compounds compared to hydrolysable fractions⁹⁷. In irrigated soils, the soil moisture increase may have favoured the decomposition of tea leaves, resulting from increased microbial activity. Overall, irrigation is therefore expected to reduce carbon sequestration⁹⁸. Priming may thus have both short- and long-term effects on soil carbon dynamics, finally enhancing carbon release into the atmosphere. Priming may further change the microbial community composition favouring decomposition⁹⁹. On the other hand, irrigation also stimulates the absorption of nutrients^{83,84}, which in turn promotes plant growth¹⁰⁰ and increase carbon quantity in the soil by adding plant biomass⁸⁸.

Neither the biomass of fungi, actinobacteria and microbial eukaryotes nor the fungi/bacteria ratio were affected by irrigation. Previous studies carried out in other agroecosystems have produced different results, with fungi responding positively to irrigation^{101,102}. However, our results are not entirely surprising, as fungi can be drought-resistant^{93,103}. The effects may further depend on the water quantity, as drip irrigation in vineyards does not provide sufficient water amount to change fungal quantities²⁶. Vineyard management practices such as fungicide applications in spring may also limit the effect of irrigation. Actinobacteria are known to be positively affected by irrigation¹⁰⁴ which was not the case in our study. Actinobacteria may have already disappeared before sampling. The effect of water addition on actinobacteria is only visible for few minutes after irrigation begins and disappears rapidly⁵⁷.

Similar to most microorganisms, irrigation highly increased mesofauna abundance. Irrigation has been shown to strongly favour mesofauna and underscores the vital role of water in enhancing soil biodiversity^{29,34}. Mite and springtail abundances increased rapidly but this irrigation-mediated increase disappeared within three weeks after the end of irrigation. The rapid response to irrigation suggests that zones of higher soil moisture may attract mites and springtails. They may have moved from deeper to upper soil layers^{59,105,106} or horizontally within the rhizosphere^{107,108}. As microbiota-feeding organisms, springtails and mites may have benefitted from the increase in microbial biomass^{42,46}. The concomitant increase in microbial and microarthropod abundances in irrigated plots suggests potential synergistic interactions mediated by increased soil moisture. Springtails and oribatid mites, in particular, are known to stimulate microbial activity through litter comminution and grazing, which may enhance microbial turnover and nutrient mineralization. Conversely, microorganisms, including bacteria, are key dietary components for many edaphic microarthropods. Thus, irrigation may promote a positive feedback loop, in which increased microbial biomass supports higher microarthropod densities, which in turn further stimulates microbial processes, collectively enhancing soil functional activity. As evidence of this enhanced soil functional activity, we observed a higher rate of organic matter decomposition in the irrigated plots. This suggests that the combined increase in microbial and microarthropod communities may contribute to more active detritus processing and nutrient cycling under irrigated conditions.

The abundance of springtails and mites in non-irrigated plots increased after the first late summer rainfalls, reaching similar abundances to those in irrigated plots. Several springtail species survive drought periods as eggs

and recolonize the habitat after rainfall^{33,109}. Other springtails and mites avoid drought by moving to deeper soil layers^{110,111}. However, prolonged drought conditions may hamper the survival of mites and springtails^{29,112}. With ongoing climate change, drought periods may increase in duration and intensity, and the adaptation of vineyard irrigation practices may change mesofauna communities leading to different dynamics in soil ecosystems.

The effects of irrigation on ground-dwelling arthropods were less pronounced than on soil microorganisms and mesofauna, and temporal dynamics was different. Regardless of irrigation, overall abundance of ground-dwelling arthropods decreased late July and reached the previous level after the first rainfall in September. There was a lag phase in the irrigation response occurring only two days after irrigation. In contrast to the soil mesofauna the irrigation effect remained significant until September. These temporal dynamics of irrigation effects were mainly driven by springtails and mites. Springtails and mites living on the soil surface may show different responses than soil organisms of the same groups, and more long-lasting effects are documented. In an experimental manipulation of precipitation, Lensing et al. (2005) found that the activity-density (mean number caught in pitfall traps per sampling date) of springtails was approximately 60% lower in drought plots than in those receiving increased precipitation. In the high-rainfall plots, springtail activity-density in the top litter layers was three times higher than in the drought plots. Using a similar experimental approach, a positive effect of irrigation on all studied springtail species except one was observed, whereas the effect of a spring drought was negative¹⁰⁵. Effects of spring precipitation persisted for the 97-day period of the study. Rapid responses driven by movements may have been complemented by higher reproduction resulting in a delay of response^{31,113}.

Ground-dwelling predator abundance was negatively affected by irrigation in the beginning. This effect was primarily driven by mites and may be the result of changes in soil surface structure. Irrigation water has the potential to significantly influence soil structural properties and infiltration¹¹⁴, which in turn may affect mite populations¹¹⁵. During irrigation (S2), the creation of puddles may have removed predator mites from the plots. However, the effect was only short-term and disappeared already two days after irrigation. No effect of irrigation was found for other arthropods such as spiders, beetles, harvestmen and ants. Similarly, inconsistent irrigation effects have been reported in other studies, ranging from positive^{35,36} to absent¹¹⁶.

Conclusion

Irrigation and associated effects on microclimatic conditions, resulted in a rapid transformation of vineyard soil, leading to an immediate increase in microbial biomass, mesofauna abundance, and small ground-dwelling arthropods, such as springtails and mites. Interestingly, the effect rapidly vanished for microorganisms and mesofauna living in the soil, but persisted for ground-dwelling springtails and mites. Moderate irrigation as typical management practice of our study region did not result in legacy effects on the analysed organisms and functions. However, our findings suggest possible shifts in carbon dynamics, species-specific and functional composition of microorganism or mesofauna communities if vineyards are irrigated for longer periods within and across years. Studies over several years that focus on these components of the agroecosystem are required to better understand potential long-term effects on vineyard soil ecosystems and functions.

Data availability

The datasets analysed during the current study available from the corresponding author on reasonable request.

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Author contributions

E.M.: conceptualization, data acquisition, formal analysis, writing original draft. M.N.: data acquisition, formal analysis. L.R.: conceptualization, data acquisition. A.B., R.G., O.B.: conceptualization, formal analysis, writing and editing supervisions. All authors approved the final manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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