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RESEARCH PAPER

Severe drought and conventional farming affect detritivore feeding activity and its vertical distributionM.Pilar Gavín-Centol^{a,*}, Diego Serrano-Carnero^b, Marta Montserrat^b,
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Abstract

Soil invertebrates are key to decomposition, a central ecosystem process related to soil health. In many temperate areas climate change will decrease soil water content, which strongly modulates biological activity. However, data are lacking on how shifts in rainfall patterns affect soil biota and the ecosystem processes they provide. Here, we used the bait-lamina test to experimentally assess how a severe drought event influenced detritivore feeding activity, during a wheat growing season, in soils under long-term organic or conventional farming. Additionally, biotic and abiotic soil parameters were measured. Feeding activity was reduced under extreme drought and conventional management, although no climate-management synergies were found. Vertical migrations of Collembola and Oribatida partially explained the unexpectedly higher bait consumption at shallower depths in response to drought. Exploratory mixed-effects longitudinal random forests (a novel *machine learning* technique) were used to explore whether the relative abundances of meso-, microfauna and microbes of the decomposer food web, or abiotic soil parameters, affected the feeding activity of detritivores. The model including meso- and microfauna selected four Nematoda taxa and explained higher variance than the model with only microbiota, indicating that detritivore feeding is closely associated with nematodes but not with microbes. Additionally, the model combining fauna and microbiota explained less variance than the faunal model, suggesting that microbe-fauna synergies barely affected detritivore feeding. Moreover, soil water and mineral nitrogen contents were found to strongly determine detritivore feeding, in a positive and negative way, respectively. Hence, our results suggest that severe drought and conventional farming impair the feeding activity of soil detritivores and thus, probably, decomposition and nutrient mineralization in soils. Furthermore, machine learning algorithms arise as a powerful technique to explore the identity of potential key drivers relating biodiversity to ecosystem functioning.

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Introduction

Central Europe has experienced recurrent severe mid-spring droughts in recent years, with an average reduction of 50–60%, and decreases reaching up to 80% of the precipitation during April (Micale et al., 2015; Ionita et al., 2020). In the coming decades, drought episodes will probably increase across Europe, especially in spring and summer (Spinoni et al., 2018). Drought seriously affects soil fauna, both directly, through negative effects on animal reproduction and development (Lindberg & Bengtsson, 2005), and indirectly, by modifying the population growth and composition of plant (Kardol et al., 2010) and microbial communities (Schimel, 2018). In addition, intensification within arable cropping systems often implies increased use of pesticides and fertilisers. Pesticides affect non-target soil fauna, disrupting a large part of the soil food web (Pisa et al., 2021), whereas fertilisers may have both negative (e.g., soil acidification) and positive (e.g., increased food resources) effects on soil faunal populations (Crotty, 2020).

The effects of agricultural inputs and labours depend not only on their composition, quantity, and frequency, but also on current and subsequent weather conditions (Crotty, 2020). For instance, drought may prolong the effects of pesticides, as the active compounds remain on the soil for longer periods of time (Ng et al., 2014). Therefore, climate change and agricultural management may thus interactively alter soil fauna. But this also implies that negative impacts of climate change on biodiversity could be reduced by implementing certain agricultural practices, such as restricting the use of fertilisers and pesticides (Pisa et al., 2021; Crotty, 2020), or reducing tillage intensity (Betancur-Corredor et al., 2022). In line with this, previous studies either support (Siebert et al., 2019; Meyer et al., 2021) or refute (Yin et al., 2019; Sünemann et al., 2021) the existence of interactive effects between climate change and farm management on soil fauna.

Soil detritivores comprise several large groups of invertebrates that are involved in numerous soil processes. For instance, they build and maintain structural porosity and aggregates of soils, and may control microbial communities and plant performance (Lavelle et al., 2006). Therefore, invertebrate detritivores and other decomposers support a wide range of ecosystem services, such as nutrient mineralization, chemical detoxification or erosion control (Lavelle et al., 2006). Recently, research by Birkhofer et al. (2021) performed in the same field experiment that concerns us here, found that extreme drought reduced detritivore feeding activity, an ecosystem process associated to decomposition (Reinecke et al., 2008; Sünemann et al., 2021). From this same experiment, Meyer et al. (2021) revealed that

collembolans and non-oribatid mites moved downwards in the soil in response to a severe drought, while oribatid mites moved upwards.

Here, we follow up on the studies by Meyer et al. (2021) and Birkhofer et al. (2021) to experimentally explore how severe drought (natural precipitation vs. 65% precipitation reduction) and farming management (organic vs. conventional) jointly affect the feeding activity of invertebrate detritivores, by means of bait-lamina tests, in a context of arable agriculture (winter wheat crops). We also evaluate whether the depth at which feeding activity occurs is associated with migrating mesofauna. Finally, using up-to-date machine learning algorithms (mixed-model random forests), we explore potential drivers of feeding activity. We hypothesised that (i) the effects of a severe drought on detritivore feeding activity would be exacerbated by conventional farming; (ii) under severe drought the feeding activity of detritivores will be explained by the vertical movements of mesofauna documented above; (iii) meso- and microfauna would be more strongly associated with the detritivore feeding than soil microbiota; and (iv) soil water content, highly dependent on precipitation; and mineral nitrogen, closely related to conventional farming inputs, would be the main drivers of the feeding activity of detritivores.

Materials and methods

Site description

This study was part of the SoilClim project (<https://www.biodiversa.org/976>) and was carried out in 2017 at the DOK trial in Therwil, Switzerland (47° 30' 09.3" N, 7° 32' 21.5" E, 300 m above sea level). The DOK trial is an agricultural long-term experiment comparing biodynamic, organic and conventional farming systems for more than 40 years (Krause et al., 2020). The soil is a Haplic Luvisol (16% clay, 72% silt and 12% sand) on deep deposits of alluvial loess. Mean annual precipitation is 842 mm, and mean annual temperature is 10.5 °C (Krause et al., 2020). For the current study, plots within winter wheat fields (*Triticum aestivum* L. cv. “Wiwa”) were used.

Experimental design

The experiment consisted of eight fields, in which plots were under three different rainfall regimes: a partial rainout shelter (Roof; 2.5 × 2.5 m, 1.3–1.7 m height) that reduced precipitation 65%; a rainout shelter control (Roof Control), which did not reduce precipitation, but allowed knowing possible artefacts derived from the shelters; or an open field

(Control) without a shelter. The rainout shelters were installed from mid-March to June 2017, shortly before wheat harvesting. Details on the design and installation of the rainout shelters are available in [Kundel et al. \(2018\)](#). These eight fields were paired, each pair consisting of a biodynamic (BIODYN) and a conventional (CONMIN) field. Biodynamic agriculture is a type of certified organic system, but since previous studies in the DOK trial ([Mäder et al., 2002](#)) found no significant differences between organic and biodynamic practices on soil quality and biodiversity, hereafter we will refer to the biodynamic system simply as organic. All plots were under the same 7-year crop rotation (with soybean as preceding crop) and equivalently sown (415 grains/m²), as well as under the same stubble working, ploughing (20 cm depth) and rolling. Differences and similarities followed in both farming systems are listed in the supplementary materials (see Appendix A), but see [Kundel et al. \(2020\)](#) for more details. In total there were 24 experimental plots (i.e., four replicated fields in two farming systems with three drought treatments each).

Sampling procedure, soil analysis and feeding activity assessment

The soil biota sampling and the evaluation of associated ecosystem processes were performed three times throughout the wheat growing season of 2017: in mid-April (T1), mid-May (T2) and mid-June (T3). Most samples were taken from the core area of the plots (1.5 × 1.5 m), leaving a margin of 0.5 m to avoid edge effects, such as possible moisture intrusion through roof sides. Sampling and laboratory methods, apart from those concerning the detritivore feeding activity, are detailed in the Supplementary materials (see Appendix A) and in the description of the open access databases of this study (see below).

The feeding activity of soil invertebrate detritivores was surveyed by means of bait-lamina tests after [Törne \(1990\)](#). Bait-lamina test consists of PVC strips (120 × 5 × 1 mm) with 16 bait-filled holes of 1.5 mm Ø, separated 5 mm from each other along the strip. Commercial bait was used, a mixture powder of 70% cellulose, 27% bran flakes and 3% active coal (Terra Protecta GmbH, Berlin). This powder was mixed with tap water to obtain a cement-like texture and fill the PVC strip holes in three passes, to avoid gaps inside the holes. In the field, nine bait-lamina strips were inserted vertically and equidistantly into the top soil of each plot, in a 3 × 3 grid (20 × 20 cm). Top and bottom holes were at 0.5 and 8.0 cm depth, respectively. After fourteen days, bait-laminas were removed, wrapped with plastic film and stored at 4 °C. In the lab, bait consumption was assessed under a dissection microscope, determining the percentage of the bait area consumed. The final value of bait consumption was counted as 0, 25, 50, 75 or 100% of consumption in each hole, with 0% indicating a hole full of bait and 100% indicating an empty hole. In total, 810 bait-lamina strips and

12,960 holes were assessed. Bait consumption was recorded by two independent observers since between-observer repeatability, measured across 9 bait-laminas and 144 holes, was very high ($R = 0.996$, $P < 0.0001$; package ‘rptR’ in R; [Stoffel et al., 2017](#)).

Statistical analyses

All statistical analyses were performed in R 4.2.2 (R Core Team, 2022). To evaluate possible factors and drivers affecting detritivore feeding activity we ran different types of models depending on the question and the nature of the data. The effects of drought and farming systems were assessed using the highly flexible ‘glmmTMB’ package ([Brooks et al., 2017](#)) to run Generalised Linear Mixed Models (GLMM) based on Template Model Builder (TMB; [Kris-tensten et al., 2016](#)). The dependent variable was detritivore feeding activity (i.e., percentage of bait consumption) converted to binomial, since its distribution on a hole-by-hole basis was bimodal ([Tabachnick & Fidell, 1996](#)) due to the many zeros. We thus converted all bait consumption data above 0 to 1 (consumption present), and kept the zeros as such (consumption absent). Fixed effects were drought treatment (natural precipitation [Roof control and Control] vs. 65% precipitation reduction [Roof]), farming system (organic [BIODYN] vs. conventional [CONMIN]), sampling time (T1 - T3), depth (hole number [1 - 16], as an ordinal variable) and interactions among them. Following a previous publication on this experiment ([Birkhofer et al., 2021](#)), we focused on contrasting the severe drought (Roof) vs. both control treatments (Roof control and Control), the latter pooled for all analyses. Since we expected time of the season to affect bait consumption, sampling time was included as a categorical covariate, allowing us to test for higher order interactions involving time. Random factors included identifiers (ID) of blocks, fields, plot-time and bait-laminas, which were implicitly nested. The need for their inclusion was tested by comparing the Akaike Information Criterion (AIC) of models with and without random factors, free of fixed effects (i.e., with intercept only). Finally only plot-time and bait-laminas IDs were included. In order to choose a final model we performed backward elimination, starting with a model including the 4-way interaction and retaining only significant interactions and the terms conforming them. The fit of the final glmmTMB model (e.g., overdispersion) was assessed by simulation using the package ‘DHARMA’ ([Hartig, 2022](#)). Effects were extracted from the ‘effects’ library ([Fox & Weisberg, 2019](#)) and displayed at identical scales using ‘ggplot2’ ([Wickham, 2016](#)).

The relative vertical position of detritivore feeding activity into the soil, as well as that of the abundance of migrating mesofauna, were estimated by means of an index; hereafter, the Relative Activity (or Abundance) Index (RAI). The RAI follows from the relative interaction index of [Armas et al. \(2004\)](#), an index with robust statistical properties, finite

limits $[-1, +1]$ and symmetric around zero, which is defined as follows:

$$RAI = \frac{\text{upper value} - \text{deeper value}}{\text{upper value} + \text{deeper value}}$$

Therefore, the RAI ranges from -1 (implying that the activity or abundance occurred only in the deeper soil layer) to $+1$ (implying that the activity or abundance occurred only in the upper soil layer). The soil layers that we refer to as upper and deeper were between 0.5 - 4 cm and 4.5 - 8 cm for bait consumption, and between 0 - 5 and 5 - 10 cm for mesofaunal abundances. To test if mesofaunal vertical movements were associated to the position of bait consumption, we calculated separate RAIs for the total abundance of the three migrating mesofaunal groups (i.e., total Collembola, Oribatida mites, and pooled Pro-, Meso- and Astigmata mites) and another for bait consumption. In order to normalize model residuals we applied the Box-Cox transformation (Box & Cox, 1964) to the dependent variable through the ‘boxcox’ function in the ‘MASS’ R package (Venables & Ripley, 2002). We then ran General Linear Models (GLM) also with the ‘glmmTMB’ R package (Brooks et al., 2017), including bait RAI as dependent variable and RAIs for migrating mesofauna as independent variables. If the downward migration of mesofauna was responsible for increased feeding activity in the deeper layer, we predicted a positive relationship between the bait RAI and the RAIs for total Collembola and non-Oribatida mites. In contrast, if the upward migration of mesofauna was responsible for increased feeding activity in the upper layer, we predicted a positive relationship between the RAI for Oribatida mites and that of bait consumption. Since we expected time of the season to affect the depth of bait consumption, we included sampling time as a categorical covariate. Using AIC and procedures explained above, we determined that the inclusion of random effects was unnecessary. Treatment effects were extracted from the ‘effects’ library (Fox & Weisberg, 2019) and continuous predictors (i.e., mesofauna RAI) displayed as partial regression plots (Moya-Laraño & Corcobado, 2008), all using ‘ggplot2’ (Wickham, 2016).

Finally, we explored whether the relative abundances of meso-, microfauna and microbes of the decomposer food web influenced detritivore feeding activity, either directly (i.e., through feeding) or indirectly (e.g., affecting detritivore abundances and/or behavior). For this purpose, we ran mixed-effects longitudinal Random Forests (RF) using the R library ‘LongituRF’ and the function ‘REEMforest’ (Random Effects Expectation Maximization forest; Capitaine, 2020). This approach makes the best of random forests, i.e. finds which predictors could be more important at predicting bait consumption after evaluating complex synergies with the rest of independent variables, while accommodating high dimensional data (e.g., the number of predictors can be higher than the number of cases). Additionally, ‘REEMforest’ includes random effects and accounts for repeated

(longitudinal) measures on each of the random subjects (plots). We explicitly assumed a Brownian motion for the stochastic process through time (Capitaine et al., 2020). The dependent variable was average bait consumption, for which we first averaged bait consumption across the 16 holes of each bait-lamina, and then obtained a single value per plot and date by averaging across the 9 bait-lamina strips values. Sampling time was included as an ordinal variable (T1 - T3) in the “Time” argument, and plot ID was included as a random factor. No time-plot dependent covariates were included for analysis. We ran different RF models relating different sets of variables to bait consumption. The first model (RF1) included the relative abundance of all four mesofaunal groups (epigeic Collembola, total Collembola, Oribatida mites and the pool of Pro-, Meso- and Astigmata mites) and that of the 43 families/genera of nematodes. The second model (RF2) included the relative abundance of the top most abundant 50 bacteria and top 50 fungi genera. A third model (RF3) with both soil fauna and microbes was ran to test whether microbiota-fauna synergies could explain bait consumption. All data on relative abundances were Hellinger transformed to account for biases of rare taxa (Legendre & Gallagher, 2001). Lastly, to explore how abiotic soil parameters affected detritivore feeding we ran a fourth model (RF4) including soil properties as independent variables (i.e., water, sand, silt, clay, pH, phosphorous, phosphates, total organic carbon, total nitrogen, mineral nitrogen, water holding capacity and bulk density). We ran all RF models using three different computer seeds (i.e., 1, 73 and 976) to call the pseudo-random number generator. This allowed us to test the robustness of our analyses and to obtain predictors common to each set of three models. To select variables potentially driving bait consumption we applied the ‘vsurf’ algorithm from the ‘VSURF’ R library (Genuer et al., 2019). Because we previously observed some inconsistency among runs, ‘vsurf’ was run 10 times and only the predictors consistently appearing in all runs were selected. To obtain a p-value for each RF model we used the function ‘rf.significance’ within the ‘rfUtilities’ package (Evans & Murphy, 2019). Partial dependence plots (Friedman, 2001) relating final RF1 and RF4 predictors of bait consumption, which have the largest explained variances, were drawn extracting the data from the function ‘partial-Plot’ of the ‘randomForest’ package (Liaw & Wiener, 2002) and displayed in ‘ggplot2’ (Wickham, 2016).

Results

The model on bait consumption showed no interaction between severe drought and farming systems, but it did show an interaction between drought, sampling time and depth (Fig. 1A, Table 1). Simulated drought strongly reduced detritivore feeding activity, especially in the middle (T2) and late (T3) growing season (Fig. 1A). Furthermore,

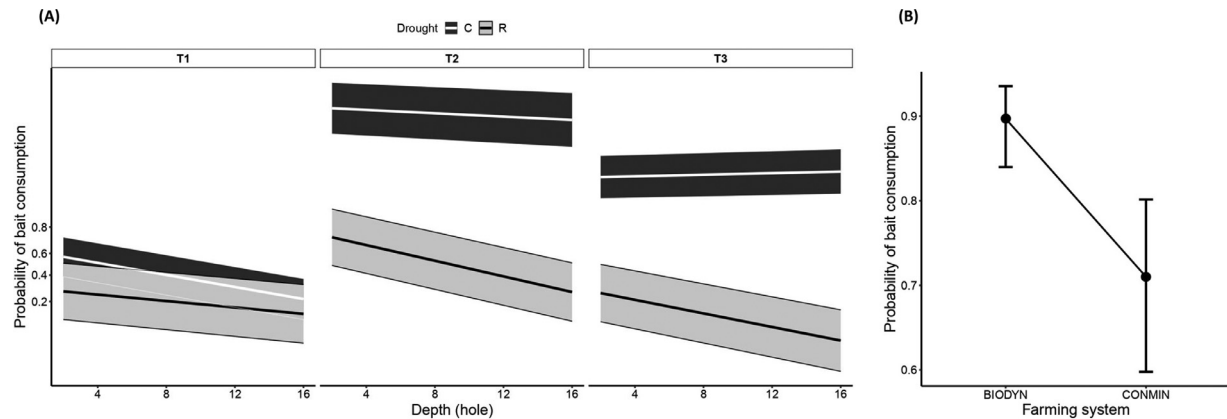


Fig. 1. Probability of bait consumption (binomial distribution). For each bait-lamina hole, the detection of some bait consumption was transformed to 1, and undetected bait consumption to 0. (A) Effect of severe drought (natural precipitation [Control] vs. 65% precipitation reduction [Roof]), across three sampling times (T1-T3: April, May and June 2017) and along soil depth (from 0.5 cm [hole 1] to 8 cm [hole 16]). (B) Effect of farming system (organic [BIODYN] vs. conventional [CONMIN]). Effects shown are estimates with the Y-axis kept at the logit scale, even though the Y-labels are logits transformed to probabilities for ease of interpretation. For statistical analysis, see Table 1.

feeding activity increased with depth under drought at T2 and T3 (Fig. 1A). And regarding the farming system, feeding activity was also reduced in conventional relative to organic managed fields (Fig. 1B, Table 1).

The model on the bait-lamina RAI revealed that the relative vertical position of the feeding activity was negatively related to that of total Collembola (Fig. 2A, Table 2) and positively related to that of Oribatida mites (Fig. 2B, Table 2). The RAI of all other mites (Pro-, Meso- and Astigmata) was not related to the bait-lamina RAI (the variable was discarded by backward elimination). Moreover, the feeding activity decreased vertically into the soil (i.e., bait RAI declined) as the season progressed (Fig. 2C).

Regardless of depth, mixed-model longitudinal random forests revealed which other components of the soil fauna were associated with bait consumption. The model including meso- and microfauna (RF1) explained 42.7 - 58.18% of the

variance in bait consumption ($P < 0.001$; Table 3). In order of importance, variable selection analysis retained the relative abundance of four Nematoda taxa: *Rhabditis*, *Helicotylenchus*, *Rotylenchus* and Qudsianematidae. Bait consumption was partially and negatively related to *Rhabditis* and *Helicotylenchus*, which are bacterivorous and herbivorous nematodes, respectively (Fig. 3A,B). This decrease in bait consumption, however, only occurred in a specific range of their abundances (Fig. 3A, range 0.2 - 0.4; Fig. 3B, range 0.1 - 0.2). In contrast, bait consumption were partially and positively related to *Rotylenchus* and Qudsianematidae, herbivorous and omnivorous nematodes, respectively (Fig. 3C, B). Both of these nematode taxa were more linearly related to bait feeding activity, albeit with a marked up-and-down in the case of *Rotylenchus* (Fig. 3C, range 0.1 - 0.3). The model using only microbial relative abundances (RF2) had the lowest explained variance of bait consumption (15.87 - 17.39%, $P \leq 0.001 - 0.004$; Table 3). This model

Table 1. Coefficients of the Generalised Linear Mixed Model (GLMM) on the probability of bait consumption. For each bait lamina hole, the detection of some consumption of bait was transformed to 1, and undetected bait consumption to 0. Model formula: $\text{glmmTMB}(\text{binomial bait consumption} \sim (\text{drought} * \text{time} * \text{depth}) + \text{farming system} + (1|\text{plot-time ID}) + (1|\text{bait-lamina ID}), \text{family} = \text{binomial})$.

| Effect | Term | Variance | Estimate | S.E. | Chisq (χ^2) | D.f. | P-value |
|--------|--------------------|----------|----------|-------|--------------------|------|---------|
| Fixed | Intercept | | 1.135 | 0.418 | 7.367 | 1 | 0.007 |
| | Drought | | -1.393 | 0.659 | 4.475 | 1 | 0.034 |
| | Time | | | | 74.601 | 2 | <0.001 |
| | Depth | | -0.112 | 0.013 | 76.463 | 1 | <0.001 |
| | Farming system | | -1.269 | 0.358 | 12.559 | 1 | <0.001 |
| | Drought*Time | | | | 12.513 | 2 | 0.002 |
| | Drought*Depth | | 0.053 | 0.023 | 5.457 | 1 | 0.019 |
| | Time*Depth | | | | 37.873 | 2 | <0.001 |
| | Drought*Time*Depth | | | | 34.798 | 2 | <0.001 |
| Random | Plot-time ID | 1.50 | | | | | |
| | Bait-lamina ID | 4.59 | | | | | |

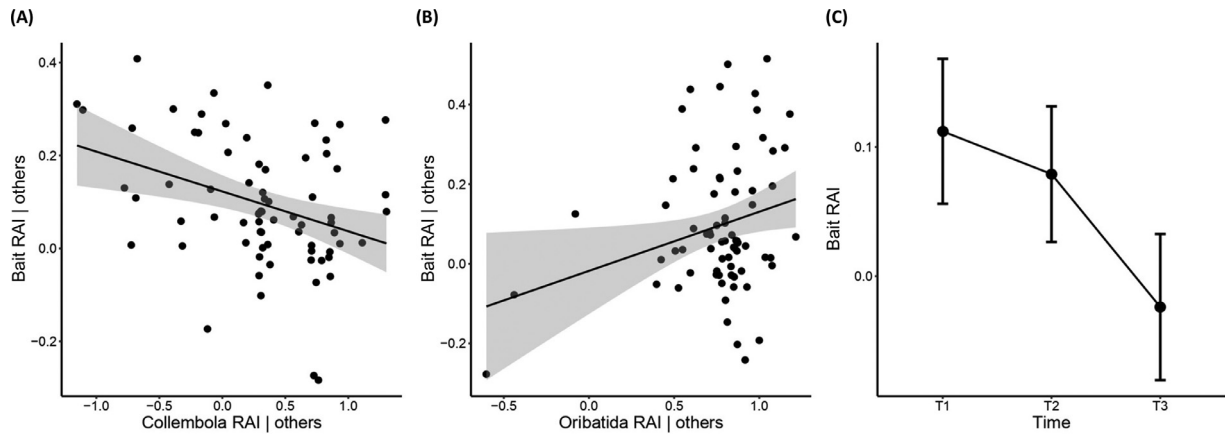


Fig. 2. Effects of the Relative Abundance Indices (RAI) of migrating mesofauna and sampling time on the bait-lamina Relative Activity Index (RAI). The bait-lamina RAI ranged from -1 (i.e., feeding activity occurred only in the deeper soil layer [ca. 0 - 4 cm]) to $+1$ (i.e., feeding activity occurred only in the upper soil layer [ca. 4.5 - 8.0 cm]). The RAIs of (A) total Collembola and (B) Oribatida mites were calculated using abundances (number of individuals per m^2) in the upper and deeper soil layers (0 - 5 and 5 - 10 cm, respectively). Effects depicted for continuous variables are partial regression plots. "Others" refers to the other independent variables in the model; that is, the effects are conditional (independent) on all other predictors. (C) Effect of sampling time (least-square means) on bait-lamina RAI, in April (T1), May (T2) and June (T3). For statistical analysis, see Table 2.

selected five bacterial genera (in order of importance: *Ferruginibacter*, *Gemmatimonas*, *Reyranella* and *Bdellovibrio*), but none of the fungal genera. The model combining fauna and microbiota (RF3) explained less variance (32.43 - 40.89%, $P < 0.001$; Table 3) than the model including only fauna. In order of importance, this model selected four bacterial genera (*Ferruginibacter*, *H16*, *Gemmatimonas* and *Reyranella*) and one nematode genus (*Rhabditis*). Besides, soil properties (RF4) had the largest effect on bait consumption, explaining 72.13 - 74.65% of its variance ($P < 0.001$; Table 3). Variable selection analysis of the latter model revealed that soil water and mineral nitrogen contents, in that order of importance, were the final two explanatory variables. Bait consumption had a strong and positive partial dependence on soil water (Fig. 3E), although this trend was only patent at water contents beyond ca. 22%. Mineral nitrogen strongly and negatively affected bait consumption, albeit this trend was only obvious for the lower part of the mineral nitrogen range (0–10 $\mu\text{g/g}$; Fig. 3F).

Discussion

Severe drought and conventional farming negative effects on detritivore feeding activity

Our results revealed that short-term simulated extreme drought considerably reduced detritivore feeding activity, as previously reported by Birkhofer *et al.* (2021). Consistently, prior studies reported that feeding activity is substantially affected by drought (e.g., Sünneemann *et al.*, 2021), though not always in an additive manner (e.g., Siebert *et al.*, 2019). Additionally, detritivore feeding activity was substantially higher in soils under long-term organic management than in the conventional system. This result is also corroborated by previous studies (e.g., Reinecke *et al.*, 2008), but refuted by others (e.g., Diekötter *et al.*, 2010; Sünneemann *et al.*, 2021). Nevertheless, Meyer *et al.* (2021) found organic management to buffer the negative effects of severe drought on soil microarthropods, but this was not paralleled by detritivore feeding

Table 2. Coefficients of the Generalised Linear Model (GLM) testing the effects of the Relative Abundance Indices (RAI) of migrating mesofauna and sampling time on the bait-lamina Relative Activity Index (RAI). The bait-lamina RAI ranged from -1 (i.e., feeding activity occurred only in the deeper soil layer [ca. 0 - 4 cm]) to $+1$ (i.e., feeding activity occurred only in the upper soil layer [ca. 4.5 - 8.0 cm]). The RAIs of total Collembola, Oribatida mites, and other mites (i.e., Pro-, Meso- and Astigmata) were calculated using abundances (number of individuals per m^2) in the upper (0 - 5 cm) and deeper (5 - 10 cm) soil layers. Sampling times were in April (T1), May (T2), and June (T3) 2017. Model formula: glmmTMB (bait RAI ~ total Collembola RAI + Oribatida mites RAI + time).

| Term | Estimate | S.E. | Chisq (χ^2) | D.f. | P-value |
|----------------------|----------|-------|--------------------|------|---------|
| Intercept | 0.061 | 0.041 | 2.202 | 1 | 0.138 |
| Total Collembola RAI | -0.086 | 0.027 | 9.908 | 1 | 0.002 |
| Oribatida mites RAI | 0.103 | 0.050 | 4.167 | 1 | 0.041 |
| Time | | | 11.255 | 2 | 0.004 |

Table 3. Coefficients of the mixed-effects longitudinal Random Forests (RF) that selected the potential drivers of bait consumption, calculated from different computer seeds (1, 73 or 976). Original scales of the predictors were: individuals/100 g dry soil for Nematoda abundance, selected genera of microbes from the most abundant genera of Bacteria and Fungi, percentage of soil water and $\mu\text{g/g}$ soil of mineral nitrogen. Abbreviations are: Ba, bacterivores; He, herbivores; Om, omnivores; and B, bacteria.

| Random Forest models | RF (1) | | RF (73) | | RF (976) | | Common predictors across RF models |
|---|----------|---------|----------|---------|----------|---------|--|
| | Variance | P-value | Variance | P-value | Variance | P-value | |
| RF1 – mesofauna and nematodes | 58.18 | 0.001 | 44.71 | 0.001 | 42.7 | 0.001 | Rhabditis (Ba) Helicotylenchus (He) Rotylenchus (He) Qudsianematidae (Om) |
| RF2 – microbes: bacteria and fungi | 17.21 | 0.002 | 17.39 | 0.001 | 15.87 | 0.004 | Ferruginibacter (B) Gemmatimonas (B) Reyranella (B) Bdellovibrio (B) |
| RF3 – mesofauna, nematodes and microbes | 40.89 | 0.001 | 32.43 | 0.001 | 34.27 | 0.001 | Ferruginibacter (B) H16 (B) Gemmatimonas (B) Reyranella (B) Rhabditis (Ba) |
| RF4 – soil properties | 74.65 | 0.001 | 73.59 | 0.001 | 72.13 | 0.001 | Soil water Mineral nitrogen |

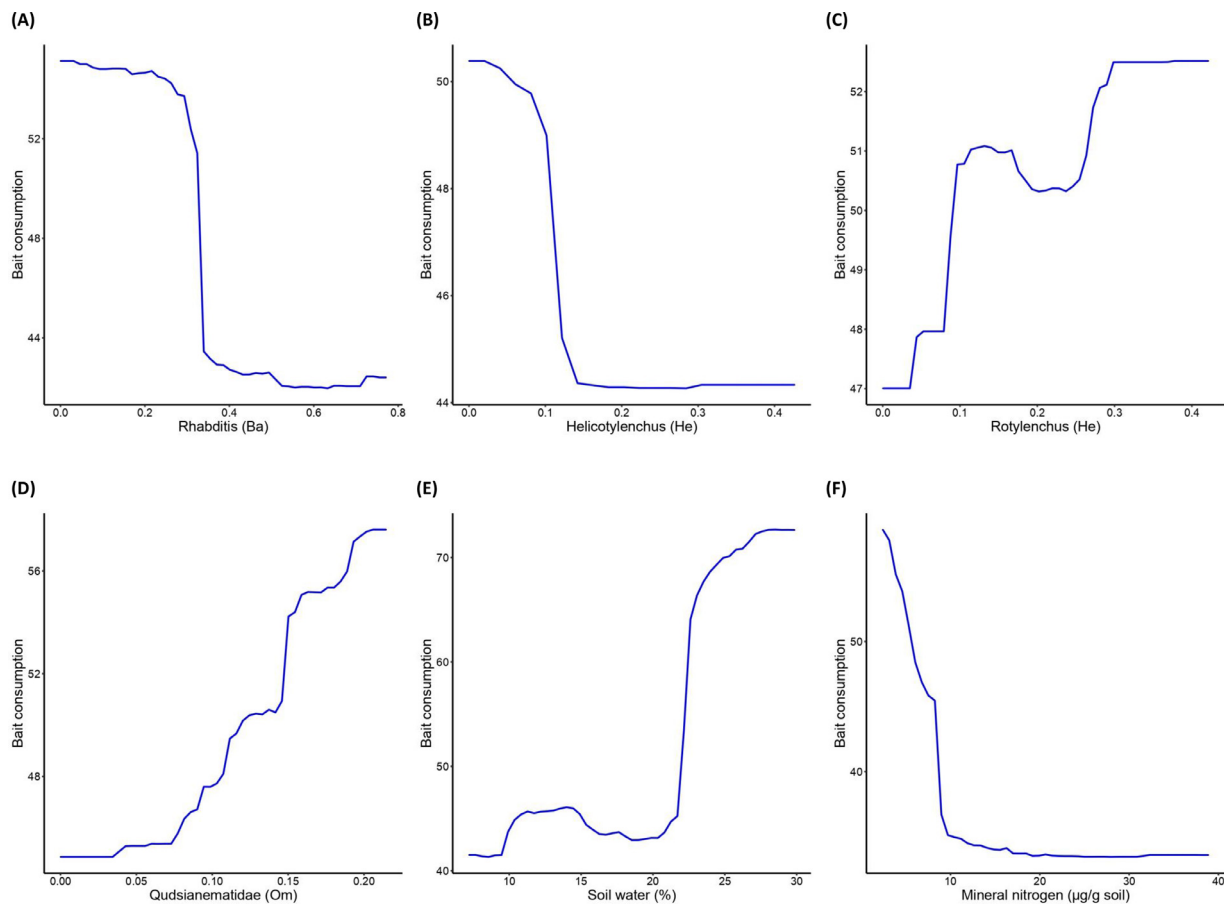


Fig. 3. Partial dependence plots showing the potential drivers of bait consumption. Potential drivers were selected by means of mixed-effects longitudinal Random Forests (RF). (A–D) selected nematoda taxa (from RF1) and (E,F) selected soil abiotic properties (from RF4). The original abundance scales for microfauna were individuals/100 g dry soil. (A) *Rhabditis*, (B) *Helicotylenchus*, (C) *Rotylenchus*, (D) *Qudsianematidae*, (E) soil water (%), and (F) mineral nitrogen ($\mu\text{g/g}$ soil). Abbreviations are: Ba, bacterivores; He, herbivores; and Om, omnivores. For statistical analysis, see Table 3.

activity. We only documented additive effects of drought and farming systems, thus conventional management did not exacerbate drought effects on detritivore feeding, failing to support our first hypothesis (i). Furthermore, it should be noted that all crops in our study system were subjected to the same type and depth of tillage (ploughed to 20 cm depth). If crops under different types of tillage (e.g., conventional tillage, conservation tillage, no-tillage) had been compared, bait consumption by detritivores would probably have been highly dependent on this factor, as it greatly disturbs the soil fauna (Betancur-Corredor *et al.*, 2022).

Depth of detritivore feeding activity and migrating mesofauna

We found that severe drought reduced bait consumption in the deeper soil layers, which seems contradictory since soil upper layers dry up more rapidly. However, we also found that this increase in bait consumption in the upper layers was closely related to the downward migration of collembolans and the upward migration of oribatid mites inside the soil. Hence, given our results and those of Meyer *et al.* (2021), and consistent with our second hypothesis (ii), we propose that the increased feeding activity in the upper soil layer might be explained by vertical migrations of soil fauna in response to drought.

Soil collembolans and oribatids are known to primarily feed on litter, roots and fungi, although some others are phytophages, predators or scavengers (Potapov *et al.*, 2022). However, the negative relationship between the position of bait consumption and that of collembolans could be either the result of an indirect effect mediated by drought conditions, or the response of other fauna that moved upwards, such as oribatids, which are more resistant to desiccation due to their thicker cuticles (Meyer *et al.*, 2021). On the contrary, the vertical position of detritivore feeding activity was not related to that of non-oribatid mites. Astigmata mites are also considered to be mostly microbivores-detritivores or omnivores, but these were classified together with Mesosoma and Prostigmata that are essentially fluid-feeders (Potapov *et al.*, 2022). Nevertheless, detritivore feeding activity does not only depend on faunal abundance, but further reflects the accessibility of bait material and the utilization of alternative resources (Birkhofer *et al.*, 2022). Besides, relationships between soil animals and bait consumption were probably related to complex soil food web dynamics, as we further develop next.

Faunal and microbial main determinants of detritivore feeding activity

Our results suggest that detritivore feeding activity may have been promoted by soil organisms other than mesofauna. Regarding microfauna, bait consumption was

associated with the abundance of four nematode taxa, probably reflecting indirect effects mediated by other fauna of the soil decomposer food web. More importantly, the faunal model explained higher variance than either the microbiota model or the combined faunal-microbiota model. Therefore, our third hypothesis (iii) is supported since strong relationships probably link detritivore feeding to nematodes, but not to microbes. Qudsianematidae are omnivorous nematodes known to feed on soil fungi (McSorley, 2012) thus, as fungal growth was observed over the bait, these nematodes may have fed on such fungi growing on the bait. However, the associations between bait-lamina tests and other soil nematode taxa might be indirect and difficult to interpret, as is the case for *Rhabditis* (bacterivores) as well as for *Rotylenchus* and *Helicotylenchus* (herbivores). In any case, it is noteworthy that although previous studies analysed bait-lamina tests along with soil nematodes, to our knowledge, none have previously reported associations between the abundance of any nematode taxa and the bait-lamina test.

With respect to soil microbes, we found five bacteria genera partially related to detritivore feeding activity. However, the fact that the microbial model was that with the lowest explained variance is consistent with the hypothesis that bait-lamina tests are not indicative of microbial activity (van Gestel *et al.*, 2003). In addition, the difference between the model with only fauna and that with fauna and microbes indicates that microbe-fauna synergies were of little relevance to bait consumption. Still, another possibility is that the different depths at which soil sampling for microbial analyses (0 - 20 cm) and bait-lamina test (0.5 - 8 cm) was performed may have obscured such relationships.

Soil abiotic key drivers of detritivore feeding activity

Detritivore feeding was positively influenced by soil water, which was dramatically reduced by rainout shelters in both farming systems (Kozjek *et al.*, 2021). Moreover, under non-drought conditions, soil water was higher in organic compared to conventional fields (Kundel *et al.*, 2020). Therefore, the adverse effects of drought and conventional farming were probably mediated by soil water. In line with this, higher aggregate stability characterises soils under organic management in the DOK trial (Mäder *et al.*, 2002), which usually entails greater infiltration and flow of water through soils. By contrast, soil mineral nitrogen was negatively related to detritivore feeding activity, a parameter that probably depends largely on the differing fertilization strategies between both farming systems (see Appendix A). Actually, the latter agrees with a previous study stating that feeding activity decreases under high NPK fertilization (Siebert *et al.*, 2019). These findings are, in any event, consistent with our last hypothesis (iv), according to which both soil water and soil mineral nitrogen are probably key drivers of detritivore feeding activity.

Conclusions

Our results provide experimental evidence on how extreme drought events and conventional agricultural practices, albeit separately, negatively impact the feeding activity of detritivorous fauna in wheat fields, which has the potential to severely affect important soil processes such as decomposition and nutrient cycling. Besides, detritivore feeding activity was negatively related to soil depth under drought. The relative vertical positions of collembolans and oribatids were associated with that of bait consumption within the soil. Studying not only the abundance but also the vertical distribution of soil fauna and its feeding activity, appears thus paramount for understanding soil food web dynamics and its associated ecosystem processes under drought conditions. Additionally, by means of mixed-effects longitudinal random forests, we found strong associations between soil detritivory and the abundance of various taxa (i.e., four nematodes and five bacteria), as well as with two abiotic parameters (i.e., soil water and nitrogen). Hence, machine learning emerges as a powerful technique with which to delve into the relationship between biodiversity and ecosystem processes.

Declaration of Competing Interest

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

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Author contributions

KB, AF, JM, SS, JT and DK made substantial contributions to the conception and design of the study. DSC and MM recorded bait consumption. AF and DK collected field data. DK and JT did the microbial databases. SSM made the nematodes databases, while SM and SS did the mesofauna ones. JML wrote the R code. JML and PGC performed the data analyses and wrote the initial draft of the manuscript, and all authors contributed substantially to the final version.

Data availability

The data are available at <https://doi.org/10.20350/digitalCSIC/14570>.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2023.03.006](https://doi.org/10.1016/j.baae.2023.03.006).

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