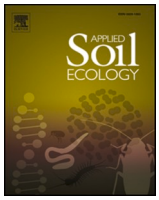
Applied Soil Ecology 170 (2022) 104254

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Integrating perennial bahiagrass into the conventional rotation of cotton and peanut enhances interactions between microbial and nematode communities

Kaile Zhang [a,b], Lesley Schumacher [c,d], Gabriel Maltais-Landry [b], Zane J. Grabau [c], Sheeja George [a], David Wright [a], Ian M. Small [a], Hui-Ling Liao [a,b,*]

[a] North Florida Research and Education Center, University of Florida, 155 Research Road, Quincy, FL 32351, USA
[b] Soil and Water Sciences Department, University of Florida, Gainesville, FL 32611, USA
[c] Entomology and Nematology Department, University of Florida, Gainesville, FL 32611, USA
[d] USDA, Agricultural Research Service, Crop Genetics Research Unit, 605 Airways Blvd, Jackson, TN 38301, USA

ARTICLE INFO

Keywords:
Sod-based rotation
Conventional rotation
Rotational diversity
Perennial grass
Soil food webs
Soil trophic interactions

ABSTRACT

Integrating two years of bahiagrass (*Paspalum notatum* Flugge) into the peanut (*Arachis hypogea* L.) and cotton (*Gossypium hirsutum* L.) cropping system improves soil quality and crop production as compared to a conventional peanut-cotton-cotton rotation (CR). However, it is unclear if this system, known as a sod-based rotation (SBR), affects soil biological communities (e.g., soil microorganisms and nematodes) and their trophic interactions. Furthermore, how soil trophic groups respond to agricultural management (e.g., irrigation) is understudied. In April 2017, we collected pre-planting soil samples (0–30 cm) from cotton plots located in Quincy (Florida, United States) that had been under CR (cotton grown in two consecutive years) and SBR (cotton grown only once) for 17 years. We used amplicon sequencing to investigate soil microbial communities and an inverted microscope technique to quantify nematodes. Compared to CR, SBR significantly increased nematode alpha diversity (one-way ANOVA; $P < 0.05$) and induced different nematode communities. In contrast, there were no significant differences in the diversity and structure of bacterial communities between SBR and CR. SBR plots were significantly enriched in Nitrospira, while the second of two consecutive years of cotton growth in CR had a higher relative abundance of Alphaproteobacteria (one-way ANOVA; $P < 0.05$). Plant-parasitic (848 counts per 100 g dry soil) and bacterial-feeding nematodes (798 counts per 100 g dry soil) had a similar abundance in SBR, while plant-parasitic nematodes (7772 counts per 100 g dry soil) were predominant in CR (<1000 counts per 100 g dry soil for all other taxa). SBR exhibited a greater number of significant paired Pearson correlations ($P < 0.05$) among functional groups of bacteria and nematodes compared to CR systems. Irrigation had no effect on the diversity and structure of bacterial and nematode communities in SBR, although some soil bacterial and nematode groups responded to irrigation. Overall, these results suggest that integrating bahiagrass to diversify the conventional peanut-cotton rotation is a sustainable approach to enhance soil biodiversity, with more diverse nematode communities and complex soil trophic interactions that will affect the response to crops and irrigation. Thus, future crop rotations should increase plant functional trait diversity (e.g., by adding perennial grasses) to maximize benefits to soil communities.

1. Introduction

Peanut (*Arachis hypogea* L.) and cotton (*Gossypium hirsutum* L.) are important crops worldwide, providing food, industrialized products, fiber, seed, and/or oil (Ahmad and Hasanuzzaman, 2020; Ganguly et al., 2020). The US is a major producer of peanut and cotton (Perea-Moreno et al., 2018; Himanshu et al., 2019), and they are major summer agronomic crops in the Southeast US, accounting for approximately 75% (1.3 million hectares) and 35% (2.5 million hectares) of the total US peanut and cotton production (2005–2018), respectively (Carlisle et al., 2019). However, farmers in this area face major challenges to maintain yield and profitability in the traditional crop rotation system of cotton-cotton-

* Corresponding author at: North Florida Research and Education Center, University of Florida, 155 Research Road, Quincy, FL 32351, USA.
E-mail address: sunny.liao@ufl.edu (H.-L. Liao).

https://doi.org/10.1016/j.apsoil.2021.104254
Received 2 February 2021; Received in revised form 15 August 2021; Accepted 2 October 2021

peanut (CR). A major issue is that soils are coarse-textured, low in soil organic matter (SOM) and water holding capacity (WHC), and prone to compaction and soil erosion, resulting in fertility and moisture deficits (Katsvairo et al., 2007a, 2007b, 2009).

Perennial grasses are beneficial to many soil functions in agroecosystems (Lodge, 1994; Abraham et al., 2009), which is partly due to their ability to develop deep root systems. These strong and vigorous root systems can penetrate through compacted soil layers, increasing soil aeration, water infiltration, and structure (Reeves, 1997; Katsvairo et al., 2006). Simultaneously, perennial grasses translocate 33% of the carbon (C) they fix to belowground structures and exudates on average, improving soil organic C and nitrogen (N) status relative to annual crops (Reeves, 1997; Katsvairo et al., 2006; Pausch and Kuzyakov, 2018). Because of these traits, integrating two years of perennial bahiagrass (*Paspalum notatum*) in the CR system, referred to as a sod-based rotation (SBR), has been proposed in the Southeast US since the early 2000s (Katsvairo et al., 2007a, 2007b, 2009; Zhao et al., 2009; Dourte et al., 2016). Previous studies have demonstrated that SBR provides many benefits relative to CR (Katsvairo et al., 2007a, 2007b, 2009; Zhao et al., 2009). For example, SBR can substantially increase crop yields while reducing the use of fertilizers, pesticides, and irrigation, due to greater SOM and N use efficiency, lower pressure of pests and disease, higher activity of nutrient cycling enzymes (e.g., β-glucosidase, β-glucosaminidase, acid and alkaline phosphatases, and arylsulfatase), and enhanced soil physical properties relative to the CR system (Katsvairo et al., 2006, 2007a, 2007c; Zhao et al., 2009; Dourte et al., 2016; Schumacher et al., 2020). However, the long-term effects of SBR on the diversity and structure of soil belowground communities remain understudied, despite the critical role of microbial communities in biogeochemical cycles and plant productivity (Fierer, 2017; Crowther et al., 2019).

Including bahiagrass in crop rotations may also suppress the growth of plant-parasitic nematodes (PPN), especially reniform nematodes (*Rotylenchulus reniformis*). Reniform nematodes are significant pathogens of cotton and are estimated to cause a 60% yield loss worldwide (Tsigbey et al., 2009; Doshi et al., 2010; Schumacher et al., 2020). However, little is known about how the conversion to SBR affects free-living nematode communities in the long term. Free-living nematodes are the most diverse group of soil mesofauna and they occupy key trophic positions in soil food webs, leading to pronounced effects on soil ecological processes through their interactions with other soil microorganisms (Osler and Sommerkorn, 2007; Neher, 2010). For example, bacterial-feeding nematodes (BFN) may enhance nitrification by altering ammonia-oxidizing bacteria community composition (i.e., *Nitrosomonas* sp. and *Nitrosospira* sp. (Xiao et al., 2010). Fungal-feeding nematodes and BFN release N compounds when grazing on decomposed microbes, directly affecting C and N mineralization (Anderson et al., 1983). Free-living nematodes also disseminate microbial propagules in the soil, accelerating the colonization of substrates and their mineralization, which releases nutrients (Bouwman et al., 1994; Jiang et al., 2018). Although overgrazing of bacteria and fungi may decrease the overall activity of microorganisms, trophic interactions among predators, omnivores, BFN, and fungal-feeding nematodes typically stimulate nutrient cycling (Bouwman et al., 1994; Jiang et al., 2017).

Nematode metabolic footprints (NMFs) are used to estimate the contribution of different nematode groups to ecosystem services and functions. In particular, these indices can provide information in terms of the biomass, metabolic activity, and magnitude of C and energy flow driven by different nematode groups in soil food webs (Ferris et al., 2012; da Silva et al., 2021; Karuri, 2021). Despite these findings, the long-term effects of different crop rotations on biotic interactions between microorganisms and nematodes remain poorly known, including how these interactions affect nutrient cycling and soil fertility. This is because most previous research focusing on the effects of cropping systems and management on soil belowground communities mostly studied a single trophic-level community (e.g., microorganisms or nematodes; Chen et al., 2020a, 2020b; Guo et al., 2020; Schumacher et al., 2020; Van Nguyen et al., 2020).

Agricultural water management, including irrigation, is an important determinant of soil belowground communities as it alters soil moisture and water availability (Prado and Airoldi, 1999; Drenovsky et al., 2004; Falkowski et al., 2008; Franco and Gherardi, 2019). For example, soil moisture can directly affect bacterial physiological status (Harris, 1981), and microbial community composition, structure, and biomass are primarily controlled by soil moisture (Brockett et al., 2012; Shen et al., 2018; Frindte et al., 2019). Nematode communities are also affected by soil moisture given the high impact of soil water on movement and activity (Franco and Gherardi, 2019) and on the regulation of substrate availability, which modulates soil communities and their activity (Prado and Airoldi, 1999). As integrating bahiagrass in SBR increases SOM and WHC and decreases irrigation requirements compared to CR (Dourte et al., 2016), this could affect soil microbial and nematode communities. Integrating perennial grasses into crop rotations also increases plant functional trait diversity and soil biodiversity (Lange et al., 2015; Faucon et al., 2017), and this higher biodiversity could increase resistance to environmental stress and anthropogenic disturbances, as seen in other ecosystems (Isbell et al., 2015; Beaury et al., 2020; Philippot et al., 2021). Therefore, SBR can be posited to have a greater tolerance to fluctuations in water content.

This study focuses on the long-term effects (17 years) of CR and SBR systems on soil microbial and nematode communities during the cotton phases of these systems. Our objectives were to 1) identify the dominant microbial and nematode communities in SBR and CR systems; 2) characterize differences in soil biological communities and trophic interactions in soil food webs between SBR and CR; and 3) determine the responses of bacterial and nematode communities to irrigation under different crop rotation systems. We hypothesized that 1) SBR would increase the diversity of microbial and nematode communities and enhance trophic interactions between microbial and nematode communities as increasing plant functional traits should increase soil biodiversity; 2) SBR would decrease PPN population and increase the abundance of free-living nematodes due to an increase in predatory nematodes that can control PPN abundance; and 3) soil biological communities would be more sensitive to irrigation in CR relative to SBR because the greater soil biodiversity found with a more diverse rotation should reduce the vulnerability of soil organisms to water scarcity.

2. Materials and methods

2.1. Experimental site and design

The experimental site was established in 2000 at the North Florida Research and Education Center, Quincy, Florida (30°32.79′N, 84°35.50′W), on a soil mapped as a Dothan sandy loam soil (fine-loamy, kaolinitic, thermic Plinthic Kandiudult) (Dourte et al., 2016). The experiment used a strip-plot experimental arrangement with a randomized complete block design. There were two main crop rotation systems, bahiagrass-bahiagrass-peanut-cotton (SBR) and peanut-cotton-cotton (CR), arranged in seven main plots (i.e., each rotation phase of the two systems) in each of three blocks, with 45.7 × 18.3 m^2 plots. Every rotation phase was represented every year, with three replicated plots for each rotation phase of the two systems. Each of the three experimental blocks combined two contiguous sections of 128 × 45.7 m^2, where one section was irrigated and the other was rainfed only. Thus, each main plot was divided into an irrigated and a rainfed subplot. Irrigated subplots received 3 cm of water every week (the dates for irrigation can be found in Schumacher et al., 2020) via a lateral line overhead irrigation system, following the recommendations from the Georgia Crop Production Guide, unless there was substantial rainfall (Dourte et al., 2016).

Cotton and peanut have been planted between early April and mid-May every year since 2000. A 5-10-15 (N-P_2O_5-K_2O) fertilizer was

applied in the bahiagrass plots at a rate of 28 kg ha^{-1} N, 24 kg ha^{-1} P, and 84 kg ha^{-1} K, broadcast immediately before seeding bahiagrass. The first-year bahiagrass was mowed twice for hay in early July and late August, and the second-year bahiagrass was cut three times for hay in early July, late August, and mid-October. A 5-10-15 fertilizer was also applied in all cotton plots at seeding at the same rate as the bahiagrass plots, and an additional 67 kg N ha^{-1} was side-dressed at the first square stage each year. Peanut received no fertilizers based on the Florida peanut production recommendations and soil tests that did not indicate deficiencies (Zhao et al., 2010).

After harvesting cotton and peanut or killing bahiagrass with glyphosate [*N*-(phosphonomethyl) glycine; 1.1 kg active ingredient ha^{-1}] in late September to October, oat (*Avena sativa* L.) was planted as a winter cover crop in all plots, except bahiagrass completing its first year of growth, using a Great Plains no-till drill at a seeding rate of 67 kg ha^{-1} (Great Plains Mfg., Assaria, Kansas) and fertilized with ammonium nitrate at a rate of 45 kg N ha^{-1}. Cover crops were killed in early spring with glyphosate (1.1 kg active ingredient ha^{-1}) each year.

2.2. Soil sampling

Three cotton phases were sampled for this study, one from SBR and two from CR (first- and second-year cotton). Supplementary Table S1 shows the history (2012–2017) of rotation phases for all plots that were under cotton in 2017 for each system. Surface soil samples (0-30 cm) were collected using an Oakfield tube before cotton planting in April 2017 in order to analyze soil microbial and nematode communities. Ten soil cores (diameter = 2 cm) were taken per subplot, and five of these cores were mixed to form a composite subsample while the other five cores were mixed to make a different composite subsample. When conducting statistical analyses, we integrated these two subsamples as an individual sample using the average for each variable. In total, there were 18 samples (3 cotton phases × 2 irrigation conditions × 3 replicates). A subsample for each soil sample was sieved through a screen with 0.64 cm apertures, and each sample was transferred to 2 ml Eppendorf tubes and stored at −80 °C prior to DNA extraction.

2.3. Nematode identification, quantification, and determination of metabolic footprints

The extraction of soil nematodes followed the sucrose-centrifugation method (Jenkins et al., 1964). Nematode samples were fixed in 2% formalin before counting with an inverted microscope (Zeiss Inc., Oberkochen, Germany) and identified morphologically using a key (Bongers and Bongers, 1998). Soil nematodes were functionally grouped into bacterial-feeding, fungal-feeding, plant-parasitic, omnivorous, and predatory nematodes based on feeding habits (Yeates et al., 1993). Nematode populations were expressed as individuals per 100 g of dry soil.

Nematode metabolic footprints (NMFs) were used to estimate the amount of C and energy entering food webs through specific nematode groups and can be calculated using these formulas:

$$W = \left(D^2 \times L\right) / \left(1.6 \times 10^6\right), \quad (1)$$

$$NMFs = \Sigma \left(N_t \left(0.1\ W_t / m_t + 0.273 \left(W^{0.75}\right)\right)\right), \quad (2)$$

where W is total nematode biomass (μg) per individual, and D and L are maximum body diameter (μm) and body length (μm), respectively, which were determined using an ocular micrometer. Nt represents the number of taxa in each trophic group, W_t is the body weight, and m_t is the colonizer-persister (cp) value (Ferris, 2010; Ferris et al., 2012; Guan et al., 2018). The cp value for each genus was determined by life-history characteristics (Bongers and Bongers, 1998). The enrichment footprint is the metabolic footprint of lower trophic levels (cp of 1-2), where nematodes respond to enrichment in C resources (Ferris, 2010). The structure footprint is the metabolic footprint of higher trophic levels (cp of 3-5; Ferris, 2010; Ferris et al., 2012). The herbivore, bacterivore, and fungivore metabolic footprints are nematode indicators of C and energy flow entering the soil food webs through their respective channels (shown by a specific cp value for each functional nematode group; Ferris, 2010).

2.4. Soil DNA extraction and amplicon sequencing

Soil DNA was extracted using the DNA PowerSoil kit (MoBio, Carlsbad, California, USA) following the manufacturer's instructions. Three-step PCR was modified according to the study of Chen et al. (2019). Briefly, bacterial 16S rRNA gene fragments were amplified using primer sets to target the V4-V5 variable region. The forward primer was 515F (5′- GTGCCAGCMGCCGCGGTAA -3′) linked with a sample-specific 10-bp barcode sequence at the 3′end of primers, and the reverse primer was 806R (5′- GGACTACHVGGGTWTCTAAT -3′) (Bates et al., 2011; Caporaso et al., 2011). Each sample was amplified in triplicate, and the reaction products were pooled and purified using bead-cleanup (AMPure-XP, Beckman Instruments, Brea, California, USA). The quantity of PCR products was assessed by spectrophotometry (NanoDrop™, Thermo Fisher Scientific, Thermo Scientific™). The size and quality of PCR products were verified by screening on 1% (w/v) agarose gels. All amplicons were pooled at equimolar concentrations (20 ng μl^{-1}), and the index sequencing of paired-end 250 bp was performed on an Illumina Miseq (v2 250bp, 6Gb sequencing capacity) (Illumina Inc., San Diego, California, USA). The raw sequence data were deposited in the NCBI Sequence Read Archive (http://trace.ncbi. nlm.nih.gov/Traces/sra/) under Study PRJNA600872.

2.5. Assembly of DNA amplicon sequence data

Data of bacterial 16 s rRNA gene sequencing were processed by QIIME 2 (Bolyen et al., 2019). High-quality sequences were filtered according to Caporaso et al. (2011) and mapped to operational taxonomic units (OTUs) using the "*vsearch*" function. Taxonomy at the species level was assigned to OTUs at a 97% identity threshold using the RDP classifier with the Greengenes database as a reference and a confidence cutoff of 0.8 for bacteria and archaea (Version 2018). All datasets were rarefied to 5000 sequences per sample prior to analysis to prevent potential bias caused by different sequencing depths. For this study, we divided bacterial communities into C-associated (e.g., Acidobacteria, Actinobacteria, Bacteroidetes, and Proteobacteria) and N-associated (e.g., ammonia-oxidizing bacteria and archaea, and nitrite-oxidizing bacteria) taxa.

2.6. Statistical analyses

Statistical analyses were performed in R, version 3.5 (Hector, 2015; Xia et al., 2018). Alpha diversity of bacterial and nematode communities was determined with the Shannon index (Zhang et al., 2017). For beta diversity, the dissimilarity of bacterial and nematode communities among all samples was calculated using Bray-Curtis distances at the OTU level (Zhang et al., 2015), and nonmetric multidimensional scaling (NMDS) ordination was used to visualize the differences in bacterial and nematode communities. Permutation multivariate analysis of variance (PERMANOVA) and analysis of similarity (ANOSIM) were used to assess the statistical significance of compositional differences of bacterial and nematode communities. Computations for alpha and beta diversity, PERMANOVA, and ANOSIM were made using the *vegan* package (Xia et al., 2018). Linear mixed models (LMM) were used to analyze the effects of crop rotation, irrigation, and their interactive effects on bacterial and nematode-associated variables, with field plot number used as a random effect (package: *lmerTest*; Zhao et al., 2019). Shapiro-Wilk's and Levene's test were used to examine the normality and homogeneity of variance within the treatments, respectively. When crop rotation by

irrigation interactions were significant in the LMM, the effect of crop rotation was determined for irrigated and rainfed plots separately, using a one-way ANOVA followed by a Tukey HSD test at $P < 0.05$, and the effects of irrigation were determined with a *t*-test comparing irrigated and rainfed conditions for each cotton phase individually. For variables in which only the main effect of crop rotation was significant, a Tukey HSD test was used among cotton phases regardless of irrigation, when variances within cotton phases were normally distributed and homogeneous. In addition, Pearson correlations were computed between irrigation, bacterial and nematode diversity and community composition, and dominant bacterial and nematode groups, using the "cor" function (package: *corrplot*; Wei et al., 2017); *P*-values were adjusted by the Bonferroni-Holm method for these correlations.

Structural equation modeling (SEM) was used to quantify the importance of crop rotation and irrigation on microbial and nematode diversity and NMFs. Crop rotation variables were created by assigning the following values: 2 to SBR, 1 to first-year cotton phase in CR (1st-year CR), and 0 to second-year cotton phase in CR (2nd-year CR) based on the level of previous crop diversity. For irrigation variables, irrigated and rainfed treatments were assigned the value 1 and 0, respectively. Bacterial and nematode alpha diversity were represented by its corresponding Shannon index. All variables were standardized by *Z* transformation (mean = 0, standard deviation = 1) using the "*scale*" function. All NMFs were reduced in dimension using NMDS, and the variance of NMFs was represented by the first axis of NMDS (Zhao et al., 2019; Zhang et al., 2020). SEM was constructed and analyzed in AMOS 24.0 (SPSS, Chicago, IL, USA) using the covariance matrix of these variables fitted by a maximum likelihood evaluation method (Zhang et al., 2020). A nonsignificant Chi-square test ($P > 0.05$), high goodness-of-fit index (GFI > 0.90), and low root mean square error of approximation (RMSEA < 0.05) were used to indicate a SEM that fitted the data well (Byrne, 2016).

3. Results

3.1. Soil microbial community composition and diversity

A total of 181,815 high-quality sequences ranging from 5626 to 13,587 sequences per sample (10,101 sequences on average) were obtained from all soil samples after quality filtering (Supplementary Table S3). Of these, 96.0% were classified as bacteria, 1.6% as archaea, and 2.4% remained unclassified. The dominant C-associated bacterial taxa, including Acidobacteria, Actinobacteria, Bacteroidetes, and Proteobacteria, accounted for 57.7–87.8% of the total sequences (Fig. 1A). Among C-associated taxa, irrigation only affected the relative abundance of Actinobacteria, with a greater relative abundance in rainfed plots compared to irrigated plots (Table 1; *t*-test; $P < 0.05$). Only two C-associated bacterial taxa were impacted by crop rotation (Table 1): the relative abundance of Deltaproteobacteria was significantly enriched under SBR and 2nd-year CR relative to 1st-year CR plots, and 2nd-year CR exhibited a higher relative abundance of Alphaproteobacteria compared to SBR and 1st-year CR plots (Fig. 1A; one-way ANOVA; $P < 0.05$).

All N-associated microorganisms identified in all soil samples were either ammonia-oxidizing archaea (*Nitrosotalea* and Ca. *Nitrosophaera*) or nitrite-oxidizing bacteria (Nitrospira), comprising 2.2-20.3% of the total sequences found across treatments (Fig. 1B). There was a significant rotation by irrigation interaction for the relative abundance of Nitrospira (Table 1). Among irrigated treatments, the relative abundance of Nitrospira was higher in SBR than CR systems. The effect of irrigation was significant only in SBR ($P < 0.001$), where irrigated plots had a higher relative abundance of Nitrospira than rainfed plots. The relative abundance of Ca. *Nitrosophaera* was significantly higher in 2nd-year CR as compared to SBR and 1st-year CR plots ($P < 0.05$). There was no significant difference among treatments for the relative abundance of *Nitrosotalea* (less than 0.12%), which was only present in 1st-year CR and irrigated treatments of 2nd-year CR.

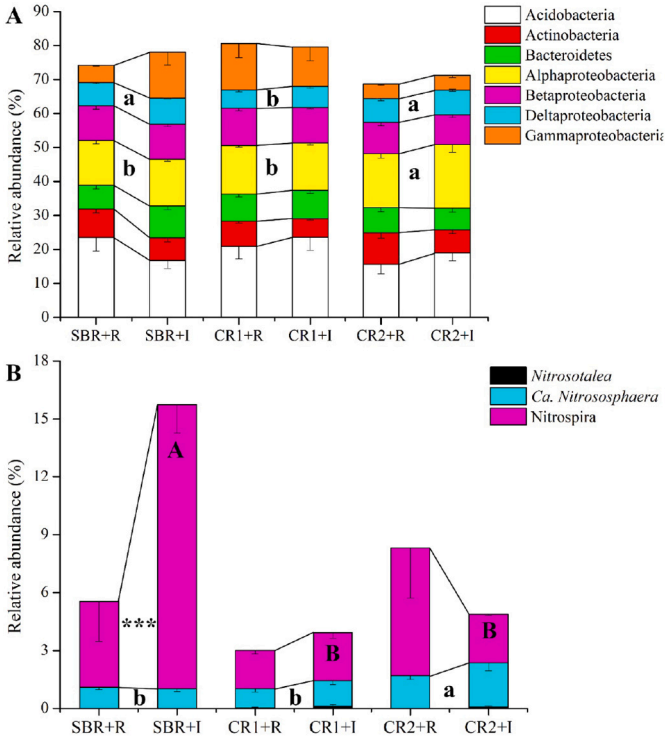


Fig. 1. Relative abundance (mean ± standard error) of dominant carbon (A) and nitrogen (B) associated bacterial taxa under SBR and CR. Lowercase letters indicate significant differences ($P < 0.05$) among cotton phases in crop rotations where the main effect of crop rotation was significant. Uppercase letters indicate significant differences ($P < 0.05$) among cotton phases in crop rotations where crop rotation by irrigation interaction was significant. Asterisks (***) shown in Nitrospira indicate a significant difference ($P < 0.001$) between irrigated and rainfed conditions within the cotton phase in SBR. R: rainfed, I: irrigation, CR1: 1st - year CR, CR2: 2nd - year CR.

Bacterial alpha diversity, calculated with Shannon's index, was not significantly affected by either crop rotation or irrigation (Fig. 2A; Table 1). Similar to alpha diversity, differences in bacterial communities among rotation phases or between irrigated and rainfed treatments ($P > 0.05$) were not significant based on PERMANOVA and ANOSIM tests (Fig. 2B; Table 3, and Supplementary Table S4).

3.2. Nematode community and metabolic footprints

The total population of nematodes varied from 850 to 16,155 individuals per 100 g dry soil (mean 6240; Supplementary Table S3), which were classified into 45 genera. Nematode communities were primarily dominated by PPN and BFN in the SBR system, accounting for over 80% of total nematode abundance (Fig. 3). On average, PPN abundance in CR was ten-fold greater than in the SBR system, accounting for more than 80% of total nematode abundance as opposed to roughly 45% for SBR. Crop rotation had a significant effect on PPN, as PPN population density was greatest in 2nd-year CR (9821 counts per 100 g dry soil) and lowest in SBR (848 counts per 100 g dry soil). Although BFN abundance was similar between SBR (798 counts per 100 g dry soil) and CR systems (636 counts per 100 g dry soil; one-way ANOVA, $P > 0.05$), the relative abundance of BFN (expressed as a % of total nematode population) was substantially lower in CR relative to SBR plots. The enrichment, herbivore, and bacterivore footprints were the main NMFs found in this study (Fig. 4; Table 2). Regardless of irrigation, enrichment and bacterivore footprints were significantly lower and HF was significantly higher under 2nd-year CR relative to SBR and 1st-year CR (one-way ANOVA, $P < 0.05$). There was no significant difference between SBR and 1st-year CR for enrichment and bacterivore

Table 1
Effects of crop rotation and irrigation on the alpha diversity and composition of the bacterial community based on a linear mixed model, where the field plot number was used as a random effect.

	Rotation		Irrigation		Rotation × irrigation	
	F	*P*	F	*P*	F	*P*
Bacterial alpha diversity	0.29	0.75	0.66	0.43	0.41	0.68
Alphaproteobacteria	**6.59**	**0.01***	1.33	0.27	1.12	0.36
Betaproteobacteria	0.04	0.96	1.14	0.31	0.81	0.47
Gammaproteobacteria	3.51	0.07	0.20	0.66	1.12	0.36
Deltaproteobacteria	**4.17**	**0.04***	1.90	0.19	0.21	0.82
Acidobacteria	1.80	0.21	0.02	0.91	2.29	0.14
Actinobacteria	1.00	0.40	**6.21**	**0.03***	0.15	0.86
Bacteroidetes	0.02	0.98	0.28	0.61	2.20	0.15
Ca. Nitrososphaera	**8.74**	**<0.01****	1.95	0.19	0.96	0.41
Nitrosotalea	2.30	0.14	3.79	0.08	0.96	0.41
Nitrospira	**11.95**	**<0.01****	**11.03**	**<0.01****	**7.83**	**<0.01****

*, **, and *** represent significant effects (marked in bold) at $P < 0.05$, 0.01 and 0.001, respectively.

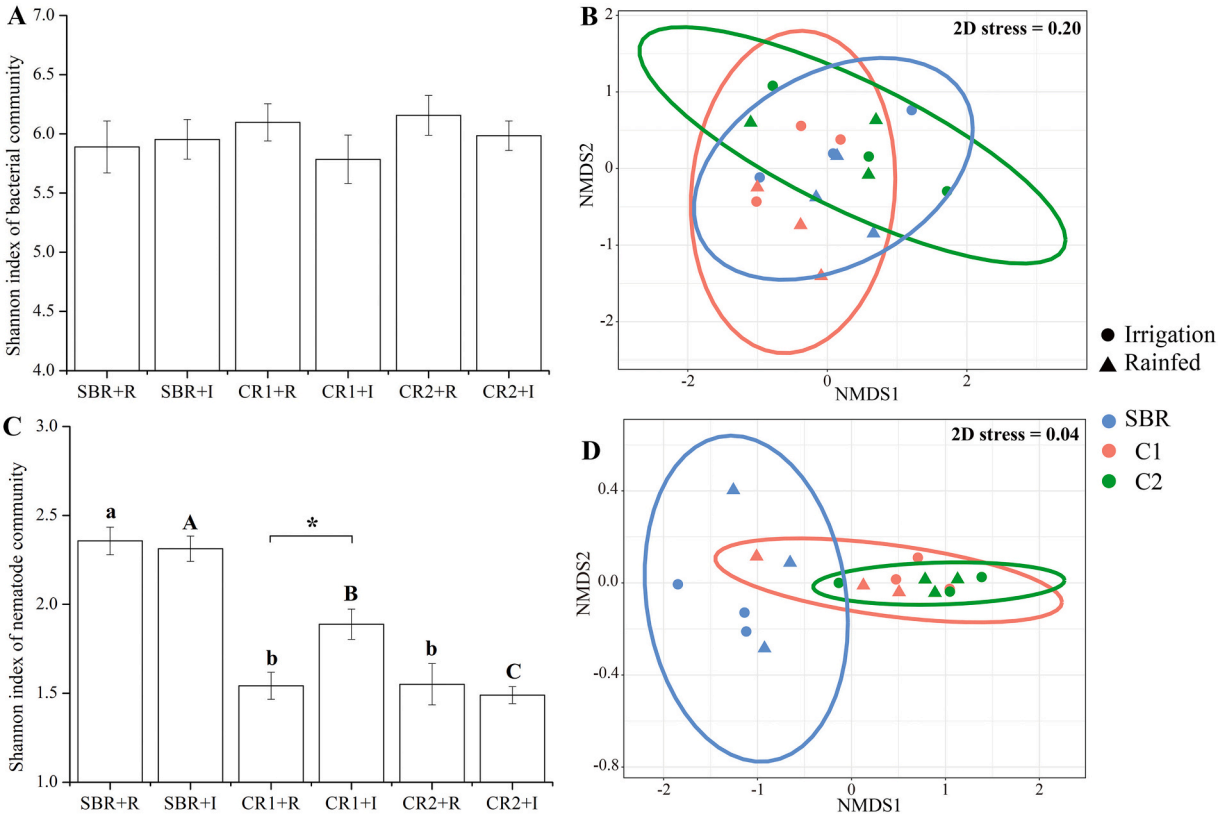


Fig. 2. Alpha (mean ± standard error) and beta diversity of bacterial (A and B) and nematode communities (C and D). In A and C, uppercase and lowercase letters indicate significant differences ($P < 0.05$) among cotton phases in crop rotations in irrigated and rainfed plots, respectively. The asterisk indicates a significant difference ($P < 0.05$) between irrigated and rainfed conditions within the 1st-year CR. For beta diversity (B and D), ellipses indicate 95% confidence intervals for each cotton phase in crop rotation systems. R: rainfed, I: irrigation, SBR: sod-based rotation, CR1: 1st – year CR, CR2: 2nd – year CR.

footprints, but SBR showed lower herbivore footprint than 1st-year CR (one-way ANOVA, $P > 0.05$).

The alpha diversity of nematodes at the genus level was significantly affected by the interaction of rotation by irrigation (Table 2). The alpha diversity of nematode communities was higher under SBR as compared to CR plots (Fig. 2C). 1st-year CR plots had higher nematode alpha diversity than 2nd-year CR under irrigated conditions, although there was no difference under rainfed conditions. Nematode alpha diversity was significantly higher under irrigation relative to rainfed conditions only in 1st-year CR. Besides, PERMANOVA and ANOSIM tests showed that nematode communities were significantly affected by rotation ($R^2 = 0.59$, $P < 0.001$), and SBR induced distinct nematode communities relative to CR systems (Fig. 2D; Table 3, and Supplementary Table S4).

3.3. Effect of cropping systems on trophic interactions

Linear correlations were used to correlate irrigation, bacterial and nematode diversity and community composition, and major NMFs under each cropping system (Fig. 5). In the SBR system, irrigation, NMFs, and the relative abundance of some microbial taxa and nematode functional groups were significantly correlated (Fig. 5A). In particular, irrigation had a significant and positive effect ($P < 0.05$) on the relative abundance of dominant microbial taxa (e.g., Gammaproteobacteria, Deltaproteobacteria, and Nitrospira) and the abundance of nematode functional groups (e.g., BFN and omnivorous nematodes). There were also significant correlations between C- and N-associated bacterial taxa: the relative abundance of Ca. *Nitrosophaera* was correlated with that of

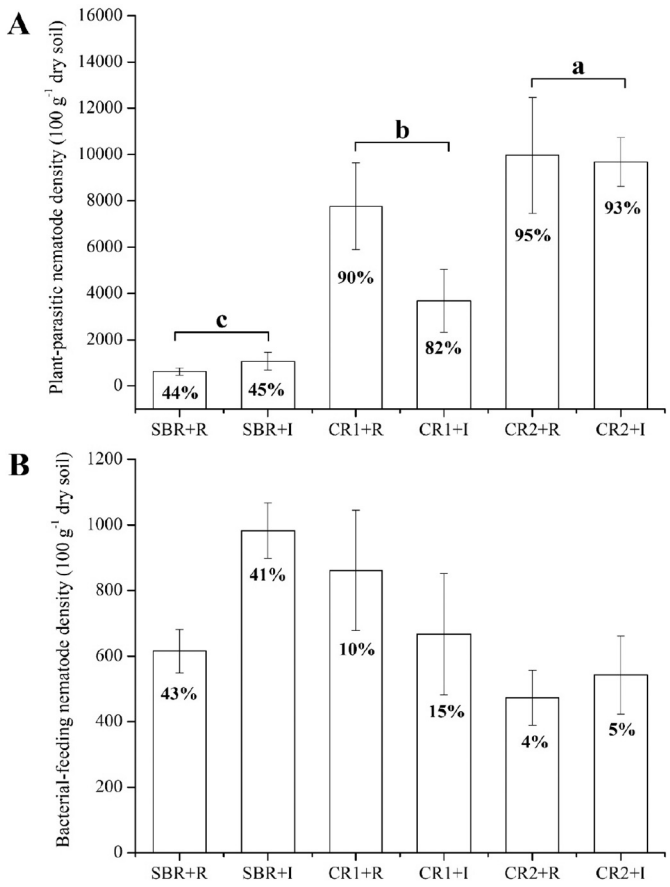


Fig. 3. Density (mean ± standard error) of dominant nematode groups in cotton plots under sod-based rotation (SBR) and conventional rotation (CR) systems. The percentage inside each bar indicates the percent of total nematode abundance that this group accounts for. Lowercase letters indicate significant differences ($P < 0.05$) among cotton phases in crop rotations, based on a significant main effect of crop rotation in the ANOVA. R: rainfed, I: irrigation, CR1: 1st - year CR, CR2: 2nd - year CR.

Actinobacteria (r = 0.70, $P = 0.01$) and Betaproteobacteria (r = −0.78, $P < 0.01$), and the relative abundance of Nitrospira was associated with that of Deltaproteobacteria (r = 0.61, $P = 0.03$), Bacteroidetes (r = 0.85, $P < 0.001$), and Acidobacteria (r = −0.68, $P = 0.01$). In addition, free-living nematodes had strong relationships with bacterial communities: BFN and omnivorous nematodes were positively associated with the relative abundance of Gammaproteobacteria (r = 0.88, $P < 0.001$; r = 0.62, $P = 0.03$) and Nitrospira (r = 0.67, $P = 0.01$; r = 0.73, $P < 0.01$), and there was also a positive correlation between omnivorous nematodes and the relative abundance of Bacteroidetes (r = 0.77, $P < 0.01$).

In contrast to SBR, there were stronger correlations between irrigation and bacterial or nematode diversity and community composition in CR plots than between irrigation and individual taxa or groups (Fig. 5B and C). Specifically, nematode diversity and community composition were sensitive to irrigation in 1st-year CR, and irrigation significantly affected bacterial diversity in 2nd-year CR. However, the trophic associations between bacterial and nematode communities were weaker in CR relative to SBR. In 1st-year CR, nematode alpha diversity was positively correlated to the relative abundance of Nitrospira (r = 0.64, $P = 0.03$) and negatively linked to PPN abundance (r = −0.86, $P < 0.001$), whereas the opposite trend occurred between nematode community composition and Nitrospira (r = −0.75, $P < 0.01$) and PPN (r = 0.93, $P < 0.001$). In 2nd- year CR, nematode alpha diversity was negatively linked to the relative abundance of Actinobacteria (r = −0.72, $P < 0.01$), nematode community composition (r = −0.98, $P < 0.001$), and PPN (r = −0.94, $P < 0.001$), but positively related to bacterial community composition (r = 0.71, $P < 0.01$) and the relative abundance of Acidobacteria (r = 0.75, $P < 0.01$). In contrast to nematode alpha diversity, nematode community composition had contrasting correlations with the bacterial community composition (r = −0.64, $P = 0.02$), the relative abundance of Acidobacteria (r = −0.71, $P < 0.01$) and Actinobacteria (r = 0.66, $P = 0.02$), and PPN (r = 0.92, $P < 0.001$).

A structural equation model (SEM) was constructed to further quantify the effects of crop rotation and irrigation on the bacterial and nematode diversity as well as NMFs (Fig. 6). Nematode alpha diversity (path coefficient = 0.88, $P < 0.001$) was more sensitive to crop rotation than bacterial alpha diversity (path coefficient = −0.19). Rotation (path coefficient = −0.96, $P < 0.001$) and nematode alpha diversity (path coefficient = −0.84, $P < 0.001$) had significant negative effects on NMFs. However, there were no significant effects of irrigation on bacterial (path coefficient = −0.22) and nematode (path coefficient = 0.11) alpha diversity and NMFs (path coefficient = 0.08).

4. Discussion

4.1. Microbial community composition and interactions

There were no significant differences in terms of microbial diversity and community composition when comparing SBR, 1st-year, and 2nd-year CR, in contrast to previous studies (Chamberlain et al., 2020; Chen et al., 2020a, 2020b), where cropping systems distinctly influenced soil bacterial community assembly. This may be because the effect of cover crops on bacterial communities was stronger than legacy effects of crop rotations, as we collected soil samples before planting cash crops and after cover cropping taking place in all plots. However, the relative abundance of some dominant microbial taxa changed in response to crop rotation systems and associated management. For example, SBR and 1st-CR had a higher relative abundance of Gammaproteobacteria (marginally significant at $P < 0.1$) but a significantly lower relative abundance of Alphaproteobacteria in comparison to 2nd-year CR. This could be due to the previous crop being peanut in SBR and 1st-CR vs. cotton in 2nd-year CR. Specifically, peanut has higher litter quality than cotton (e.g., higher N concentration, lower C/N ratio and concentration of phenol and lignin), which facilitates the growth of copiotrophic bacteria, such as Gammaproteobacteria (Ho et al., 2017; Pan et al., 2019). In contrast, cotton residues with lower N and P concentrations should favor the growth of oligotrophic bacteria, e.g., Alphaproteobacteria (Ho et al., 2017; Pan et al., 2019).

The higher relative abundance of Nitrospira under SBR than CR systems indicates that Nitrospira, and potentially nitrification, was of greater importance in the SBR system. This greater relative abundance of Nitrospira may be driven by greater N release from the decomposition of peanut residues under SBR than under CR systems (Supplementary Table S2; Katsvairo et al., 2007c, 2009; Zhao et al., 2010). In addition, Nitrospira can be a dominant nitrite oxidizer or comammox (where one kind of nitrifier drives the complete oxidation of ammonia to nitrate) in agroecosystems (Attard et al., 2010; Han et al., 2017, 2018; Wang et al., 2019). This suggests a greater reliance on microbial-derived N transformations in SBR systems relative to CR, although this would need to be confirmed in future studies.

The greater number of significant paired Pearson correlations ($P < 0.05$) among different microbial groups in SBR compared to CR systems suggests that higher rotational diversity under SBR can stimulate microbial interaction complexity. In addition, we found that some interactions among microbial communities existed in the cotton phase of rotation systems specifically. For example, Nitrospira had significant relationships with Acidobacteria and Bacteroidetes in SBR, but Nitrospira and Deltaproteobacteria were tightly related in 1st-year CR. These results are consistent with previous studies where changes in plant diversity affected soil microbial interactions (Bakker et al., 2013; Schlatter et al., 2015). This indicates that diverse plant communities may increase

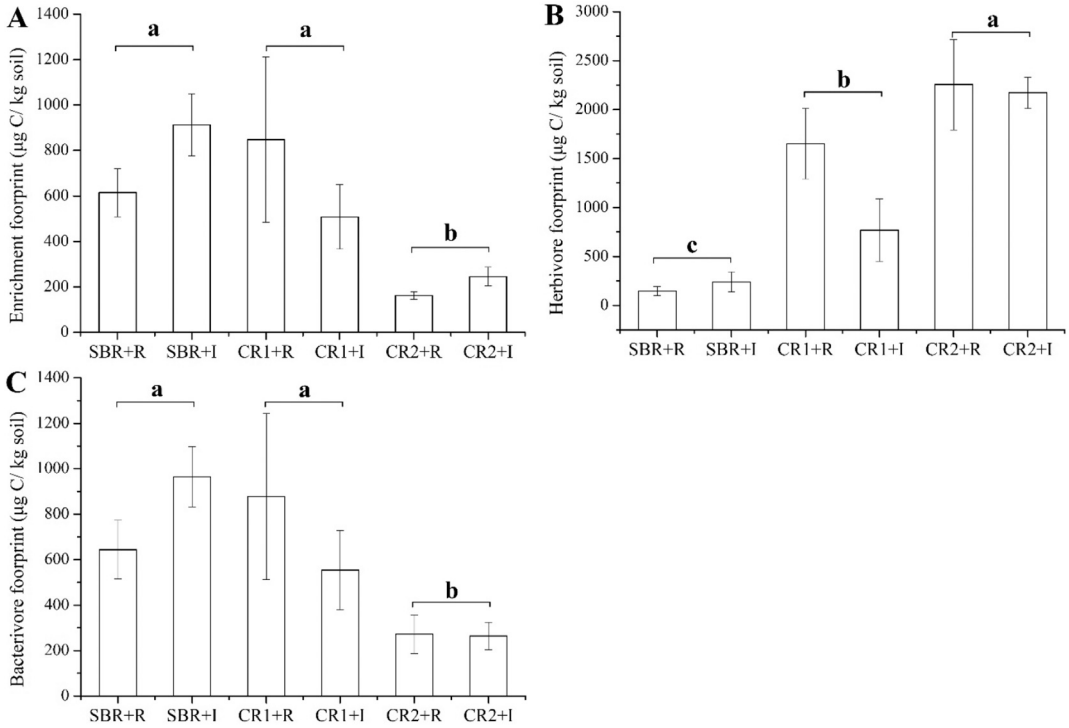


Fig. 4. Major nematode metabolic footprints (NMFs, mean ± standard error) under conventional (CR) and sod-based rotation (SBR). Lowercase letters indicate a significant difference ($P < 0.05$) among cotton phases in crop rotations, based on a significant main effect of crop rotation in the ANOVA. R: rainfed, I: irrigation, CR1: 1st - year CR, CR2: 2nd - year CR.

Table 2
Effect of crop rotation and irrigation on the alpha diversity of all identified nematode taxa, the major functional nematode groups and dominant metabolic footprints based on a linear mixed model, where the field plot number was used as a random effect.

	Rotation		Irrigation		Rotation × irrigation	
	F	*P*	F	*P*	F	*P*
Nematode alpha diversity	**61.28**	**<0.001*****	1.64	0.23	**4.50**	**0.03***
Plant-parasitic nematodes	**17.59**	**<0.001*****	0.70	0.42	0.84	0.46
Bacterial-feeding nematodes	2.72	0.11	0.25	0.63	2.39	0.13
Enrichment footprint	**6.32**	**0.01***	0.01	0.92	1.83	0.20
Herbivore footprint	**30.95**	**<0.001*****	1.92	0.19	2.05	0.17
Bacterivore footprint	**5.32**	**0.02***	0.01	0.98	1.67	0.23

*, **, and *** represent significant effects (marked in bold) at $P < 0.05$, 0.01 and 0.001, respectively.

Table 3
The effects of crop rotation and irrigation on bacterial and nematode communities based on PERMANOVA.

		Rotation	Irrigation	Rotation × irrigation
Bacterial community	R^2	0.13	0.06	0.11
	P	0.25	0.28	0.47
Nematode community	R^2	0.59	0.01	0.09
	P	**<0.001*****	0.50	0.15

*** represents significant effects (marked in bold) at $P < 0.001$.

the number of microbial interactions by creating different environments, which could impact soil resources (e.g., C, N, SOM) that play a critical role in shaping microbial interactions (Schlatter et al., 2015; Trivedi et al., 2020).

4.2. Rotational effects on microbial-nematode interactions

Some nematode functional groups (e.g., omnivorous and predatory nematodes) were absent or had a low abundance under CR, and CR also had a lower Shannon diversity for nematodes compared with SBR. This implies that the greater crop diversity in SBR systems sustained a more diverse soil community and thereby fostered more robust and complex soil food webs, which could help control PPN through top-down regulation (Delgado-Baquerizo et al., 2017; da Silva et al., 2018; Zhang et al., 2021). A more diverse soil community also increases the likelihood that plants develop strong relationships with beneficial soil communities that could inhibit the attack of herbivores or pathogens (van der Heijden et al., 2008). This is consistent with the substantially lower abundance of PPN observed in SBR compared to CR. Besides, there are fewer host crops in SBR for the growth of PPN, such as reniform nematodes, resulting in lower PPN abundance (Schumacher et al., 2020).

The positive relationships observed between BFN and soil bacterial taxa (e.g., Gammaproteobacteria and Nitrospira) under SBR differ from previous studies (Castillo et al., 2017; Neher, 2010), where bacterial communities were negatively correlated with their predators due to top-down control. Positive biological linkages between bacterial taxa and their predators in SBR systems can be interpreted as bottom-up control driven by resource availability at the base of soil food webs, where the greater abundance of lower trophic levels leads to greater productivity at higher trophic levels (Hoekman, 2010). This is consistent with Scherber et al. (2010), who reported that plant diversity had a strong bottom-up effect on multitrophic interaction networks. Besides, positive relationships between higher trophic levels (e.g., omnivorous and predatory nematodes) and some microbial taxa (e.g., Nitrospira, Gammaproteobacteria, Deltaproteobacteria, and Bacteroidetes) suggest that bottom-up trophic cascades also occurred under SBR systems, which indirectly mediated higher trophic levels. Given that trophic network complexity can be a valid proxy for ecosystem functions and processes (McDaniel et al., 2014; Bender et al., 2015; Yang et al., 2018), these results suggest that the SBR system may increase C content and soil

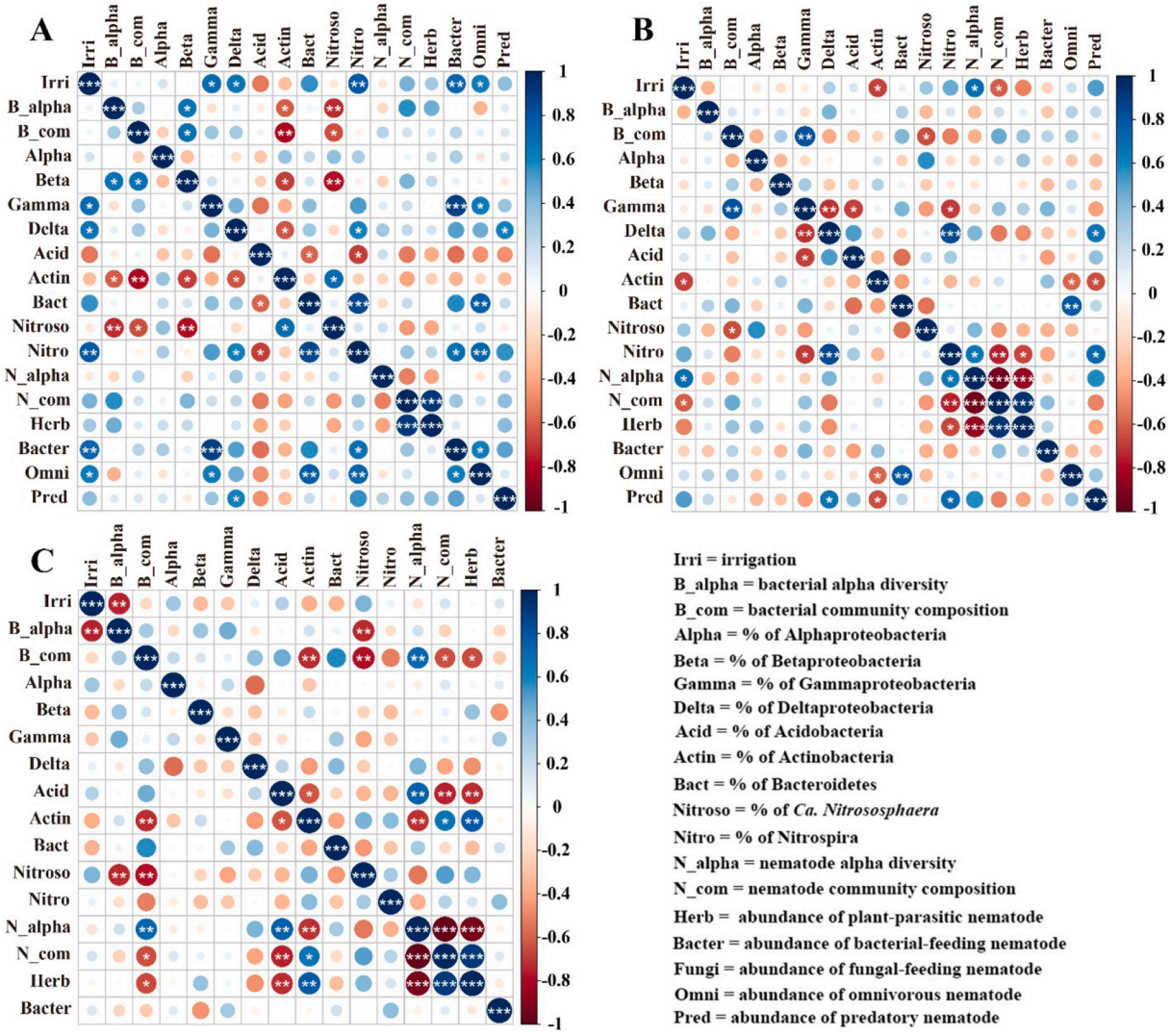


Fig. 5. Pearson correlations among irrigation, major microbial taxa, nematode functional groups, and nematode metabolic footprints (NMFs) in cotton plots under sod-based rotation (A), 1st- year (B) and 2nd - year (C) conventional rotation system. *, **, and *** mark significance at $P < 0.05$, 0.01, and 0.001, respectively, after correction for multiple comparisons using the Bonferroni-Holm method. %: relative abundance.

nutrient availability (Supplementary Table S2). Similarly, a meta-analysis conducted by King and Blesh (2018) concluded that integrating perennial crops into rotations increased soil organic C by 6.2% on average relative to grain-only rotations. Although direct measurements of C and nutrient cycling would be required to confirm this link between changes in soil communities and ecosystem function, the greater N and P acquisition previously found in cotton plots for SBR compared to CR systems at this site are consistent with this interpretation (Supplementary Table S2; Katsvairo et al., 2007a, 2007b, 2009; Zhao et al., 2009; Dourte et al., 2016).

Moreover, nematode metabolic footprints that represent C and energy flow in soil food webs based on functional guilds (Ferris, 2010) showed that SBR had a higher bacterivore and enrichment footprint compared to 2nd-year CR. This indicates a stronger response to C resource enrichment that includes the activity of primary decomposers and lower trophic levels of nematodes (Ferris et al., 2012; Hodson et al., 2014). Positive correlations between Gammaproteobacteria and enrichment and bacterivore footprints indicate that the flow of C and energy was driven by r-strategists for bacterivory pathways in SBR plots. These results suggest that SBR increases the quantity and quality of C resources, most likely because bahiagrass increases root biomass and root mass of subsequent crops by increasing the rooting depth, root area, and root length of subsequent crops (Wright et al., 2004; Katsvairo et al., 2007c). Additionally, the greater omnivore, predator, and structure footprints under SBR relative to 2nd-year CR indicate greater productivity and turnover rates of enrichment indicators, which could meet the growth requirements of higher trophic groups and maintain the nematode metabolic balance (Ferris, 2010).

In CR systems, a greater herbivore footprint, regardless of irrigation, suggests that resources entered soil food webs mainly through herbivory pathways. Furthermore, PPN abundance was tightly correlated with some bacterial taxa, including k-strategist bacteria (e.g., Acidobacteria and Nitrospira) and r-strategists (Actinobacteria). This could be driven by a greater release of root exudates due to PPN damage, generating a labile C source that would stimulate the growth of r-strategist bacteria (Denton et al., 1998; Gebremikael et al., 2016; Zhang et al., 2021). Simultaneously, lower root biomass and root mass observed in the PPN-enriched CR system should decrease inputs of recalcitrant root C into the soil (Wright et al., 2004; Katsvairo et al., 2007c), which should be less conducive to the growth of k-strategist bacteria (Verbon and Liberman, 2016).

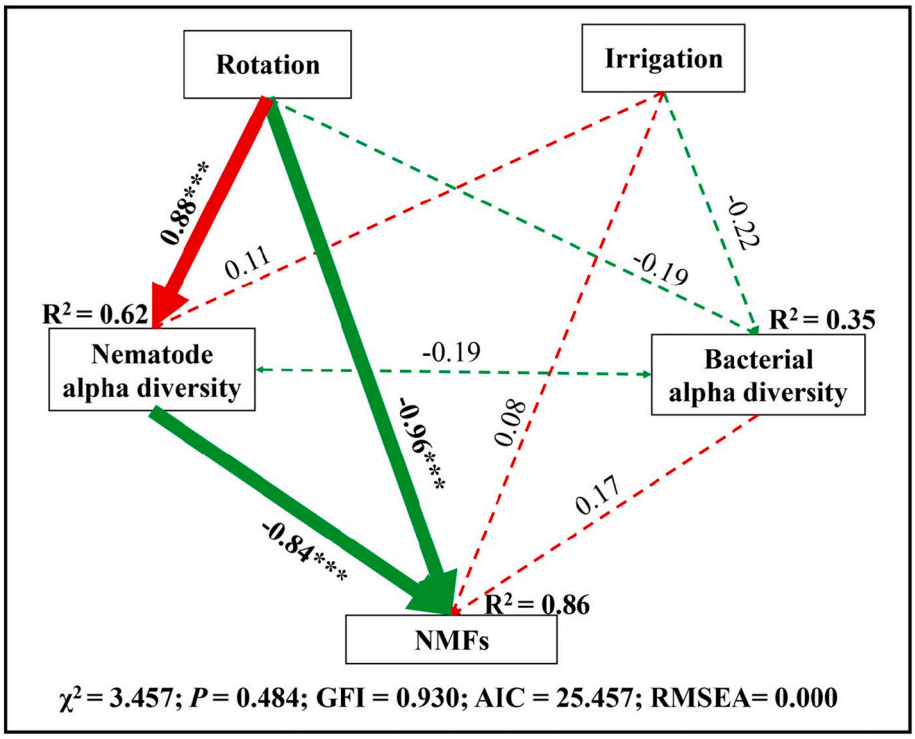


Fig. 6. Structural equation model (SEM) illustrating the effects of irrigation and crop rotation on bacterial and nematode diversity and nematode metabolic footprints (NMFs). Continuous and dashed arrows show significant and nonsignificant relationships between two measured variables, respectively. Arrows with two heads indicate the interplay between two measured variables. Values adjacent to the arrows represent path coefficients, and the width of arrows shows the strength of path coefficients. *, **, and *** indicate significance at $P < 0.05$, 0.01, and 0.001, respectively. Red and green arrows indicate positive and negative relationships of two variables, respectively. R^2 shows the proportion of variance explained by the model for each variable. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.3. Response of soil communities to irrigation under different cropping systems

Previous studies indicated that SBR can reduce irrigation requirements due to greater water infiltration and WHC at shallow depths, along with the deeper and extensive root systems of bahiagrass that can overcome soil compaction at deeper depths (Katsvairo et al., 2006, 2007a; Dourte et al., 2016). However, these studies did not assess how SBR and irrigation affected microbial community structure and their associations with dominant soil fauna (e.g., nematodes). Several studies have demonstrated that water availability was a major driver that altered the composition, diversity, and abundance of soil organisms (Brockett et al., 2012; Holland et al., 2013; Sorensen et al., 2013; Frindte et al., 2019). However, our results showed that irrigation only stimulated the growth of some soil microbial groups (e.g., Gammaproteobacteria, Deltaproteobacteria, and Nitrospira) under SBR. This could be due to the higher water infiltration rate as well as greater C and N inputs found in SBR systems (Katsvairo et al., 2007a, 2007c, 2009; Zhao et al., 2010), providing adequate resources and ultimately stimulating their growth (Supplementary Table S2; da Silva et al., 2021; Karuri, 2021). Our study also found a direct correlation between water availability and the abundance of some nematode groups (e.g., BFN and omnivorous nematodes), in agreement with the large water requirements of nematodes for movement and activity (Franco and Gherardi, 2019). This is consistent with a recent study reporting lower nematode abundance with increasing aridity in grassland ecosystems (Xiong et al., 2019).

Irrigation had no effect on bacterial and nematode diversity (as measured by Shannon's index) and structure (as measured by the NMDS) under the SBR system, although some soil bacterial and nematode groups were associated with irrigation. In contrast, irrigation exerted a great impact on nematode diversity and structure in 1st-year CR and bacterial diversity in 2nd-year CR. These results are consistent with previous studies where irrigation significantly influenced soil belowground communities under low-diversity cropping systems (Porazinska et al., 1998; Ma et al., 2020), suggesting that soil belowground communities underpinned by high rotational diversity in SBR may develop greater resistance to changes in soil water content (Dourte et al., 2016; Isbell et al., 2015; Beaury et al., 2020). This is probably due to the greater water availability in the SBR system caused by increased SOM and lower bulk density that result in better water retention and ultimately lower irrigation demand relative to CR (Katsvairo et al., 2007a; Dourte et al., 2016).

5. Conclusion

Overall, we found a strong influence of cropping systems on soil community assembly, especially nematode diversity and community structure. Our first hypothesis was partially supported, as integrating bahiagrass into the peanut and cotton rotation system increased nematode diversity and resulted in different nematode communities compared to CR, but it had no effect on the diversity and structure of bacterial communities. There was also a greater number of significant paired correlations between bacterial and nematode communities in SBR relative to CR systems, suggesting SBR led to more complex trophic interactions between bacterial and nematode communities. Consistent with our second hypothesis, SBR suppressed the growth of PPN but promoted free-living nematode populations (e.g., fungal-feeding nematodes and predatory nematodes). Simultaneously, irrigation had no effect on the diversity and structure of bacterial and nematode communities under the SBR system, although some soil bacterial and nematode groups were associated with irrigation. This implies that soil belowground communities in SBR may develop greater resistance to changes in soil water content, which supports our third hypothesis. Ultimately, our study demonstrated that high rotational diversity associated with the SBR system can foster robust soil food webs with complex soil trophic interactions, which could promote agroecosystem functions and processes (e.g., increasing nutrient availability and defense against plant pathogens) and reduce requirements in external resources (e.g., fertilization, irrigation, and fumigation) (Fig. 7). Future studies are needed that combine data on soil biological communities and C and nutrient cycling to validate the connections outlined in this study and better quantify the role of soil communities in greater crop rotation complexity with higher functional trait diversity.

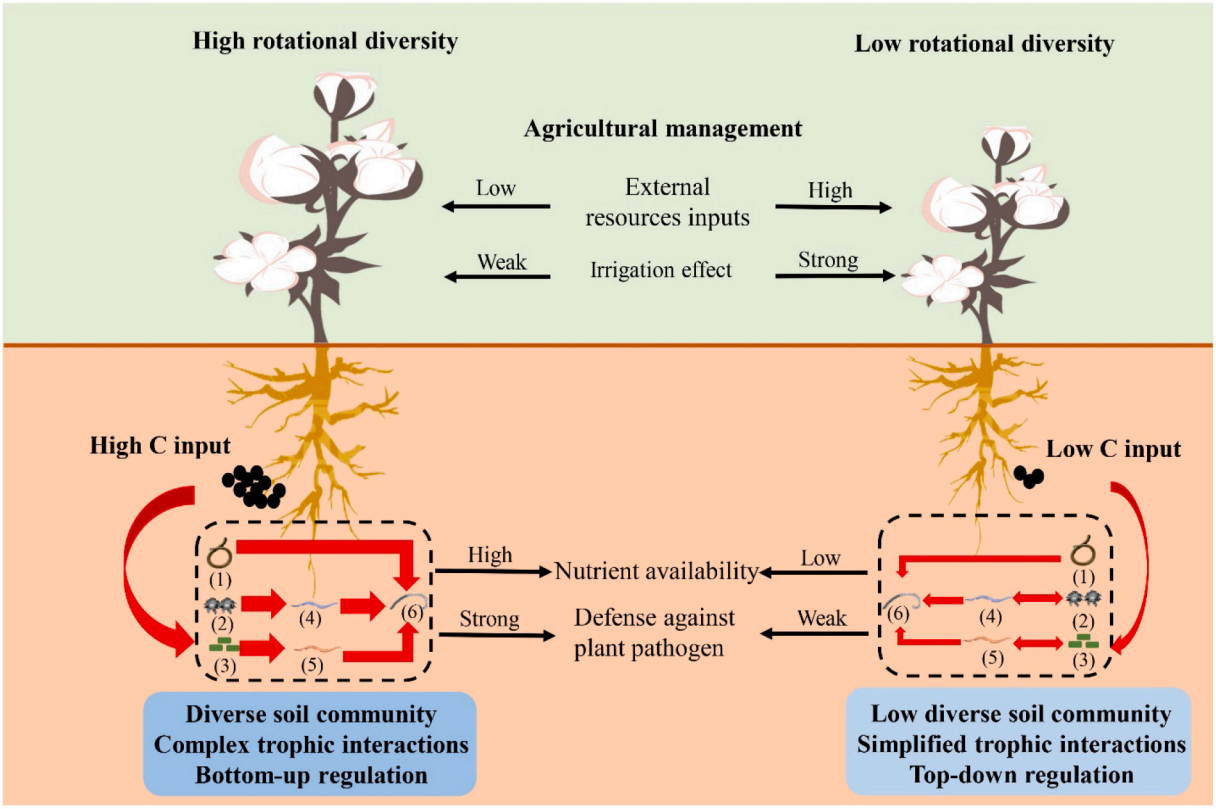


Fig. 7. Conceptual diagram of the relationships between rotational diversity, agroecosystem processes, and agricultural management. This diagram combines our results with previous studies (Katsvairo et al., 2009; Zhao et al., 2010; Dourte et al., 2016). (1) plant-parasitic nematodes, (2) fungi, (3) bacteria, (4) fungal-feeding nematodes, (5) bacterial-feeding nematodes, (6) omnivorous and predatory nematodes. Red arrows represent C, nutrient, and energy flows to higher trophic levels, and the width of the arrows indicates the magnitude of these flows. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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.

Acknowledgements

This work was supported by USDA/SSARE grant (2017-38640-26914) to H. Liao, Z. Grabau, D. Wright, and I. Small, USDA/SSARE grant (2019-38640-29878) to H. Liao and K. Zhang, USDA-NIFA grant (2019-67013-29107) to H. Liao, USDA-NIFA, Hatch project (FLA-SWS-005733) to G. Maltais-Landry, and a University of Florida Graduate School Funding Award to K. Zhang. We thank Ko-Hsuan Chen for assistance with data analysis, Chih-Ming Hsu for support and help with laboratory work, and the staff at the North Florida Research and Education Center for maintenance of the long-term rotation at Quincy. This work was supported in part by the U.S. Department of Agriculture, Agricultural Research Service. USDA is an equal opportunity provider and employer.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104254.

References

Abraham, J.K., Corbin, J.D., D'Antonio, C.M., 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. In: Van der Valk, A.G. (Ed.), Herbaceous Plant Ecology: Recent Advances in Plant Ecology. Springer, Netherlands, Dordrecht, pp. 81–92.

Ahmad, S., Hasanuzzaman, M. (Eds.), 2020. Cotton Production and Uses: Agronomy, Crop Protection, and Postharvest Technologies. Springer, Singapore.

Anderson, R.V., Gould, W.D., Woods, L.E., Cambardella, C., Ingham, R.E., Coleman, D.C., 1983. Organic and inorganic nitrogenous losses by microbivorous nematodes in soil. Oikos 75–80.

Attard, E., Poly, F., Commeaux, C., Laurent, F., Terada, A., Smets, B.F., Recous, S., Roux, X.L., 2010. Shifts between nitrospira-and nitrobacter-like nitrite oxidizers underlie the response of soil potential nitrite oxidation to changes in tillage practices. Environ. Microbiol. 12, 315–326.

Bakker, M.G., Otto-Hanson, L., Lange, A.J., Bradeen, J.M., Kinkel, L.L., 2013. Plant monocultures produce more antagonistic soil streptomyces communities than high-diversity plant communities. Soil Biol. Biochem. 65, 304–312.

Bates, S.T., Berg-Lyons, D., Caporaso, J.G., Walters, W.A., Knight, R., Fierer, N., 2011. Examining the global distribution of dominant archaeal populations in soil. ISME J. 5, 908–917.

Beaury, E.M., Finn, J.T., Corbin, J.D., Barr, V., Bradley, B.A., 2020. Biotic resistance to invasion is ubiquitous across ecosystems of the United States. Ecol. Lett. 23, 476–482.

Bender, S.F., Franz Bender, S., van der Heijden, M.G.A., 2015. Soil biota enhance agricultural sustainability by improving crop yield, nutrient uptake and reducing nitrogen leaching losses. J. Appl. Ecol. 52, 228–239.

Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A., Alexander, H., Alm, E.J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J.E., Bittinger, K., Brejnrod, A., Brislawn, C.J., Brown, C.T., Callahan, B.J., Caraballo-Rodríguez, A.M., Chase, J., Cope, E.K., Da Silva, R., Diener, C., Dorrestein, P.C., Douglas, G.M., Durall, D.M., Duvallet, C., Edwardson, C.F., Ernst, M., Estaki, M., Fouquier, J., Gauglitz, J.M., Gibbons, S.M., Gibson, D.L., Gonzalez, A., Gorlick, K., Guo, J., Hillmann, B., Holmes, S., Holste, H., Huttenhower, C., Huttley, G.A., Janssen, S., Jarmusch, A.K., Jiang, L., Kaehler, B.D., Kang, K.B., Keefe, C.R., Keim, P., Kelley, S.T., Knights, D., Koester, I., Kosciolek, T., Kreps, J., Langille, M.G.I., Lee, J., Ley, R., Liu, Y.-X., Loftfield, E., Lozupone, C., Maher, M., Marotz, C., Martin, B.D., McDonald, D., McIver, L.J., Melnik, A.V., Metcalf, J.L., Morgan, S.C., Morton, J.T., Naimey, A.T., Navas-Molina, J.A., Nothias, L.F., Orchanian, S.B., Pearson, T., Peoples, S.L., Petras, D., Preuss, M.L., Pruesse, E., Rasmussen, L.B., Rivers, A., Robeson 2nd, M.S., Rosenthal, P., Segata, N., Shaffer, M., Shiffer, A., Sinha, R., Song, S.J., Spear, J.R., Swafford, A.D., Thompson, L.R., Torres, P.J., Trinh, P., Tripathi, A., Turnbaugh, P.J., Ul-Hasan, S., van der Hooft, J.J.J., Vargas, F., Vázquez-

Baeza, Y., Vogtmann, E., von Hippel, M., Walters, W., Wan, Y., Wang, M., Warren, J., Weber, K.C., Williamson, C.H.D., Willis, A.D., Xu, Z.Z., Zaneveld, J.R., Zhang, Y., Zhu, Q., Knight, R., Caporaso, J.G., 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat. Biotechnol. 37, 852–857.
Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239–251.
Bouwman, L.A., Bloem, J., van den Boogert, P.H.J.F., Bremer, F., Hoenderboom, G.H.J., de Ruiter, P.C., 1994. Short-term and long-term effects of bacterivorous nematodes and nematophagous fungi on carbon and nitrogen mineralization in microcosms. Biol. Fertil. Soils 17, 249–256.
Brockett, B.F.T., Prescott, C.E., Grayston, S.J., 2012. Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada. Soil Biol. Biochem. 44, 9–20.
Byrne, B.M., 2016. Structural equation modeling with AMOS: basic concepts, applications, and programming, Third edition. Routledge.
Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Lozupone, C.A., Turnbaugh, P.J., Fierer, N., Knight, R., 2011. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. Proc. Natl. Acad. Sci USA 108, 4516–4522.
Carlisle, L., De Wit, M.M., DeLonge, M.S., Calo, A., Getz, C., Ory, J., Munden-Dixon, K., Galt, R., Melone, B., Knox, R., Iles, A., Press, Daniel, 2019. Securing the future of US agriculture: the case for investing in new entry sustainable farmers. Elem. Sci. Anth. 7, 17.
Castillo, J.D., Vivanco, J.M., Manter, D.K., 2017. Bacterial Microbiome and Nematode Occurrence in Different Potato Agricultural Soils. Microb. Ecol. 74, 888–900.
Chamberlain, L.A., Bolton, M.L., Cox, M.S., Suen, G., Conley, S.P., Ané, J.-M., 2020. Crop rotation, but not cover crops, influenced soil bacterial community composition in a corn-soybean system in southern Wisconsin. Appl. Soil Ecol. 154, 103603.
Chen, K.-H., Liao, H.-L., Bellenger, J.-P., Lutzoni, F., 2019. Differential gene expression associated with fungal trophic shifts along the senescence gradient of the moss Dicranum scoparium. Environ. Microbiol. 21, 2273–2289.
Chen, J., Gong, J., Xu, M., 2020. Implications of continuous and rotational cropping practices on soil bacterial communities in pineapple cultivation. Eur. J. Soil Biol. 97, 103172.
Chen, X., Henriksen, T.M., Svensson, K., Korsaeth, A., 2020. Long-term effects of agricultural production systems on structure and function of the soil microbial community. Appl. Soil Ecol. 147, 103387.
Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. Science 365.
da Silva, J.C.P., de Medeiros, F.H.V., Campos, V.P., 2018. Building soil suppressiveness against plant-parasitic nematodes. Biocontrol Sci. Tech. 28, 423–445.
da Silva, J.V.C.de L., Ferris, H., Cares, J.E., Esteves, A.M., 2021. Effect of land use and seasonality on nematode faunal structure and ecosystem functions in the Caatinga dry forest. Eur. J. Soil Biol. 103, 103296.
Delgado-Baquerizo, M., Powell, J.R., Hamonts, K., Reith, F., Mele, P., Brown, M.V., Dennis, P.G., Ferrari, B.C., Fitzgerald, A., Young, A., Singh, B.K., Bissett, A., 2017. Circular linkages between soil biodiversity, fertility and plant productivity are limited to topsoil at the continental scale. New Phytol. 215, 1186–1196.
Denton, C.S., Bardgett, R.D., Cook, R., Hobbs, P.J., 1998. Low amounts of root herbivory positively influence the rhizosphere microbial community in a temperate grassland soil. Soil Biol. Biochem. 31, 155–165.
Doshi, R.A., King, R.L., Lawrence, G.W., 2010. Classification of Rotylenchulus reniformis numbers in cotton using remotely sensed hyperspectral data on self-organizing maps. J. Nematol. 42, 179–193.
Dourte, D., Bartel, R.L., George, S., Marois, J.J., Wright, D.L., 2016. A sod-based cropping system for irrigation reductions. Renewable Agric. Food Syst. 31, 485–494.
Drenovsky, R.E., Vo, D., Graham, K.J., Scow, K.M., 2004. Soil water content and organic carbon availability are major determinants of soil microbial community composition. Microb. Ecol. 48, 424–430.
Falkowski, P.G., Fenchel, T., Delong, E.F., 2008. The microbial engines that drive Earth's biogeochemical cycles. Science 320, 1034–1039.
Faucon, M.-P., Houben, D., Lambers, H., 2017. Plant functional traits: soil and ecosystem services. Trends Plant Sci. 22, 385–394.
Ferris, H., 2010. Form and function: metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46, 97–104.
Ferris, H., Sánchez-Moreno, S., Brennan, E.B., 2012. Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production. Appl. Soil Ecol. 61, 16–25.
Fierer, N., 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. Nat. Rev. Microbiol. 15, 579–590.
Franco, A.L.C., Gherardi, L.A., 2019. Drought suppresses soil predators and promotes root herbivores in Mesic, but not in xeric grasslands. Proc. Natl. Acad. Sci. U. S. A. 116, 12883–12888.
Frindte, K., Pape, R., Werner, K., Löffler, J., Knief, C., 2019. Temperature and soil moisture control microbial community composition in an arctic–alpine ecosystem along elevational and micro-topographic gradients. ISME J. 13, 2031–2043.
Ganguly, P., Sengupta, S., Das, P., Bhowal, A., 2020. Synthesis of cellulose from peanut shell waste and its use in bioethanol production. In: Ghosh, S.K., Sen, R., Chanakya, H.N., Pariatamby, A. (Eds.), Bioresource Utilization and Bioprocess. Springer Singapore, Singapore, pp. 81–91.
Gebremikael, M.T., Steel, H., Buchan, D., Bert, W., De Neve, S., 2016. Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. Sci. Rep. 6, 32862.
Guan, P., Zhang, X., Yu, J., Cheng, Y., Li, Q., Andriuzzi, W.S., Liang, W., 2018. Soil microbial food web channels associated with biological soil crusts in desertification restoration: the carbon flow from microbes to nematodes. Soil Biol. Biochem. 116, 82–90.
Guo, Z., Wan, S., Hua, K., Yin, Y., Chu, H., Wang, D., Guo, X., 2020. Fertilization regime has a greater effect on soil microbial community structure than crop rotation and growth stage in an agroecosystem. Appl. Soil Ecol. 149, 103510.
Han, S., Luo, X., Liao, H., Nie, H., Chen, W., Huang, Q., 2017. Nitrospira are more sensitive than nitrobacter to land management in acid, fertilized soils of a rapeseed-rice rotation field trial. Sci. Total Environ. 599–600, 135–144.
Han, S., Zeng, L., Luo, X., Xiong, X., Wen, S., Wang, B., Chen, W., Huang, Q., 2018. Shifts in nitrobacter- and nitrospira-like nitrite-oxidizing bacterial communities under long-term fertilization practices. Soil Biol. Biochem. 124, 118–125.
Harris, R.F., 1981. In: Effect of water potential on microbial growth and activity. Water potential relations in soil microbiology, 9, pp. 23–95.
Hector, A., 2015. The new statistics with R: an introduction for biologists. Oxford University Press.
Himanshu, S.K., Ale, S., Bordovsky, J., Darapuneni, M., 2019. Evaluation of crop-growth-stage-based deficit irrigation strategies for cotton production in the southern High Plains. Agric. Water Manag. 225, 105782.
Ho, A., Di Lonardo, D.P., Bodelier, P.L.E., 2017. Revisiting life strategy concepts in environmental microbial ecology. FEMS Microbiol. Ecol. 93, fix006.
Hodson, A.K., Ferris, H., Hollander, A.D., Jackson, L.E., 2014. Nematode food webs associated with native perennial plant species and soil nutrient pools in California riparian oak woodlands. Geoderma 228, 182–191.
Hoekman, D., 2010. Turning up the heat: temperature influences the relative importance of top-down and bottom-up effects. Ecology 91, 2819–2825.
Holland, T.C., Reynolds, A.G., Bowen, P.A., Bogdanoff, C.P., Marciniak, M., Brown, R.B., Hart, M.M., 2013. The response of soil biota to water availability in vineyards. Pedobiologia 56, 9–14.
Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577.
Jenkins, W., et al., 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 48, 692.
Jiang, Y., Liu, M., Zhang, J., Chen, Y., Chen, X., Chen, L., Li, H., Zhang, X.-X., Sun, B., 2017. Nematode grazing promotes bacterial community dynamics in soil at the aggregate level. ISME J. 11, 2705–2717.
Jiang, Y., Zhou, H., Chen, L., Yuan, Y., Fang, H., Luan, L., Chen, Y., Wang, X., Liu, M., Li, H., Peng, X., Sun, B., 2018. Nematodes and microorganisms interactively stimulate soil organic carbon turnover in the macroaggregates. Front. Microbiol. 9, 2803.
Karuri, H., 2021. Nematode community structure and functional guilds differ in tea fields and tropical forest. Geoderma 392, 115006.
Katsvairo, T.W., Wright, D.L., Marois, J.J., Hartzog, D.L., Rich, J.R., Wiatrak, P.J., 2006. Sod-livestock integration into the Peanut-cotton rotation: a systems farming approach. Agron. J. 98, 1156–1171.
Katsvairo, T.W., Wright, D.L., Marois, J.J., Hartzog, D.L., Balkcom, K.B., Wiatrak, P.P., Rich, J.R., 2007a. Cotton roots, earthworms, and infiltration characteristics in sod–peanut–cotton cropping systems. Agron. J. 99, 390.
Katsvairo, T.W., Wright, D.L., Marois, J.J., Hartzog, D.L., Balkcom, K.B., Wiatrak, P.P., Rich, J.R., 2007b. Performance of Peanut and cotton in a bahiagrass cropping system. Agron. J. 99, 1245.
Katsvairo, T.W., Wright, D.L., Marois, J.J., Rich, J.R., 2007c. Transition from conventional farming to organic farming using bahiagrass. J. Sci. Food Agr. 87, 2751–2756.
Katsvairo, T.W., Wright, D.L., Marois, J.J., Rich, J.R., Wiatrak, P.P., 2009. Comparative plant growth and development in two cotton rotations under irrigated and non-irrigated conditions. Crop Sci. 49, 2233.
King, A.E., Blesh, J., 2018. Crop rotations for increased soil carbon: perenniality as a guiding principle. Ecol. Appl. 28, 249–261.
Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez, P.G., Malik, A.A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B.C., Trumbore, S.E., Gleixner, G., 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nat. Commun. 6, 6707.
Lodge, G.M., 1994. The role and future use of perennial native grasses for temperate pastures in Australia. N. Z. J. Agric. Res. 37, 419–426.
Ma, G., Kang, J., Wang, J., Chen, Y., Lu, H., Wang, L., Wang, C., Xie, Y., Ma, D., Kang, G., 2020. Bacterial community structure and predicted function in wheat soil from the North China plain are closely linked with soil and plant characteristics after seven years of irrigation and nitrogen application. Front. Microbiol. 11, 506.
McDaniel, M.D., Tiemann, L.K., Grandy, A.S., 2014. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. Ecol. Appl. 24, 560–570.
Neher, D.A., 2010. Ecology of plant and free-living nematodes in natural and agricultural soil. Annu. Rev. Phytopathol. 48, 371–394.
Osler, G.H.R., Sommerkorn, M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88, 1611–1621.
Pan, Z., Zhang, R., Zicari, S., 2019. Integrated processing Technologies for Food and Agricultural by-Products. Academic Press.
Pausch, J., Kuzyakov, Y., 2018. Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. Glob. Chang. Biol. 24, 1–12.

Perea-Moreno, M.-A., Manzano-Agugliaro, F., Hernandez-Escobedo, Q., Perea-Moreno, A.-J., 2018. Peanut Shell for energy: properties and its potential to respect the environment. Sustainability 10, 3254.
Philippot, L., Griffiths, B.S., Langenheder, S., 2021. Microbial community resilience across ecosystems and multiple disturbances. Microbiol. Mol. Biol. Rev. 85.
Porazinska, D.L., McSorley, R., Duncan, L.W., Graham, J.H., Wheaton, T.A., Parsons, L. R., 1998. Nematode community composition under various irrigation schemes in a citrus soil ecosystem. J. Nematol. 30, 170–178.
Prado, A.G.S., Airoldi, C., 1999. The influence of moisture on microbial activity of soils. Thermochim. Acta 332, 71–74.
Reeves, D.W., 1997. The role of soil organic matter in maintaining soil quality in continuous cropping systems. Soil Tillage Res. 43, 131–167.
Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.-M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M., Tscharntke, T., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553–556.
Schlatter, D.C., Bakker, M.G., Bradeen, J.M., Kinkel, L.L., 2015. Plant community richness and microbial interactions structure bacterial communities in soil. Ecology 96, 134–142.
Schumacher, L.A., Grabau, Z.J., Wright, D.L., Small, I.M., Liao, H.-L., 2020. Nematicide influence on cotton yield and plant-parasitic nematodes in conventional and sod-based crop rotation. J. Nematol. 52, 1–14.
Shen, Q., Zhang, K., Song, J., Shen, J., Xu, J., Inubushi, K., Brookes, P.C., 2018. Contrasting biomass, dynamics and diversity of microbial community following the air-drying and rewetting of an upland and a paddy soil of the same type. Biol. Fertil. Soils 54, 871–875.
Sorensen, P.O., Germino, M.J., Feris, K.P., 2013. Microbial community responses to 17 years of altered precipitation are seasonally dependent and coupled to co-varying effects of water content on vegetation and soil C. Soil Biol. Biochem. 64, 155–163.
Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T., 2020. Plant–microbiome interactions: from community assembly to plant health. Nat. Rev. 18, 607–621.
Tsigbey, F.K., Rich, J.R., Marois, J.J., Wright, D.L., 2009. Effect of bahiagrass (Paspalum notatum Fluegge) on nematode populations in the field and their behavior under greenhouse and laboratory conditions. Nematropica 111–120.
van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310.
Van Nguyen, S., Nguyen, P.T.K., Araki, M., Perry, R.N., Ba Tran, L., Minh Chau, K., Min, Y.Y., Toyota, K., 2020. Effects of cropping systems and soil amendments on nematode community and its relationship with soil physicochemical properties in a paddy rice field in the vietnamese Mekong Delta. Appl. Soil Ecol. 156, 103683.
Verbon, E.H., Liberman, L.M., 2016. Beneficial microbes affect endogenous mechanisms controlling root development. Trends Plant Sci. 21, 218–229.
Wang, Z., Cao, Y., Zhu-Barker, X., Nicol, G.W., Wright, A.L., Jia, Z., Jiang, X., 2019. Comammox nitrospira clade B contributes to nitrification in soil. Soil Biol. Biochem. 135, 392–395.
Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., 2017. Package 'corrplot'. Statistician 56, e24.
Wright, D., Marois, J., Katsvairo, T., Wiatrak, P., Rich, J., 2004. Value of perennial grasses in conservation cropping systems. In: Proc. of the 26th Southern Conservation Tillage Conference for Sustainable Agriculture, Raleigh, NC, pp. 8–9.
Xia, Y., Sun, J., Chen, D.G., 2018. Statistical analysis of microbiome data with R. Springer, Singapore.
Xiao, H., Griffiths, B., Chen, X., Liu, M., Jiao, J., Hu, F., Li, H., 2010. Influence of bacterial-feeding nematodes on nitrification and the ammonia-oxidizing bacteria (AOB) community composition. Appl. Soil Ecol. 45, 131–137.
Xiong, D., Wei, C., Jasper Wubs, E.R., Veen, G.J., Liang, W., Wang, X., Li, Q., Putten, W. H., Han, X., 2019. Nonlinear responses of soil nematode community composition to increasing aridity. Glob. Ecol. Biogeogr. 29, 117–126.
Yang, G., Wagg, C., Veresoglou, S.D., Hempel, S., Rillig, M.C., 2018. How soil biota drive ecosystem stability. Trends Plant Sci. 23, 1057–1067.
Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera-an outline for soil ecologists. J. Nematol. 25, 315–331.
Zhang, X., Guan, P., Wang, Y., Li, Q., Zhang, S., Zhang, Z., Martijn Bezemer, T., Liang, W., 2015. Community composition, diversity and metabolic footprints of soil nematodes in differently-aged temperate forests. Soil Biol. Biochem. 80, 118–126.
Zhang, K., Chen, L., Li, Y., Brookes, P.C., Xu, J., Luo, Y., 2017. The effects of combinations of biochar, lime, and organic fertilizer on nitrification and nitrifiers. Biol. Fertil. Soils 53, 77–87.
Zhang, K., Chen, L., Li, Y., Brookes, P.C., Xu, J., Luo, Y., 2020. Interactive effects of soil pH and substrate quality on microbial utilization. Eur. J. Soil Biol. 96, 103151.
Zhang, K., Maltais-Landry, G., Liao, H.-L., 2021. How soil biota regulate C cycling and soil C pools in diversified crop rotations. Soil Biol. Biochem. 156, 108219.
Zhao, D., Wright, D.L., Marois, J.J., 2009. Peanut yield and grade responses to timing of bahiagrass termination and tillage in a sod-based crop rotation. Peanut Sci. 36, 196–203.
Zhao, D., Wright, D.L., Marois, J.J., Mackowiak, C.L., Brennan, M., 2010. Improved growth and nutrient status of an oat cover crop in sod-based versus conventional peanut-cotton rotations. Agron. Sustain. Dev. 30, 497–504.
Zhao, Z., He, J., Geisen, S., Han, L., Wang, J., Shen, J., Wei, W., Fang, Y., Li, P., Zhang, L., 2019. Protist communities are more sensitive to nitrogen fertilization than other microorganisms in diverse agricultural soils. Microbiome 7, 33.