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Biosolarization restructures soil bacterial communities and decreases parasitic nematode populations

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ABSTRACT

Biosolarization is a soil disinfestation technology that combines passive solar heating and organic amendments to generate multiple pest-inactivating stressors. The objectives of this study were to assess the performance of almond (*Prunus dulcis*) processing residues in biosolarization to control infestations of root lesion (*Pratylenchus vulnus*) and ring nematodes (*Mesocriconema xenoplax*) during the pre-planting period of an almond orchard. The broader effects on soil microbial community composition were assessed by 16S rRNA gene sequencing immediately before and after biosolarization, as well as two months after treatment ended. Soil organic acids with nematicidal activity peaked after 9 days in biosolarized plots. Temperatures in biosolarized plots and solarized control plots reached maximum values 9–12 °C higher than untreated control plots. Biosolarization and solarization also enriched for specific Firmicutes, Actinobacteria, and Proteobacteria taxa associated with nematode suppression, some of which remained enriched two months post treatment. Biosolarization led to 100% mortality of *P. vulnus* in the upper 0–30 cm soil layer by 9 days of treatment. In contrast, reductions in plant-parasitic nematode densities between non-amended, solarized treatments and untreated controls were not observed until day 41 of treatment.

1. Introduction

Plant parasitic nematodes residing in soil present an enormous challenge to agriculture worldwide (Dutta et al., 2019). Pre-plant soil fumigation remains the most effective method to disinfest soil before planting high-value horticultural crops (Hodson et al., 2019). However, certain soil fumigants have been linked to cases of respiratory illness in farm workers; these include chloropicrin (Oriel et al., 2009), methyl isothiocyanate (Nakubulwa et al., 2018), and 1,3-dichloropropene (Strickland and Hogan, 2000). Furthermore, these volatile pesticides can drift from fumigation sites and create inhalation risks to surrounding communities (O'Malley et al., 2005; Oriel et al., 2009; Wofford et al., 2014). The application of fumigants can also alter soil ecology, which can ultimately leave soils open to reinfestation by pathogens (Momma et al., 2013; Ros et al., 2008). As a result, there is a need for alternative nematode control strategies (Bruggen and Semenov, 2000; Koike et al.,

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Abbreviations: cCER, cumulative carbon dioxide evolution rate; CON, negative control soil that received no treatment; HPLC, high-performance liquid chromatography; NMDS, non-metric multidimensional scaling; NP, Nonpareil variety hulls & shells; NPVC, soil amended with 1.5% Nonpareil hulls & shells and 0.6% vermicompost; OA, organic acids; PM, mixed pollinator variety hulls & shells; PMVC, soil amended with 1.5% mixed pollinator variety hulls & shells and 0.6% vermicompost; QIIME, Quantitative Insights into Microbial Ecology software; SIMPER, similarity percentage; SOL, solarization without amendment; VC, vermicompost.

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2003; Mazzola, 2007).

Biosolarization is a fumigation alternative that employs soil amendments, solar heating, and anaerobiosis to alter soil ecology and manage soil pathogens (Gamliel and Stapleton, 1993). In this process, soil is amended with labile organic matter, covered with transparent plastic tarp, and irrigated (Ros et al., 2008). The addition of organic matter initiates a rapid increase in population and activity of copiotrophs and saprophytes (Bruggen and Semenov, 2000). Irrigation and tarping limit oxygen diffusion and enrich for facultative anaerobes that can ferment soil amendments and form biopesticidal organic acid (OA) byproducts (Momma et al., 2006; Streminska et al., 2014). The anaerobic and biopesticide stresses on pests are complemented by high temperatures induced by the tarp's greenhouse heating effect, which can raise the temperature of topsoil to over 50 °C (Stapleton, 2000).

Microorganisms enriched during biosolarization may inactivate phytoparasitic nematodes directly or c outcompete them to prevent root colonization (Katan, 2014; Lamers et al., 2010; Stapleton, 2000; Strauss and Kluepfel, 2015). For example, Bacilli and Clostridia form organic acids as products of organic matter decomposition which are toxic to nematodes (Walia et al., 2000). The Bacilli class also includes *Pasteuria* spp., a diverse group of nematode parasites that can enhance nematode control when combined with soil solarization (Walia et al., 2000). One study found soils amended with *Brassica* seed meal enriched for Gammaproteobacteria such as *Pseudomonas*: these soils were suppressive to nematodes for multiple seasons, while fumigated plots saw re-emergence of plant parasites (Mazzola et al., 2016). Changes to microbial communities due to organic matter and temperature also affect nematode populations by increasing bacterivore abundance (Papatheodorou et al., 2004), which can increase bacterivore populations and in turn effect microbial ecology due to predation (De Mesel et al., 2004).

Almond (*Prunus dulcis*) orchards in California's Central Valley are of particular interest to biosolarization research for several reasons. First, young almond trees are highly susceptible to phytoparasitic nematodes. Left untreated, nematodes can damage over a third of planted acreage (McKenry, 1987). Almond yield losses in California can have a global impact as the state supplies 80% of almonds worldwide (and nearly 100% of U.S. almonds) (CDFA, 2018). Because of their high value and sensitivity to pests, the almond industry relies heavily on chemical fumigants for pre-plant soil treatment. In 2017, over one million kg of 1,3-dichloropropene were applied to almond orchards in California (DPR, 2017). Moreover, the almond industry produces a high volume of low-cost biomass: almond processing residues (hulls and shells) account for 73% of the dry weight of the almond fruit and over 2.8 billion kg are produced annually in California (ABC, 2020). Almond hulls and shells are promising biosolarization soil amendments due to their high fermentable nutrient content and nematicidal properties (Saura-Calixto et al., 1983; Fernández-Bayo et al., 2020). High biomass lability has been correlated to pest control efficacy (Achmon et al., 2017; Fernández-Bayo et al., 2018). Biosolarization may therefore offer a new circular economy approach for almond production, where almond residues may be used to as a fumigation alternative to enable additional almond production.

Biosolarization has been studied as a method for controlling fungi, weeds, nematodes, and pathogenic bacteria (Achmon et al., 2017; Butler et al., 2014; Shennan et al., 2014). However, the authors are aware of no previous studies that have translated biosolarization to a commercial orchard system for the treatment of phytoparasitic nematodes. Additionally, few studies have evaluated how both microbial and nematode communities are affected by biosolarization and how these communities recover post-treatment. The goal of this study was to measure the performance of biosolarization using almond industry byproduct soil amendments on a pre-plant commercial almond orchard. In this study, a 41-day biosolarization field trial using hull and shell amendments sourced from mixed pollinator and Nonpareil almond varieties was conducted in the Sacramento Valley of California. Among the hulls and shells tested, it was hypothesized that those with higher sugar content would contribute to greater organic acid accumulation, shifts in microbial community composition, and pest inactivation during biosolarization. Changes in the soil environment were monitored over time, including soil temperature, soil pH, and organic acid concentrations. Moreover, microbial and nematode community structure was analyzed over time. Ecological indices and bacterial relative abundances were measured before treatment, immediately after treatment, and two months post-treatment. Two major almond tree phytoparasites, *Pratylenchus vulnus* (root lesion nematodes) and *Mesocriconema xenoplax* (ring nematodes), were monitored to determine pest inactivation efficacy.

2. Materials and methods

2.1. Field, soil, and amendment properties

The field trial was conducted within a commercial almond orchard owned and operated by the Nicolaus Nut Company in Chico, California (39.803°N, −121.903°W). The soil was a Typic Haploxerert (USDA, 2005). The soil texture was a clay loam (36% sand, 36% silt, 28% clay), determined using the hydrometer method (Sheldrick and Wang, 1993). A commercial walnut orchard previously located at the site (Serr variety on black walnut rootstock) was removed in the spring of 2016 via excavator, spring-tooth chisel, and hand labor crews. A winter brassica mix cover crop [35% canola (*Brassica napus*); 15% Bracco white mustard (*B. hirtum*); 15% Nemfix yellow mustard (*B. juncea*); 20% Diakon radish (*Raphanus sativus*); 15% common yellow mustard (*B. hirtum*)] was planted in winter 2017 and disk-incorporated in March 2017. The field was then allowed to dry, the soil was laser leveled, and the field was smoothed with a land plane and float. Pre-treatment samples taken from the soil in June 2017 found all nematode feeding groups represented (Supplementary Table S1), including the plant-parasitic nematodes *P. vulnus*, *M. xenoplax* and *Meloidogyne* spp.

Almond hulls and shells collected during the 2016 Sacramento Valley harvest were obtained from two sources: a hull-rich stream from the Nonpareil variety (NP), and a hull and shell mixture (approximately 77% hull by mass) from several pollinator varieties (PM) (Carmel, Butte, Price and Aldrich almonds, with trace residues of Monterey, Padre, Mission, Peerless, and Wood Colony almonds) (North State Hulling Cooperative, Chico, California, USA). The compositional differences of the varieties have been previously reported (Palma et al., 2020): the neutral detergent fiber, starch, and sugar content was 258, 3.9, and 267.4 g kg^{-1} dry matter for Nonpareil variety, and 345, 5.2, and 178 g kg^{-1} dry matter for the pollinator mixed variety. Hulls and shells were milled in a 1000 hp. tub grinder (Morbark, Winn, Michigan, USA) to a particle size of less than 2.5 cm. Worm castings or vermicompost (VC) with a particle size of 6 mm were used as received (Vernalis, California, USA).

Properties of soil (0–30 cm) and amendments were determined using standard methods as previously described (Fernández-Bayo et al., 2020), including water-holding capacity (WHC), pH, and organic matter (OM) content. WHC was estimated as the moisture content of saturated solid material allowed to freely drain for 24 h. Soil pH was measured with a pH meter (InLab® Routine Pro ISM, 3-in-1 pH sensor, Mettler-Toledo, Columbus, Ohio, USA) for supernatants obtained by vortexing soil or amendments with water at a 1:1 mass ratio for 30 s and centrifuging at 8800*g* for 10 min. Total OM was estimated as volatile solid (VS) content, the proportion of oven-dry weight lost upon ignition for 4 h at 600 °C. Total nitrogen and carbon of materials were determined using flash combustion coupled to a thermal conductivity and infrared detector system (AOAC, 1997, 2006). Properties of the vermicompost were reported as received (A & L Western Agricultural Laboratories, Modesto, California, USA). A summary of the measured and calculated properties of the hull and shell amendments, VC, soil, and mixtures of these materials along with the predicted properties of each soil mixture calculated based on fraction of each material used are shown (Table 1).

Table 1
Properties of almond residue amendments, inoculum, and soil.

Material	% dry weight[a]			mg/kg dry weight				C/N	WHC	pH
	TC	TN	VS	NH_4	NO_3	PO_4	K			
PM[b]	43.8	0.69	94.3	10	<10	620	24,900	64	1.32	4.7
NP[b]	36.0	0.65	90.6	20	<10	680	22,200	55	1.74	4.8
VC[c]	23.9[d]	1.14[d]	76.2	*NR*	*NR*	711[d]	590[d]	21[d]	0.32	7.7[d]
Soil[e]	1.5	0.12	9.57	4.0	26	23.1	348	13	0.39	7.0
PMVC[f]	2.3	0.13	11.2	4.1	25	36.2	718	14	0.4	7.0
NPVC[f]	2.2	0.13	11.2	4.2	25	37.1	677	14	0.41	7.0

[a] Percent dry weight of total carbon (TC), nitrogen (TN), volatile solids (VS).

[b] Almond residues derived from mixed pollinator variety hulls and shells (PM) or Nonpareil hulls and shells (NP).

[c] Vermicompost (VC).

[d] Values reported as received (A & L Western Agricultural Laboratories, Modesto, CA).

[e] Soil collected from 0 to 30 cm the field site.

[f] Calculated properties of soil amended with 1.5% residues and 0.6% vermicompost based on the measured properties of the constituent materials and their abundance in the mixture.

2.2. Plot design and sampling

A 4400 m^2 subsection of the 202,300 m^2 fallow field was divided into thirty plots (3 × 295 m) arranged north-to-south in parallel, with a 3.7 m non-treated area between each plot. Plots were randomly assigned one of four soil treatments: biosolarization using 1.5% Nonpareil hulls and shells combined with 0.6% VC (NPVC), biosolarization using 1.5% pollinator mix hulls and shells combined with 0.6% VC (PMVC), solarization without amendment (SOL) or untreated negative control (CON). For biosolarized plots, almond residues (2900 kg dry weight per plot) and vermicompost (1100 kg dry weight per plot) were applied to dry soil using a truck-mounted spreader and tilled to a depth of 18 cm via rotary tiller (TX2 300 10 ft tiller, Memphis, Tennessee, USA). Biosolarized and solarized plots were leveled with a land plane and float, lined with six pressure compensating drip lines per plot (1.27 cm diameter, 30.5 cm emitter spacing, 0.001 m^3 h^{-1}). Biosolarized and solarized plots were covered with clear totally impermeable film, applied by TriCal (Hollister, California, USA). Tarps were sealed by burying edges with soil. Negative control plots received no amendment or tarp.

Biosolarization and control treatments were initiated on June 26, 2017 and the treatment lasted for six weeks (41 days). To initiate the biosolarization and solarization processes, the dry soil (11.6% moisture) was irrigated to field capacity via the pressure compensating drip hose down to 0.6 m depth. To maintain field capacity and promote continued anaerobic microbial activity, a second irrigation occurred 33 days into treatment. Irrigation occurred at a rate of 5.8 m^3 hr^{-1} for 6 h per plot (a depth of 6.7 cm h^{-1}). Of the 30 experimental plots, 12 plots were randomly selected for sampling representing three replicates for each of the four soil treatments.

Soil was sampled from plots one day before irrigation and tarping (day −1), 9 and 30 days after treatment initiation, immediately after the treatment ended (day 41), and 58 days after treatment ended (day 99). At each timepoint, six composite core samples (30 × 2.3 cm) were extracted from the north and south side of each plot. For intermediate sampling points (day 9, day 30), nylon bags filled with sand were placed around the puncture point of the core sampler to prevent oxygen contamination, and the punctures were immediately sealed with clear tape after samples were extracted. Soil cores were divided into upper 1–15 cm and lower 15–30 cm for all samples except the initial and 99-day time points. All soil samples were stored at 4 °C until analysis.

2.3. Soil respiration kinetics

To determine the effect of VC inoculum on amendment degradation, a laboratory study was conducted to measure microbial respiration for field soil with and without amended almond residues and VC. The cumulative carbon dioxide evolution rate (cCER) was used as a measure of residue degradability. The treatments included nonamended soil (CON), soil with 0.6% VC (VC), soil with 1.5% NP (NP) or PM (PM), and soil with 0.6% and 1.5% NP or PM (NPVC or PMVC). Aerobic bioreactors were prepared as previously described (Achmon et al., 2019). Briefly, soil mixtures (100 g dry) were incubated in 250 mL glass flasks at 25 °C in the dark. Moisture was held at 80% field capacity through periodic water addition to compensate for evaporation losses . Flasks were connected to a MicroOxymax respirometry system equipped with an infrared absorbance carbon dioxide sensor (Columbus Instruments, Columbus, Ohio, USA).

Effluent gas from bioreactors was measured in real time for four days (96 h). A saturation model was fit to cCER versus time data to estimate model parameters for each treatment according to the equation: $cCER = (C_t \times t) \times (c + t)^{-1}$ where C_t is the theoretical maximum amount of CO_2 that can be evolved (mg CO_2 g^{-1} dry weight), c is time needed to achieve half of C_t (hours) and t is time (hours). Cumulative carbon dioxide evolution rate (cCER, mg CO_2 g^{-1} soil) and saturation model parameters were calculated from gas effluent concentration data (Aslam and VanderGheynst, 2008; Simmons et al., 2013).

2.4. Soil organic acid, pH, and temperature measurements

Organic acids (OAs) and pH were analyzed as previously reported (Fernández-Bayo et al., 2020). Briefly, soil collected at each timepoint was extracted by vortexing with water (1:1) in duplicate, and centrifuging for 10 mins (8800 *g*, Eppendorf Centrifuge 5810R 15 Amp, Hamburg, Germany). pH values were obtained for supernatants. Each supernatant was filtered via 0.02 μm syringe filter (Thermo Fisher Scientific Inc., San Diego, California, USA).

Succinic, lactic, formic, acetic, propionic, isobutyric and butyric acid contents in soil extracts were analyzed by high-performance liquid chromatography (HPLC model UFLC-10Ai, Shimadzu, Columbia, Maryland, USA; Aminex HPX-87H column; 300 × 7.8 mm, Bio-Rad, Hercules, California, USA) coupled to a UV detector set to 210 nm (SPD-20A Prominence, Shimadzu, Columbia) according to an established method (Fernández-Bayo et al., 2020). Measured OA concentrations in soil were normalized according to the dry weight of soil used in each extraction. Individual OA concentrations in each sample were stoichiometrically added to determine total OA concentration.

To record soil temperature, miniature temperature sensor and data loggers (Thermochron iButtons model 1922 L; Embedded Data Systems, Lawrenceburg, Kentucky, USA) were buried at 2.5 and 20 cm depths in the center of three plots for each soil treatment before tarping. To measure ambient temperatures, additional temperature loggers were placed in the field 1.0 m above ground level in triplicate. Temperature loggers automatically recorded temperature every 30 min throughout the treatment duration and were extracted after the tarp removal. For temperature data, daily average temperature , minimums, and maximums were calculated for each plot over the 41-day treatment period.

2.5. DNA extraction and 16S rRNA gene sequencing

Microbial DNA was extracted from each soil sample for each of three time points (day −1, day 41, day 99) using a Powersoil DNA Isolation Kit (MO-BIO, Carlsbad, California, USA) as previously described (Achmon et al., 2019; Fernández-Bayo et al., 2019; Simmons et al., 2016). Duplicate extractions were performed for each sample and purified DNA was pooled. Sequences corresponding to the V4-V5 hypervariable region of 16S rRNA gene were amplified from extracts via PCR with the primer pairs 515F-Y 5′ GTGYCAGCMGCCGCGGTAA and 926R 5′ CCGYCAATTYMTTTRAGTTT. PCR conditions were as follows: an initial incubation at 94 °C for 3 min followed by 35 cycles of 94 °C for 45 s, 50 °C for 1 min, and 72 °C for 1.5 min. Reactions concluded with a final incubation at 72 °C for 10 min and a hold at 4 °C. Sequencing of the amplicons was performed using the Illumina MiSeq platform, as previously described (Simmons et al., 2014). Raw sequencing data are available on the JGI IMG portal (JGI, 2020) under project ID numbers 1145680 and 1145682. JGI sequence project names, sample identification numbers and corresponding treatments are listed in Supplementary Table S2.

Raw FASTQ sequences were then aligned against the Greengenes Database (version 13.8) using the Quantitative Insights into Microbial Ecology (QIIME) toolkit (V 2.0 2019.10) following the default values ($r = 3$; $P = 0.75$ total read length; $q = 3$; $n = 0$; $c = 0.005\%$) according to a previously established pipeline (Bokulich et al., 2013; QIIME 2 development team, 2018). The Greengenes database (V 13.8) was used to phylogenetically bin the operational taxonomic units (OTUs) based on a similarity threshold of 97% (Caporaso et al., 2010). Singleton OTUs with one read were removed prior to analysis.

2.6. Nematode classification and enumeration

Nematodes were extracted from 200 cm^3 of each composite soil core sample, measured volumetrically using a sieving and decanting technique followed by sugar centrifugation (Barker, 1985). The total number of nematodes in each sample was counted on a Nikon model TMS-F inverted microscope (Tokyo, Japan). The first 200 nematodes encountered on a slide were taxonomically identified at 400× magnification to the genus level according to Bongers (1988) and feeding classifications (fungivores, bacterivores, or herbivores) were assigned according to Yeates et al. (1993) (Supplementary Table S1). It should be noted that the classification ‘herbivores’ applies to both plant parasites as well as the family *Tylenchidae*, generally considered non-damaging epidermal root hair feeders (Yeates et al., 1993). Any dead nematodes noted in these samples were distinguished from live nematodes by internal degradation of the body cavity and only live nematodes were included in the enumeration analyses.

Median nematode abundances were reported, along with either the minimum or maximum values or the interquartile range (IQR), calculated by the $N + 1$ interpolation method.

2.7. Statistical analyses

ANOVA and Tukey's Honest Significant Difference post hoc test were used to compare mean values of cCER, temperature, OA, and pH measurements. Linear regression analysis was used to determine correlation between total OAs and pH. Normality of data and residuals was analyzed using the Shapiro-Wilk test ($P > 0.05$).

R studio was used to determine microbial OTU and phyla relative abundance, OTU richness, evenness, and Shannon diversity. The Vegan package version 2.5-6 (Oksanen et al., 2019) was used to generate anonmetric multidimensional scaling (NMDS) plot from the Bray-Curtis dissimilarity matrix (calculated from OTU abundance values) based on 1000 random starts. The NMDS plot was used to observe dissimilarity in the microbial communities' structure between different treatments and timepoints. The Adonis function in vegan was used to perform two-way permutational multivariate ANOVA (PERMANOVA) using the Bray-Curtis dissimilarity matrix with 999 permutations to determine soil treatment and time effects. Similarity percentage (SIMPER) analysis was carried out to identify specific OTUs that contributed most to observed Bray-Curtis dissimilarity (Clarke, 1993) between certain soil treatments and time points.

Kruskal Wallace and Dunn's multiple comparison tests were used to analyze differences in nematode abundance between treatments. Statistical analyses were performed using R Studio Version 1.1.423 and JMP-pro software at a significance level of 0.05 (version 14.0.0, SAS, Cary, North Carolina, USA).

3. Results

3.1. Laboratory measurement of soil respiration kinetics

Microbial respiration of field soil in bioreactors was affected by the addition of vermicompost (VC) (Fig. 1). ANOVA determined that without the addition of VC inoculum, cumulative respiration rate (cCER) in bioreactors was on average 34% higher for NP-amended soil compared to the PM-amended soil ($P < 0.001$). The addition of 0.6% VC by dry weight significantly increased the cCER of the PM-amended soil ($P = 0.003$) but did not affect NP-amended soil. With VC inoculation, the degradation and respiration kinetics of PM-amended soils were statistically equivalent to that of NP-amended soil.

3.2. Soil organic acids, pH, and temperature

HPLC analysis detected OAs in the top 15 cm of soil amended with both NPVC and PMVC at each timepoint (day −1, day 9, day 30 and day 41). In the top 15 cm of amended soils, OAs increased from low initial levels to peak concentrations nine days after treatment and remained detectable for the duration of the 41-day treatment (Fig. 2). Soil amended with NPVC had a peak average total OA concentration of 296 mM, significantly higher than that of PMVC amended soil according to ANOVA (100 mM, $P = 0.002$). Major organic acids included acetic, lactic, and formic acids, which together made up about 80% of total OAs

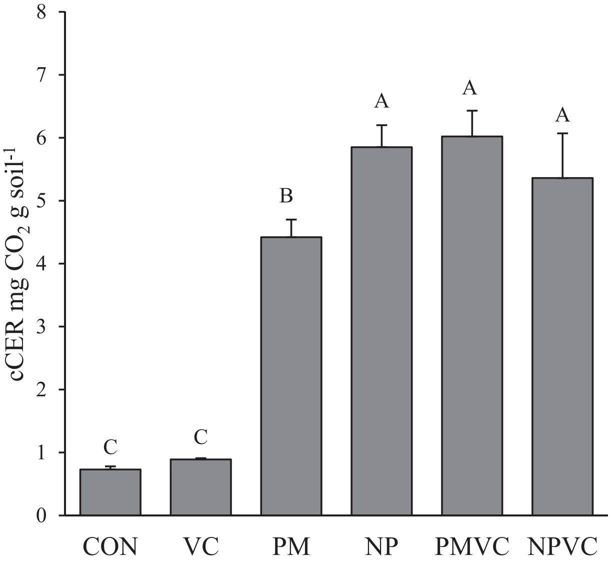

Fig. 1. Mean cumulative CO_2 respiration after 96 h of incubation. Cumulative CO_2 evolution rate (cCER) was estimated for the non-amended soil (CON), soil amended with vermicompost (VC), and soil amended with pollinator (PM) or Nonpareil (NP) hull and shell biomass lacking or including vermicompost inoculum (PMVC and NPVC). All values are reported as mean response ± one standard deviation ($n = 3$). Values that do not share a letter are significantly different ($P \leq 0.05$).

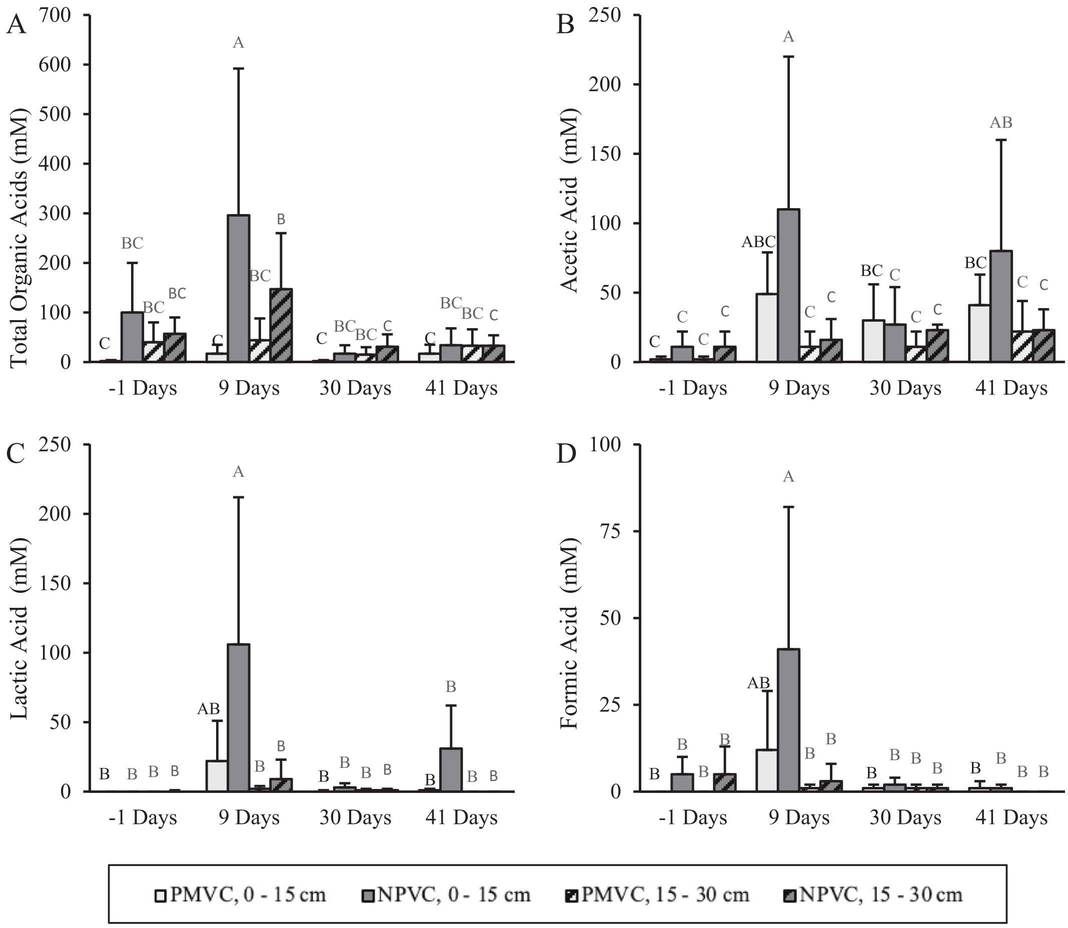

Fig. 2. Mean concentration of organic acids in soil.

Total organic acids (A), acetic acid (B), lactic acid (C), and formic acid (D) were extracted from soil. Soil OAs were extracted before treatment (−1 days), 9, 30, and 41 days after treatment commenced from amended plots at two depths: 0–15 cm soil or 15–30 cm soil. Plots were either biosolarized with 0.6% vermicompost and 1.5% hulls and shells from either Nonpareil (NPVC) or pollinator mix (PMVC). Total organic acids represent the sum of acetic, lactic, formic, propionic, and butyric acids. Error bars represent one standard deviation (n = 6). Values that do not share a letter are significantly different ($P \leq 0.05$). The y-axes have different scales for clarity.

detected nine days after treatment in the 0–15 cm layer. At this timepoint, their concentrations were 49, 22, and 12 mM in the PMVC amended soil and 110, 106, and 41 mM in the NPVC amended soil, respectively. Propionic and butyric acids were detected in lower concentrations, and unlike the three major OAs, peaked in concentration at 41 days of treatment: 8 and 5 mM for PMVC, 12 and 20 mM for the NPVC amended soil.

While OAs were also present in the deeper soil layer (15–30 cm profile), total OA concentrations remained relatively low at 18–36 mM. Total OA levels of SOL and CON treatments were nondetectable (<1 mM).

Across all treatments, depths, and timepoints, soil pH was inversely correlated to total OA concentration according to linear regression analysis ($P < 0.001$). In general, pH remained close to neutral at 6.5–7.2 for all treatments, depths, and time points (Table 2). The exception was a pH of 6.0 observed for NPVC soil in the 0–15 cm layer at nine days, where OA concentration was highest.

Regardless of depth and time, soils that underwent tarping (PMVC, NPVC, SOL) experienced daily temperatures with 8–10 °C higher averages, 7–10 °C higher minimums, and 7–13 °C higher maximums than non-tarped controls according to one-way ANOVA at each depth ($P < 0.001$, Table 2). At 2.5 cm depth, temperatures were between 37–58 °C for NPVC soils, 36–59 °C for PMVC soils, 33–60 °C for SOL soils, and 26–50 °C for negative control soils. At 20 cm, lower temperature ranges were observed where NPVC soil reached temperatures between 40–46 °C, PMVC between 41–47 °C, SOL between 40–47 °C, and controls were only 32–36 °C.

3.3. Changes in microbial community composition and diversity

Alpha diversity indicators, including species richness, evenness, and Shannon diversity were calculated for each treatment (CON, SOL, NPVC and PMVC) and time point (day −1, day 41, and day 99). According to multi-way ANOVA, all parameters were significantly affected by both treatment ($P < 0.001$ for all), and time point ($P < 0.001$ for all, Table 3).

Immediately after amendment but before tarping (day −1), CON soil had significantly higher evenness than NPVC soil ($P = 0.009$). Immediately after the treatment (41 days), CON soil had significantly higher richness than biosolarized treatments, and higher evenness and Shannon diversity than both solarized and biosolarized soil ($P < 0.05$ for all). Fifty-eight days after tarp removal (99 days), soils had statistically similar richness, evenness, and Shannon diversity ($P > 0.05$ for all Tukey's HSD comparisons).

Nonmetric multidimensional scaling (NMDS) was applied to all soil treatments and timepoints, which demonstrated dissimilarity between treated soils according to the abundance of individual identified taxa in each sample (Fig. 3). Adonis analysis found treatment and timepoint contributed significantly to these soil community differences ($P < 0.001$ for both). This was reflected in the NMDS plot, where data primarily clustered according to whether soil was solar heated (via either

Table 2
Soil temperature, moisture content, and pH responses to biosolarization with almond residue amendments. Across both depth ranges for a given response, values that do not share a letter are significantly different (P ≤ 0.05). Values represent mean ± one standard deviation.

Depth	Treatment[†]	MC[‡] (%)	pH[‡,§]	Temperature metrics[#] (°C)		
				Avg	Min	Max
0–15 cm	NPVC	19 ± 3a	6.0 ± 0.5b	46 ± 0.7a	37 ± 0.7bc	58 ± 0.1ab
	PMVC	18 ± 3ab	6.8 ± 0.2a	46 ± 0.7a	36 ± 1.2c	59 ± 0.4a
	SOL	18 ± 2ab	7.0 ± 0.04a	45 ± 1.7a	33 ± 1.3 cd	60 ± 5.8a
	CON	13 ± 4c	6.7 ± 0.2a	37 ± 1.7b	26 ± 1.8e	50 ± 5.6bc
15–30 cm	NPVC	19 ± 6a	6.8 ± 0.05a	43 ± 1.9a	40 ± 1.7a	46 ± 2.2c
	PMVC	18 ± 3ab	7.4 ± 0.1a	44 ± 1.2a	41 ± 1.3a	47 ± 1.1c
	SOL	18 ± 3ab	7.2 ± 0.2a	43 ± 0.7a	40 ± 0.6ab	47 ± 1.1c
	CON	15 ± 4bc	6.9 ± 0.2a	34 ± 0.5b	32 ± 0.4d	36 ± 0.6d
Ambient				30 ± 3	15 ± 3	45 ± 4

[†] Properties for soil biosolarized with 1.5% Nonpareil hulls and shells and 0.6% vermicompost (NPVC), soil biosolarized with 1.5% pollinator mix hulls and shells and 0.6% vermicompost (PMVC), soil solarized with no amendment (SOL), and soil that received no treatment (CON).

[‡] Moisture Content (MC) value indicates mean of composite soil core samples taken at each half plot and split between 0–15 and 15–30 cm (n = 6), analyzed in duplicate.

[§] pH value measured nine days after treatment initiation (tarping, irrigation) corresponding to peak OA concentrations.

[#] Mean of 41 daily temperature averages (Avg), minimums (Min), and maximums (Max) from 6/27/2017 to 8/06/2017 for each treatment and depth (n = 3), measured at 2.5 cm for the 0–15 cm profile or 20 cm for the 15–30 cm profile, and 1.0 m above surface for ambient.

Table 3
Species evenness, richness, and Shannon Diversity for soil microbial communities. Across all treatments and timepoints within each metric, values that do not share a letter are significantly different (P ≤ 0.05). Values represent mean ± one standard deviation for each metric (n = 3).

Diversity metric	Time point[†]		
Species richness[‡]	−1 days	41 days	99 days
CON	210 + 5 a	200 + 16 a	196 + 36 ab
SOL	211 + 10 a	178 + 6 ab	180 + 16 ab
PMVC	192 + 9 ab	130 + 25 b	127 + 17 ab
NPVC	196 + 8 ab	125 + 13 b	162 + 99 ab
Shannon diversity[‡]	−1 days	41 days	99 days
CON	7.2 + 0.1 a	6.8 + 0.2 a	5.7 + 0.5 abc
SOL	7.2 + 0.3 a	5.3 + 0.4 bc	5.6 + 0.2 abc
PMVC	6.7 + 0.3 ab	4.7 + 0.6 c	4.4 + 0.03 c
NPVC	5.6 + 0.3 abc	4.7 + 0.1 c	5.2 + 2.1 c
Species evenness[‡]	−1 days	41 days	99 days
CON	0.62 + 0.01 a	0.6 + 0.01 ab	0.54 + 0.04 abc
SOL	0.62 + 0.02 a	0.49 + 0.03 c	0.54 + 0.02 abc
PMVC	0.59 + 0.01 abc	0.47 + 0.01 c	0.45 + 0.01 c
NPVC	0.49 + 0.13 bc	0.48 + 0.05 c	0.51 + 0.02 bc

[†] Timepoints analyzed include one day before treatment initiation (−1 days), immediately following tarp removal (41 days), or 58 days after tarp removal (99 days).

[‡] Treatments analyzed include soil that received no treatment (CON), soil solarized with no amendment (SOL), soil biosolarized with 1.5% pollinator mix hulls and shells and 0.6% vermicompost (PMVC), or soil biosolarized with 1.5% Nonpareil hulls and shells and 0.6% vermicompost (NPVC).

solarization or biosolarization) and the time since solar heating. SIMPER analysis revealed that 19 OTUs represented 13% of the dissimilarity between communities of different treatments and timepoints (Table 4).

Of all identified taxa in the pooled dataset, 95.6% belonged to ten phyla, primarily Proteobacteria (29%), Actinobacteria (20%), Firmicutes (15%), Acidobacteria (10%), and Bacteroidetes (6%), but also Chloroflexi, Gemmatimonadetes, Verrucomicrobia, Planctomycetes, and the archaea Crenarchaeota (5% or less each, Fig. 4).

Community differences emerged after residues were applied, even before the tarping and subsequent heating and oxygen depletion (day −1). Nonamended soils (CON and SOL) showed significantly greater levels of Planctomycetes, Proteobacteria, Bacteroidetes, Acidobacteria, Chloroflexi, and Gemmatimonadetes compared to NPVC plots (P ≤ 0.05 for all). Non-amended soils initially had 2% or less relative abundance of Firmicutes; amendment with either NPVC or PMVC significantly enriched for Firmicutes (P < 0.001) prior to biosolarization initiation. Firmicutes made up 35% and 11% of the initial NPVC and PMVC soil communities, respectively, with nearly all belonging to the class Bacillus. Two Bacilli from the Planococcaceae family, including OTUs from the genus *Paenisporosarcina*, were enriched in amended plots and were both two-fold greater for NPVC than PMVC soil. Amended plots were also enriched in the certain Actinobacteria genera, including Arthrobacter and Streptomyces, more so for NPVC (2.0 and 0.1%) than PMVC soil (1% and <0.1%), compared to CON and SOL plots (0.3 and 0%).

After 41 days, the microbial community structures of SOL and biosolarized soils shifted. Firmicutes were enriched in all solar heated plots with the highest levels observed in NPVC treatments (50% abundance, P = 0.016) followed by PMVC (32%, P = 0.030) and SOL (27%, P < 0.001). Unlike at the initial timepoint, Firmicutes classes after treatment were composed of about 50% Bacilli and 50% Clostridia, regardless of amendments. Bacteroidetes levels in PMVC soils increased from 8 to 14%, higher than CON, SOL, and NPWM soils, but this increase was not significant (P = 0.469). Finally, certain Betaproteobacteria from the class Burkholderiales, including the families Comamonadaceae and Oxalobacteraceae, and the genus *Massilia*, were enriched in SOL, PMVC, and NPVC treated soils and contributed to high dissimilarity between treated and control soils, but significant enrichment was only observed for an OTU from the order Comamonadaceae (P = 0.039). All treated soils had significantly lower Acidobacteria, Chloroflexi, Planctomyces, and Verrucomicrobia than control soils (P < 0.001 for all).

Ninety-nine days after soil treatment initiation, in which soil was untarped for 58 days, further community restructuring was observed. At this timepoint, total Actinobacteria, Proteobacteria, and Verrucomicrobia abundances were no longer significantly different between treated and CON soils (P > 0.05 for all). However, Firmicutes relative abundance remained significantly elevated in biosolarized and SOL soils (P = 0.032), with PMVC having the highest abundance at 39%. At day 99, the OTUs that contributed most to the difference between biosolarized and CON treatments were from the Bacilli and Clostridia class, including the families Planococcaceae and Symbiobacteriaceae, as well as *Bacillus asahii*, *Caloramator*, *Clostridium tyrobutyricum*, and *Desulfosporosinus meridiei*. Certain Chloroflexi from the orders Anaerolineales and Chloroflexi also contributed to differences between biosolarized and SOL/CON treatments. CON was enriched in total Actinobacteria, although Actinobacteria from certain taxa were also enriched in treated soils: the genera *Saccharopolyspora*, *Streptomyces*, and *Micromonospora* contributed to high dissimilarity between treated and control soils, but significant enrichment was only observed for an OTU from the order Micromonosporaceae (P = 0.018).

3.4. Nematode abundance

Initially (day −1), *P. vulnus* infested all plots in the 0–30 cm soil depth, with a median of 90 counts per 200 cm^3 soil (Fig. 5A). After nine days of treatment, NPVC and PMVC soils had significantly lower viable *P. vulnus* counts than CON soils according to Dunn's multiple comparison test (P = 0.040 for both); counts in SOL plots also declined to low levels but were not significantly different from CON (P = 0.070) at this timepoint. After the full 41 days of treatment, NPVC, PMVC, and SOL

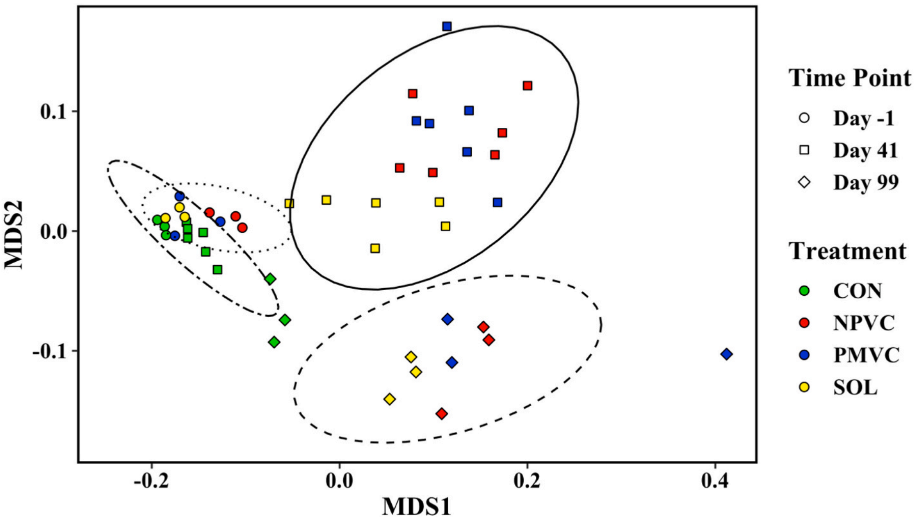

Fig. 3. Nonmetric multidimensional scaling (NMDS) biplot based on differences in OTU counts between treatments and timepoints. Points represent untreated plots (CON), solarized plots (SOL), and plots biosolarized with either Nonpareil (NPVC) or pollinator mix (PMVC). Soil was analyzed one day before treatment (day -1), immediately after tarp removal (day 41), and 58 days after tarp removal (day 99). Points were separated according to Bray-Curtis dissimilarity of OTU counts. Ellipses represent 95% confidence intervals for the centroids associated with each cluster: control soils at all timepoints, amended soils before treatment, solarized and biosolarized soils immediately after 41-day treatment, and finally solarized and biosolarized soils after 99 days of treatment initiation.

Table 4
Taxa contributing to greatest dissimilarity between treatments and their relative abundance at each sampling timepoint. OTUs are reported to the lowest resolved taxonomic level, including class (c), order (o), family (f), genus or species (italicized). Rows that contain letters indicate OTUs that showed significant differences in abundance for at least one timepoint; values that do not share a letter are significantly different ($P \leq 0.05$). Values represent mean relative abundance for each OTU expressed as percentages. ($n = 3$).

Taxonomic assignment[†]	−1 days[‡,§]				41 days[‡,§]				99 days[‡,§]			
	CON	SOL	PMVC	NPWM	CON	SOL	PMVC	NPWM	CON	SOL	PM VC	NPWM
Actinobacteria												
Arthrobacter[*]	0.3_c	0.3_c	1.0_b	2.0_a	0.9_b	1.1_b	2.0_a	1.3_{ab}	0.4	0.1	0.3	0.0
Micromonosporaceae (o)[*]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0_b	0.5_a	0.3_{ab}	0.6_a
Micromonospora	0.0	0.0	0.0	0.0	0.0	1.1	0.9	0.8	0.0	0.3	0.4	0.7
Saccharopolyspora	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.6	0.0	3.3	0.3
Streptomyces[*]	0.0_b	0.0_b	0.0_a	0.1_a	0.0	0.0	0.0	0.1	0.1	0.7	0.1	1.4
Bacteroidetes												
Rhodothermaceae (f)	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	1.1
Chloroflexi												
Anaerolineae (c)	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0	2.6	0.7
Chloroflexi (c)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3	0.8	0.6
Firmicutes												
Bacillus asahii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.7
Planococcaceae (f)[*]	0.1_b	0.3_b	2.3_b	8.1_a	0.3_c	0.5_c	1.1_b	1.7_a	0.7	1.3	7.5	1.5
Paenisporosarcina[*]	0.1_b	0.2_b	1.2_b	4.1_a	0.2_b	0.3_b	0.3_b	1.0_a	0.4	0.7	0.3	0.5
Caloramator	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.1
Clostridium tyrobutyricum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0
Desulfosporosinus meridiei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Symbiobacteriaceae (f)	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.5	0.0	0.6	0.4	0.8
Proteobacteria												
Kaistobacter	0.1	0.1	0.1	0.1	0.2	0.3	0.0	0.0	0.0	0.3	0.2	0.7
Comamonadaceae (f)[*]	0.1	0.1	0.1	0.2	0.2_b	1.4_{ab}	2.3_a	1.0_{ab}	0.2	0.3	1.0	0.1
Oxalobacteraceae (f)	0.2	0.2	0.2	0.2	0.2	2.5	1.2	0.4	0.6	0.2	0.0	0.1
Massilia	0.6	0.6	0.3	0.2	1.1	2.6	1.5	0.7	0.6	0.1	0.6	0.1
Total relative abundance for listed OTUs (%)	1.5	1.8	5.2	15.1	3.1	10.1	10.0	7.7	3.6	5.4	26.1	11.0

[*] OTU was significantly affected by the soil treatment for at least one time point ($P \leq 0.05$).

[†] List of OTUs that represented a minimum of 13% of the dissimilarity between community structures.

[‡] Timepoints analyzed include one day before treatment initiation (−1 days), immediately following tarp removal (41 days), or 58 days after tarp removal (99 days).

[§] Treatments analyzed include soil that received no treatment (CON), soil solarized with no amendment (SOL), soil biosolarized with 1.5% pollinator mix hulls and shells and 0.6% vermicompost (PMVC), or soil biosolarized with 1.5% Nonpareil hulls and shells and 0.6% vermicompost (NPVC).

treatments all showed significantly lower *P. vulnus* levels than CON ($P < 0.01$, $P = 0.02$ and $P = 0.01$ respectively) despite high variation. After the tarp had been removed for 58 days and the soil deep tilled (day 99), *P. vulnus* abundance in CON soils declined from a median of 315.6 individuals at day 41 to 4.8 counts per 200 cm^3. These levels were only significantly greater than those in the NPVC treatment ($P < 0.01$); PMVC and SOL counts remained low but were not significantly different from CON at this timepoint.

Initial counts of *M. xenoplax* were lower than those of *P. vulnus*, with a median of 30 individuals per 200 cm^3 soil (day −1, Fig. 5B). After nine days of treatment, counts were significantly lower in NPVC, PMVC, and SOL soils compared to CON according to Dunn's multiple comparison test ($P < 0.01$, $P = 0.02$ and $P < 0.01$, respectively). *M. xenoplax* abundance in CON soil declined between 9 and 41 days from 38 to 0 counts per 200 cm^3 soil, and abundance was statistically equal in all plots regardless of treatment at this time. Ninety-nine days after soil amendments were applied and the soil tilled, *M. xenoplax* levels remained near-zero and statistically equivalent.

Treatment affected the abundance of free-living nematodes as well as phytoparasites (Fig. 6). Initially, no differences were observed between

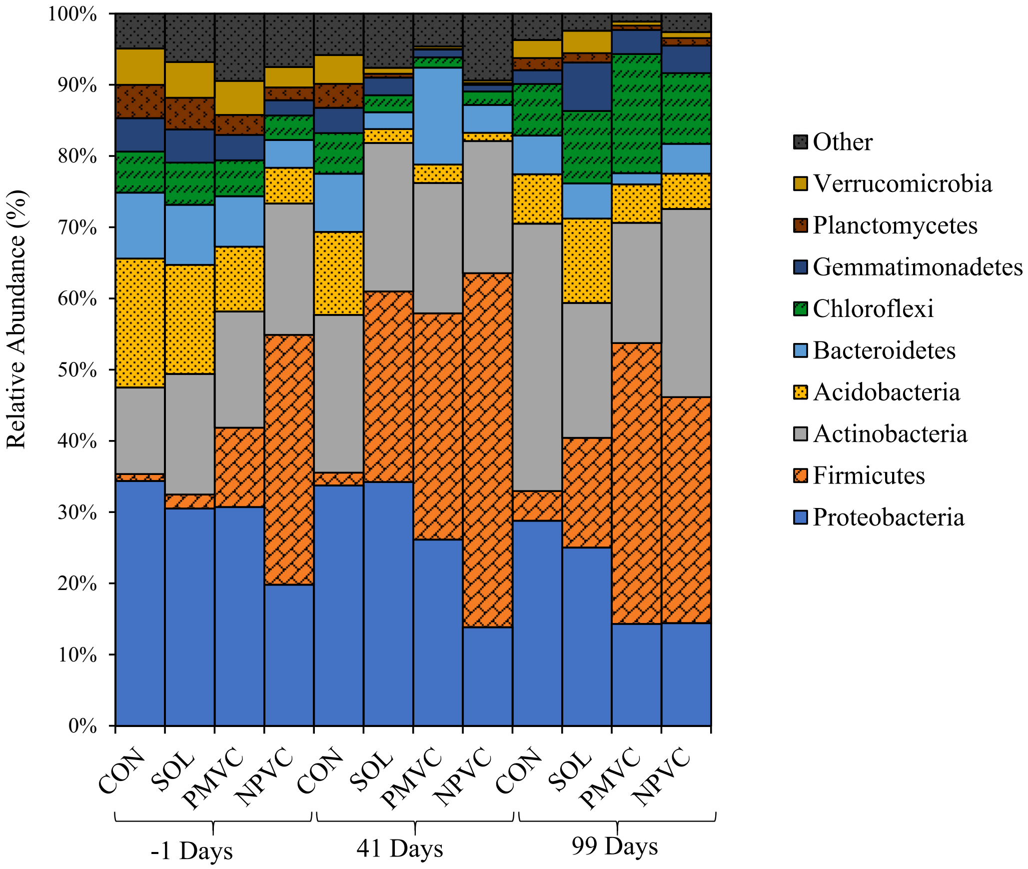

Fig. 4. Phyla relative abundance. Treatments include untreated soil (CON), solarized soil (SOL), and soil biosolarized with 0.6% vermicompost and 1.5% hulls and shells from either Nonpareil (NPVC) or pollinator mix (PMVC). Soil was analyzed one day before treatment (-1 days), immediately after six weeks of treatment (41 days), and 58 days after tarp removal (99 days). Values represent mean relative abundance for each of nine prominent phyla (representing >95% of all detected prokaryotes).

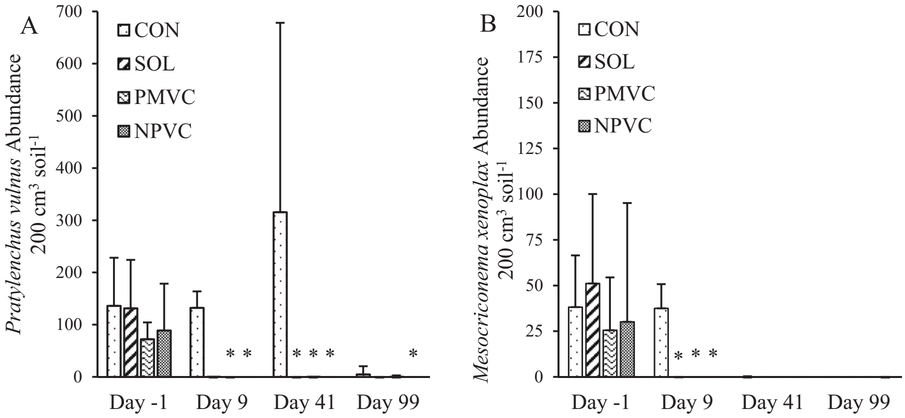

Fig. 5. Parasitic Nematode Counts in Soil. Counts of *Pratylenchus vulnus* (A) and *Mesocriconema xenoplax* (B) determined in 200 cm^3 soil of the cores sampled from 0 to 30 cm deep.
Treatments include untreated soil (CON), solarized soil (SOL), and soil biosolarized with 0.6% vermicompost and 1.5% hulls and shells from either Nonpareil (NPVC) or pollinator mix (PMVC). Soil was analyzed one day before treatment (day −1), after nine days of treatment (day 9), after six weeks of treatment (day 41), and 58 days after tarp removal (day 99). Values represent medians and error bars indicate the interquartile range (n = 6). Asterisk (*) indicates significant difference from control ($P < 0.05$) according to Dunn's multiple comparison test within the same sampling point.

plots for fungivores, bacterivores, or herbivores according to Dunn's multiple comparison test. After nine days of treatment, NPVC, PMVC, and SOL treatments saw a significant decline in the abundances of herbivores ($P = 0.04$, $P < 0.01$ and $P < 0.01$, respectively), fungivores ($P < 0.01$, $P = 0.03$, and $P = 0.020$, respectively), and bacterivores ($P < 0.01$, $P = 0.03$, and $P = 0.020$, respectively). After 41 days, the abundances of all feeding groups increased in CON soil but remained extremely low for solarized and biosolarized treatments ($P < 0.05$). After the tarp had been removed for 58 days and the soil tilled (day 99), the total abundance of nematodes declined by 95% in control plots, and counts were not statistically different among treatments.

4. Discussion

4.1. Soil respiration kinetics

Previous biosolarization trials found that inoculation with lignocellulose-degrading microbiota, such as those found in compost, improved degradation of recalcitrant organic matter amendments (Fernández-Bayo et al., 2019). Inoculation also improved efficacy via increased accumulation of biopesticidal OAs (Hestmark et al., 2019). Here, the co-amendment of vermicompost increased the respiration rate of soil amended with mixed pollinator variety hulls and shells in soil bioreactors, suggesting a benefit to biomass deconstruction and availability of amendment nutrients to endogenous and amended microorganisms in the soil. In contrast, soil amended with Nonpareil hulls and

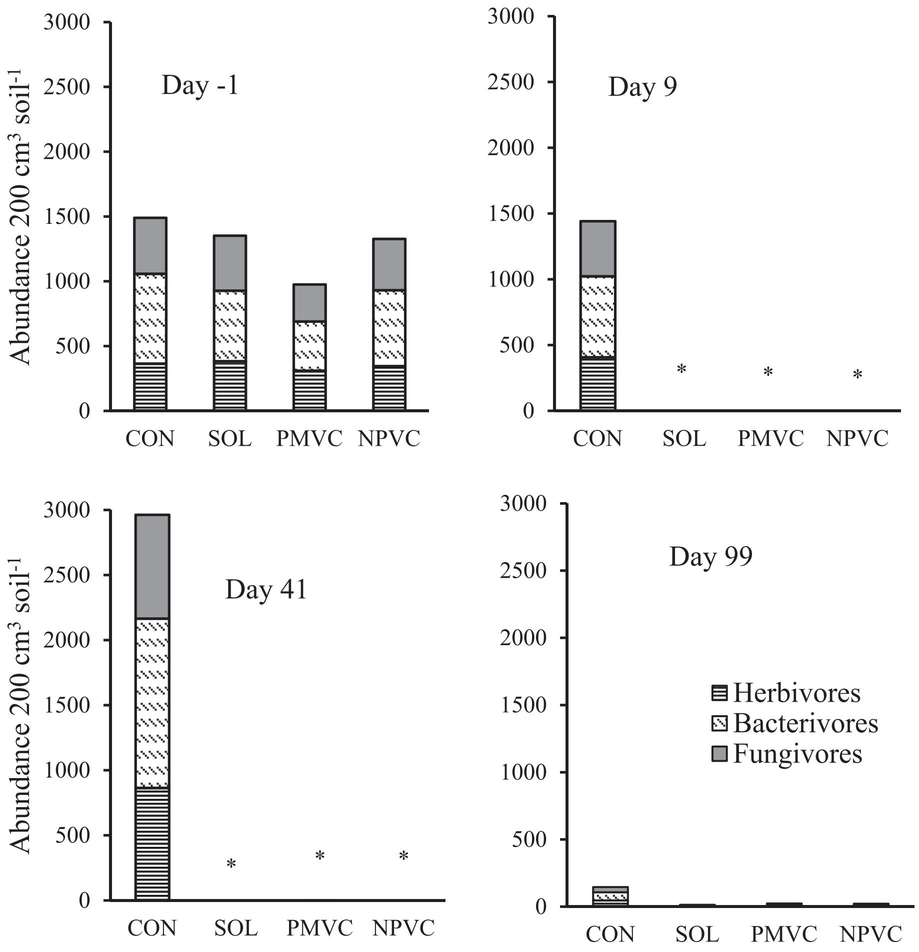

Fig. 6. Median abundance of nematodes of different feeding groups.
Nematodes were counted and identified by feeding group in 200 cm^3 soil sampled from 0 to 30 cm soil depth. Treatments include untreated soil (CON), solarized soil (SOL), and soil biosolarized with 0.6% vermicompost and 1.5% hulls and shells from either Nonpareil (NPVC) or pollinator mix (PMVC). Soil was analyzed one day before treatment (day −1), after nine days of treatment (day 9), after six weeks of treatment (day 41), and 58 days after tarp removal (day 99). Asterisk (*) indicates significant difference ($P < 0.05$) according to Dunn's multiple comparison test for total nematode abundance.

shells saw no such increase in respiration with the addition of vermicompost inoculum. This disparity is likely due to compositional differences between the pollinator variety and Nonpareil hulls and shells. Hulls and shells from pollinator varieties generally contain more lignocellulose and less labile sugar and starch compared to those from the Nonpareil variety (Palma et al., 2020). Accordingly, the addition of deconstructive microorganisms in the vermicompost may have acted to enhance degradation of the more recalcitrant fiber fraction in the mixed pollinator variety material.

4.2. Soil organic acids, pH, and temperature

Organic acid accumulation in soil is a key mechanism of pest inactivation during biosolarization (Momma et al., 2006). Overall OA levels were highest after nine days of biosolarization, in agreement with previous studies that demonstrated concentration peaks after eight days of fermentation (Achmon et al., 2016). Only the top 18 cm of soil was amended with almond hulls and shells due to the limitations of tillage for this experiment; this was reflected in the greater OA concentrations observed in the 0–15 cm depth compared to the 15–30 cm layer.

Lactic, acetic, and formic acid dominated the OA profile, coinciding with lab-scale biosolarization using these amendments (Fernández-Bayo et al., 2020), in which complete *P. vulnus* mortality was observed after a 72 h exposure to biosolarized soil extracts with 27–30 mM total OAs (Fernández-Bayo et al., 2020). Acetic and lactic acid, the most abundant OAs detected, are commonly studied biopesticides. According to bioassay studies, acetic acid has an estimated LC_{95} for *P. penetrans* of 37.8 mM (Mahran et al., 2008). Another study found that 11 mM lactic acid caused 88% nematode mortality (Abdel-Rahman et al., 2008). Though lower in concentration in this study, propionic and butyric acids are more toxic with reported LC_{95} values of 14.6 and 25.3 mM acid against *P. penetrans* respectively (Mahran et al., 2008). Soil amended with Nonpareil residues consistently exceeded nematicidal thresholds, with peak total OAs between 99 and 493 mM. Pollinator mix amendments, with lower concentration range of 10–190 mM total OAs, may have lower predictability in nematicidal performance.

High OA concentration variability can be expected due the large, heterogenous particle size of the amendments along with variations in soil oxygen (Achmon et al., 2017; Fernández-Bayo et al., 2018; Hestmark et al., 2019; Simmons et al., 2016), soil community composition, and moisture content (Zheng et al., 2011) within and among plots. Increased homogeneity of amendment particle size and applicatoion uniformity could improve the consistency of OA production. In this trial, pH showed little variation and remained between 6.0 and 7.3. It is important to note that OAs are considered more toxic when protonated, which occurs at pH <3.5–4.5 (Mahran et al., 2008).

In addition to acidification, soil heating is considered an important pest control mechanism in biosolarization. Soil temperatures achieved during solarization, with and without amendments, have been shown to be sufficient for eradication of weed seeds (Achmon et al., 2017; Peachey et al., 2001), fungal pathogens (Basallote-Ureba et al., 2016; Coelho et al., 1999; Fernández-Bayo et al., 2018; Klein et al., 2011; Otieno et al., 2003), and nematodes (Butler et al., 2012; Oka et al., 2007; Ros et al., 2008). In the current study, solarized and biosolarized treatments achieved and surpassed thermal death threshold values for a variety of soil pests (Dahlquist et al., 2007; Stapleton, 2000), with maxima of 43–49 °C in the 20 cm layer and 55–66 °C in the 2.5 cm layer. However, temperatures in untreated soils at 20 cm depth only reached maxima of 35–37 °C, survivable for mesophiles. Heating likely played a role in nematode inactivation in the present study, either through direct inactivation in the upper soil layers or via sublethal temperatures synergizing with other stresses in deeper soils. Elevated, yet sublethal, soil temperatures can weaken pathogens and make them more sensitive to biopesticides (Oka, 2010), low oxygen (Ebihara and Uematsu, 2014), and antagonism from microbes (Otieno et al., 2003). For instance, sublethal heating from solarization can make nematodes more susceptible to parasitism (Walia et al., 2000).

4.3. Changes in microbial community composition and diversity

Abundant phyla in the untreated negative control soil included Acidobacteria, Gemmatimonadetes, Verrucomicrobia, Planctomycetes, and Proteobacteria. This is consistent with several previous studies, which observed Acidobacteria in non-amended soil, attributed to the slow growth of these oligotrophs in response to high soil organic matter additions (Hewavitharana and Mazzola, 2016; Simmons et al., 2016; van Agtmaal et al., 2015). Amending soil with almond residues led to enrichment of specific taxa associated with beneficial saprophytic microbes, including OTUs belonging to the Actinobacteria and Firmicutes phyla prior to solar heating. Specifically, the genus *Streptomyces* was enriched in Nonpareil residue-amended soils, as observed in previous studies using almond shell compost amendments (Vida et al., 2016). Actinobacteria such as *Streptomyces* are known to promote formation of vitamins, humus, antibiotics, and biopesticides (Casacchia et al., 2010; Gu et al., 2007; Vida et al., 2016). Firmicutes, particularly the Bacilli class, were also abundant after Nonpareil residue amendment before any solar heating, making up almost 35% of all OTUs. Firmicutes are central to biosolarization efficacy due to their capacity for anaerobic polysaccharide degradation, fermentation, and organic acid formation (Fernández-Bayo et al., 2019; Simmons et al., 2016). Bacilli may have been present on the Nonpareil residue surface, providing another reason OA production was more robust in these plots.

After almost six weeks of either biosolarization or solarization, the microbial communities underwent additional restructuring. Evenness and Shannon diversity decreased after solarization and biosolarization treatments. One reason for this decrease was the selection of Firmicutes, which accounted for 27 to 50% of the soil bacterial community in tarped plots, potentially due to the presence of saprophytic, thermotolerant, and/or anaerobic microorganisms in this phylum (Simmons et al., 2016). Recent studies note that the abundance of saprophytes, rather than high diversity, was a greater predictor of plant disease suppression (van Agtmaal et al., 2018). Bacilli remained elevated in biosolarized soils, and Clostridia class abundance increased from near-zero initial levels to match the high Bacilli levels. Clostridia are mainly obligate anaerobes, and the presence of these taxa indicate anaerobic conditions were achieved in the solarization and biosolarization treatments (Simmons et al., 2014). Clostridia have been observed in soils biosolarized with green waste (Fernández-Bayo et al., 2019; Simmons et al., 2014), where they were associated with recalcitrant carbon biopolymer degradation and subsequent OA production. Finally, solarization and biosolarization enriched for Betaproteobacteria such as the order Burkholderiales. Previous studies also found certain Betaproteobacteria can survive the stress of biosolarization (Fernández-Bayo et al., 2019) and even pasteurization (Hewavitharana and Mazzola, 2016).

On day 99, after solarized and biosolarized soils were allowed to aerate for 58 days, further evidence of community restructuring was observed. The Shannon diversity and evenness of solarized and biosolarized soils increased and reached similar levels to that of the control soils. However, structural differences in the selected microbial community components remained between treated and non-treated soils. *Streptomyces*, abundant in soils amended with Nonpareil variety hulls and shell from before solar heating, was still 14-fold enriched two months post-treatment compared to control soils. *Micromonospora* and related taxa were also observed in high abundance in all solarized and biosolarized plots 58 days after biosolarization, perhaps due to the ability of these Actinobacteria to degrade lignocellulose and form heat-tolerant endospores (Reddy et al., 2013). Chloroflexi had been initially suppressed by the treatment, but after two months were enriched again in treated soils, indicating re-equilibration after the return of aerobic soil conditions (Simmons et al., 2014). The sustained elevation of polysaccharide-degrading taxa even after two months of treatment may also indicate a slow degradation of almond residues that has been associated with longer-term pest suppression (Akhtar and Malik, 2000).

4.4. Nematode abundance

The results of this study showed that solarization and biosolarization drastically reduced populations of nematodes in the top 30 cm of soil. After only nine days, near-zero *P. vulnus* and *M. xenoplax* numbers were detected in solarized soil, and no nematodes were detected in biosolarized soil. Previous studies found that soil amendments in conjunction with solarization controlled root knot nematodes better than solarization alone (Butler et al., 2012). Soil fumigants such as 1,3-dichloropropene can dramatically decrease free-living nematode populations within 30 days (Sánchez-Moreno et al., 2010), but bacterivorous nematodes can be resilient to this disturbance, unlike other feeding groups (Hodson et al., 2019; Sánchez-Moreno et al., 2010). Here, bacterial and fungal feeders were susceptible to solarization and biosolarization, with populations remaining low 9 through 99 days after application.

While temperature alone seemed sufficient to control nematodes at these depths, other mechanisms such as oxygen depletion, microbial shifts to favor organic acid accumulation, and enrichment of nematode antagonists may have improved efficacy at lower depths or for longer periods (Achmon et al., 2016; Browne et al., 2018; Oka, 2010). *Streptomyces* and Bacilli, enriched after soil was amended, are known to produced a diverse array of nematicidal volatile compounds that have been shown to parasitic nematodes in cultures (Gu et al., 2007). In addition to their capacity to produce organic acids, Specific Bacilli are known antagonists of nematodes: *Bacillus thuringiensis* produces thermostable toxins suppressive to nematodes (Walia et al., 2000) and *Bacillus subtilis* strains have been shown to reduce *M. incognita* egg mass on tomato roots by 62% (Adam et al., 2014). *Streptomyces* and Bacilli remained elevated in treated soils 99 days after treatment initiation. Solarization and biosolarization enriched for Betaproteobacteria such as the order Burkholderiales; previous studies found Burkholderia antagonism was one mechanism of pest suppression driven by soil amendments (Strauss and Kluepfel, 2015). Moreover, this taxa was associated with long term suppression of pathogens in avocado orchard soil amended with composted almond shells (Vida et al., 2016).

Tillage dramatically reduced all trophic groups of nematodes in all plots, including the control plots that received no amendment or solar heating. Preparing almond orchards for planting is a disruptive process that involves deep tilling and shaping raised berms where trees are planted (Flint, 2002). This degree of mechanical disturbance can decrease populations of phytoparasitic nematodes and shift nematode populations to become more dominated by bacterial feeders (Lenz and Eisenbeis, 2000; Sánchez-Moreno et al., 2006). Others have observed that tillage reduced populations of *Pratylenchus* spp. (Rahman et al., 2007; Thomas, 1978; Yeates and Hughes, 1990), but pest nematode populations slowly recover over time after tillage, in the absence of other control measures (Hodson et al., 2019). In some cases, continuous physical disturbance led to an increase in plant-feeding nematodes over time (Li et al., 2016). Longer term monitoring is required to characterize the true efficacy of biosolarization as a nematode control tactic. For example, some studies found that *Pratylenchus* populations did not differ between control and fumigated plots until two years after treatment application, at which time pest nematode populations had begun to recover from the deep tillage of orchard establishment (Hodson et al., 2019).

5. Conclusion

This study is the first report to indicate that biosolarization using almond processing byproducts can effectively increase soil temperature, promote biopesticidal compound accumulation, and promote control of certain phytoparasitic nematodes to at least 30 cm depth in a 9-day time frame, a considerably shorter duration that other fumigation alternatives. Soil heating likely played a significant role in nematode inactivation, as pest populations decreased in both amended and nonamended solar heated plots. While plots amended with hulls and shells significantly reduced *P. vulnus* compared to controls at day 9 of treatment, differences between solarized treatments and negative controls were not apparent until day 41. Microbial community analysis based on 16S rRNA gene sequencing revealed an enrichment of obligate and facultative anaerobic bacteria from the phyla Firmicutes in biosolarized and solarized soils, particularly in soil amended with Nonpareil variety hulls and shells. Soil amendments resulted in fermentative organic acid accumulation in concentrations sufficient to cause sub-lethal or lethal effects in soil nematodes. Nonpareil variety hulls and shells were more effective in producing organic acid biopesticides than those of the mixed pollinator varieties, possibly due to the presence of more labile material (i.e., sugars) in the hull-rich Nonpareil residues. The results of this field trial demonstrate that recycling agricultural waste streams as soil amendments potentially reduce the necessity of pre-plant chemical fumigants. Additionally, biosolarization using almond processing residues warrants investigation in other cropping systems.

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Declaration of competing interest

Rory Crowley is Chief Operations Officer and Executive VP of Research & Business Development at the Nicolaus Nut Company. He also served on the Strategic Ag Innovation Committee within the Almond Board of California.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104343.

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