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Organic management promotes natural pest control through altered plant resistance to insects

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Reduced insect pest populations found on long-term organic farms have mostly been attributed to increased biodiversity and abundance of beneficial predators, as well as to changes in plant nutrient content. However, the role of plant resistance has largely been ignored. Here, we determine whether host plant resistance mediates decreased pest populations in organic systems and identify potential underpinning mechanisms. We demonstrate that fewer numbers of leafhoppers (*Circulifer tenellus*) settle on tomatoes (*Solanum lycopersicum*) grown using organic management as compared to conventional. We present multiple lines of evidence, including rhizosphere soil microbiome sequencing, chemical analysis and transgenic approaches, to demonstrate that changes in leafhopper settling between organically and conventionally grown tomatoes are dependent on salicylic acid accumulation in plants and mediated by rhizosphere microbial communities. These results suggest that organically managed soils and microbial communities may play an unappreciated role in reducing plant attractiveness to pests by increasing plant resistance.

Organic farming is characterized by management practices that promote soil biodiversity and beneficial ecological interactions to offset the need for synthetic inputs such as inorganic fertilizers and biocides. Pest and nutrient management in organic agriculture is largely accomplished through various diversification methods, including cover crops, crop rotations, trap crops and promotion of active soil microbial communities[1–5]. Although organic agriculture is often thought to be less productive in terms of yield as compared to conventional farming, it offers great potential to enhance ecosystem services and agricultural sustainability[5–7].

Accumulating evidence suggests that organic management practices also reduce pest populations and increase resilience to pest damage[8,9]. Decreased insect pests on long-term organic farms have largely been attributed to practices that limit pest build-up, increase predator biodiversity, and increase the numbers of beneficial insects[9–13]. The nitrogen contents of plants grown on organic farms are often lower than those of conventional systems[11,12]. Plants that are nitrogen-limited are often less attractive to herbivores, which could also explain the lower pest pressure observed in organic systems[12,14,15]. However, very little is known about the impact of organic management for plant defence capacity.

Organic management strategies can increase microbial activity and biomass in soils[1,2,16], alter microbial communities[17] and in some cases enhance plant associations with beneficial microbes in the rhizosphere[3,4]. Microorganisms that associate with plant roots play a critical role in resistance to abiotic and biotic stress[18–20]. Mycorrhizal fungi have been shown to induce plant systemic resistance[21,22] and can reduce susceptibility to pathogens[23] and herbivores[24]. Plant growth-promoting rhizobacteria commonly found in soil microbial pools, as well as commercial inoculants, induce defences and other physiological changes in the host plant that influence above-ground herbivores[19,25–28]. Despite the known interactions between organic management, plant–microbe associations and changes in crop resistance, the potential of these interactions to reduce pest damage in agricultural systems remains largely untapped.

In this study, we report that organic management influences pest populations through changes in plant resistance. We explore linkages between insect settling and performance, rhizosphere communities and phytohormones related to plant defence with tomato (*Solanum lycopersicum*) and the beet leafhopper (*Circulifer tenellus*), an important pest of California's processing tomato industry[29]. We demonstrate that tomatoes grown using conventional management are preferentially settled by leafhopper pests and have lower salicylic acid (SA) levels compared to tomatoes grown using organic management. Our results indicate that differences in insect preference were due at least partially to changes in SA accumulation and rhizosphere microbial communities. Understanding how soil management influences plant resistance and to what extent it helps create robust and resilient systems will provide growers with new pest management tools to improve multiple sustainability outcomes for agro-ecosystems.

Results

Organic management reduced insect populations and settling on tomatoes. To determine if management influenced plant attractiveness to insects, we collected tomato branches from organic and conventional fields at the long-term experimental site (Farm RR) at Russell Ranch (Davis, California, United States) and at three commercial sites (Farms F, M and S; Supplementary Table 1) in Yolo County (northern California) in 2017. Tomato branches were used to compare beet leafhopper settling preference for the leaves paired by field (organic versus conventional; see Supplementary Fig. 1 for design). Fewer leafhoppers settled on tomato leaves from organic fields at three out of the four sites compared to tomato leaves from conventional fields (Fig. 1a; Farm RR, ~50% less; Farm M, ~40% less; and Farm S, ~36% less). Next, we surveyed insect populations using sweepnet sampling in the same organic and conventionally

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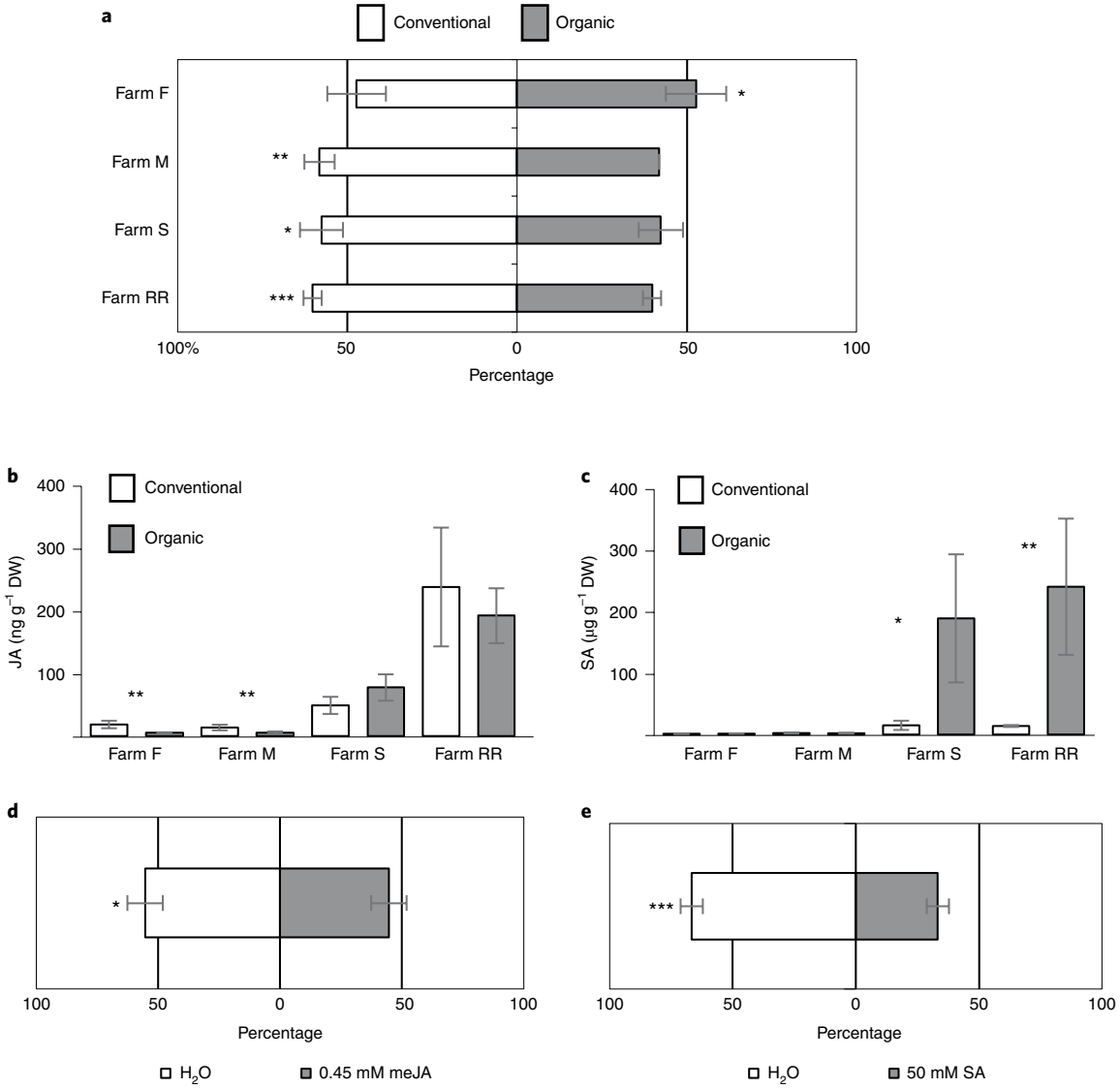

Fig. 1 | Organic management practices reduced insect settling and altered plant defence signalling pathways. a, Leafhopper settling preference for leaves collected from Farm RR and three commercial sites (Farms F, M and S) in 2017. **b**,**c**, JA (**b**) and SA (**c**) content in tomato leaves from organic and conventional fields at Farm RR and three commercial sites (Farms F, M and S) in 2017. **d**, Leafhopper settling on leaves induced with 0.45 mM of meJA or with water as a control. **e**, Leafhopper settling on leaves induced with 50 mM of SA or with water as a control. Mean ± s.e.m.; $n = 18$ for **a**, $n = 9$–24 for **b** and **c**, $n = 15$ for **d** and $n = 10$ for **e**. Binomial distribution test (**a**, **d** and **e**) and generalized linear model (GLM) at each site (**b** and **c**). $^{*}P < 0.1$, $^{**}P < 0.05$, $^{***}P < 0.001$. DW, dry weight.

managed tomato fields. We observed considerably fewer insects in organic fields compared to conventional fields at Farm RR (~2.5 times fewer) (Supplementary Fig. 2). No systematic differences in insect abundance were observed between organic and conventional fields at the other sites (Supplementary Fig. 1).

Organic management practices altered plant defence signalling pathways. The phytohormones SA and jasmonic acid (JA) are important regulators of plant defence and changes often influence insect preference[30,31]. To determine if organic management practices may be altering SA or JA accumulation in tomato, we measured both phytohormones in leaves collected from all four sites. Although site-level variation was observed, leaves from organic fields had higher SA levels than those from conventional fields ($F_{1,\ 237.6} = 6.30$, $P = 0.012$), driven by differences at Farms RR and S (Farm RR, ~17 times more, $F_{1,\ 109} = 4.56$, $P = 0.035$; and Farm S, ~12 times more, $F_{1,\ 40} = 3.66$, $P = 0.063$) but there were no differences between organic and conventional fields at Farms F and M (Fig. 1c). No main effect of soil management on JA levels was observed ($F_{1,\ 226.69} = 0.48$, $P = 0.490$) but leaves from conventional fields on Farms F and M had elevated JA levels compared to the organic paired fields (Farm F, about three times more, $F_{1,\ 36} = 6.59$, $P = 0.015$; and Farm M, about two times more, $F_{1,\ 40} = 5.01$, $P = 0.031$) (Fig. 1b). To determine if changes in SA or JA may be mediating leafhopper preference, we measured leafhopper settling on tomato leaves that had been induced with SA or methyl jasmonate (meJA) compared to uninduced leaves in settling bioassays. Leafhoppers preferred to settle on control leaves compared to meJA- or SA-induced controls (Fig. 1d,e).

Organic management practices altered plant and soil nutrient content. Organic and conventional management systems have drastically different soil fertility management. This can result in large

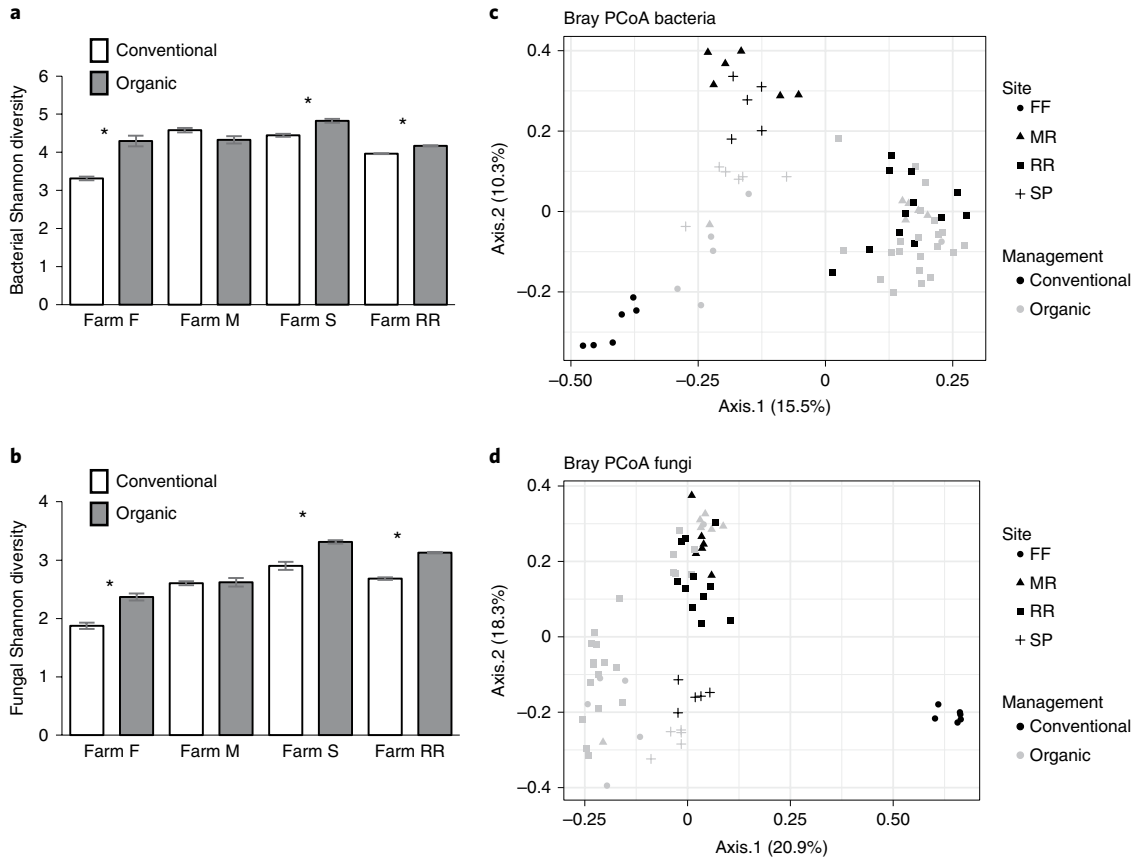

Fig. 2 | Bacterial and fungal diversity and community composition differ among organic and conventional sites. Rhizosphere microbial communities from processing tomato roots were sampled from paired organic or conventional fields at four sites, and bacteria and fungi were characterized using 16S and ITS metabarcoding. **a**,**b**, Bacterial (**a**) and fungal (**b**) Shannon diversity is greater in organic than conventional fields at three sites. **c**,**d**, Bacterial (**c**) and fungal (**d**) community composition is visualized using principal coordinates analysis (PCoA) based on Bray–Curtis dissimilarity and differs among fields (PerMANOVA $P<0.001$), between organic and conventional fields ($P<0.001$) and according to the site-management interaction ($P<0.001$). Mean ± s.e.m.; $^*P<0.05$.

variation in plant and soil nutrient content, which can directly or indirectly affect soil microbial populations and insect preference[32]. We measured 14 different nutrients in leaves and soil collected at all four paired sites (Supplementary Tables 2 and 3). There was considerable variation in plant nutrient content across the treatments and sites (Supplementary Tables 2 and 3). Although nitrogen is one of the most limiting plant nutrients for insect herbivores and often drives patterns of insect preference[33], there was no consistent difference in C:N ratios in leaves between organic or conventional fields (Supplementary Table 2). Contrary to our expectations, nitrogen content in leaves was reduced in conventionally grown plants compared to organic at three of the four sites (Supplementary Table 2; Farms RR, S and F, ~2.3 times more), however this did not correlate with insect settling data. Sulfur concentrations in leaves were higher in organically grown plants compared to conventional plants at all four sites (Supplementary Table 2; Farm RR, ~1.8 times more; Farm S, ~2.9 times more; Farm M, ~1.4 times more; Farm F, ~2.3 times more). Copper concentrations were higher in organically grown plants compared to conventional at three of the four sites (Supplementary Table 2; Farm RR, ~1.3 times more; Farm S, ~1.2 times more; and Farm M, ~1.3 times more). Conventionally managed soil had reduced total carbon, organic matter and sodium, and elevated magnesium, at three of the four sites compared to organically managed soils (Supplementary Table 3).

Rhizosphere microbial composition is associated with changes in plant nutrients and defence. Rhizosphere bacteria and fungi, which differ with management[17], have been previously shown to influence plant health by regulating defence compounds against insect herbivores[34]. We examined if differences in rhizosphere communities were associated with observed differences in plant defence hormones in plants from the different farms. For both bacteria and fungi, tomato rhizosphere communities were more diverse under organic management at three of four sites (Fig. 2a,b). Sites differed in microbial communities but organic and conventional communities remained distinct from each other at all sites (Fig. 2c,d). Mantel tests were conducted to identify correlations among plant variables (nutrient, biomass, and hormone data) and microbes (bacteria or fungal composition). Plant variables were significantly associated with microbial community composition redundancy analysis (RDA); Mantel bacteria $r=0.33$, $P<0.001$; fungi $r=0.51$, $P<.001$). Because plant response variables were also associated with soil parameters ($P<0.001$), we conducted a partial Mantel test to examine if microbial community composition remained significant after soil nutrients were included in the model. This analysis revealed that the structure of the microbial community, in particular the fungal community, was significantly associated with variation in plant traits including nutrient content and SA concentration, even when variation in soil nutrition was considered (partial Mantel $P<0.001$).

To examine if any specific microbial orders were associated with variation in plant SA concentrations, we performed a differential abundance analysis. Plants with higher SA concentrations also hosted higher relative abundances of Micrococcales (Actinobacteria) but lower relative abundances of Burkholderia,

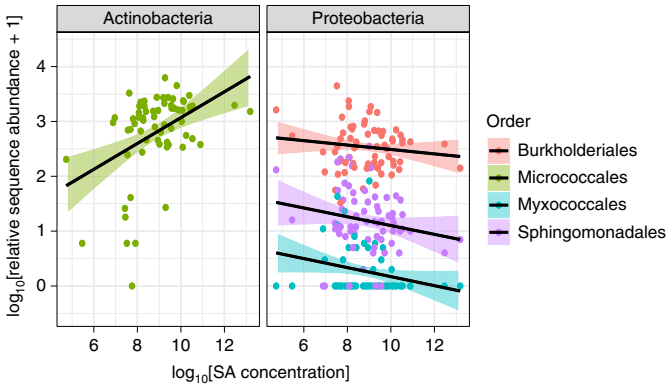

Fig. 3 | Relative abundance of bacterial orders associated with changes in SA. Relative abundance of root-associated bacterial orders from 16S survey are related to the SA concentration in tomato leaves. Relationships are positive for Micrococcales in the phylum Actinobacteria (false discovery rate (FDR) < 0.001), but negative for the members of the Burkholderiales, Myxococcales and Sphingomonadales in the phylum Proteobacteria (all FDR < 0.05). Lines represent best-fit linear regression models. Bacterial data are separated by phyla, and points are coloured by bacterial order.

Sphingomonadales and Myxococcales (Proteobacteria; Fig. 3). This correlation suggests specific changes in the composition of rhizosphere microbiome are associated with variation in plant foliar SA concentration.

Soil biota drives differences in leafhopper preference and plant resistance. To isolate the relative importance of different soil components (physical structure, biological communities and chemical properties) in plant resistance, we performed a series of bioassays in the laboratory using rhizosphere soil collected from Farm RR, the site where we observed the largest differences in insect populations, insect preference and plant resistance (Farm RR, Fig. 1 and Supplementary Fig. 1). Another reason we chose to focus on Farm RR for the soil slurries experiments was because it consists of three replicated fields for each management regime[35]. To remove effects of soil physical properties, collected soils were washed and slurries from organic or conventional soils were used to inoculate tomato plants before bioassays. Roughly 1.5 times as many leafhoppers settled on plants inoculated with conventional slurries compared to organic slurries (Fig. 4a), consistent with laboratory and field experiments (Fig. 1 and Supplementary Fig. 1). Leafhopper survival rate was about three times higher by day 6 on plants inoculated with slurries from the conventional fields, despite a sharp decline in survival over time in both treatments (Fig. 4b). These results suggest that management-based regulation of plant resistance and insect preference may occur via soil biological or chemical parameters rather than physical properties at Farm RR.

Next, we investigated if soil biota within organically managed soils affect insect preference. Half of the slurry solution for each treatment (organic and conventional) was autoclaved to kill all microbes. When slurries were autoclaved (no live microbes), no difference in leafhopper settling preference was observed (Fig. 4a). These results suggest a critical role of soil microbes in mediating insect preference. Moreover, plants grown on the biologically active organic soil slurry (live) had a 25% higher SA concentration compared to conventional but no difference in the amount of SA was found when plants were inoculated with autoclaved slurries (Fig. 4c). Levels of JA did not differ between treatments (Fig. 4d). No significant differences in nutrient content between control and autoclaved soil slurries or organic and conventional treatments were observed (Supplementary Table 5).

To determine if changes in SA or JA are responsible for differences in insect preference, we performed additional soil slurry experiments with NahG tomatoes, which are not able to accumulate SA and activate SA-mediated defences, and *def1* tomatoes, in which JA signalling and related defences are compromised. Leafhoppers had no preference between NahG plants grown using organic versus conventional soil slurries (Fig. 4e), while leafhoppers preferentially settled on *def1* and wild-type (WT) control plants that were grown in conventional soil slurries compared to the same plants grown in organic soil slurries (Fig. 4e,f). Differences were not as large for the *def1*/castlemart experiments (Fig. 4e), possibly due to cultivar differences or due to these experiments being conducted over a year after soil collection. These results collectively suggest that differences in microbial communities may mediate changes in insect preference and plant resistance levels through changes in SA signalling.

Differences in soil properties drive changes in plant resistance across plant species. To determine if the impact of organic soil slurries on insect performance is conserved across plant species, we performed additional slurry experiments with *Myzus persicae*, a generalist hemipteran aphid and three additional plant species: carrot (*Daucus carota*), *Arabidopsis thaliana* and potato (*Solanum tuberosum*). Our results show that *M. persicae* reproduction is reduced on all three plants when grown with organic soil slurries compared to conventional (Fig. 5a; *D. carota*, ~40% less; *A. thaliana*, ~70% less; and *S. tuberosum*, ~75% less). Lastly, we looked at the fitness of another type of herbivorous pest of tomato, *Manduca sexta*, which feeds by chewing, as opposed to phloem feeding, as hemipterans do. There was no significant difference in dry weight of *M. sexta* between treatments (Fig. 5b).

Discussion

Our results demonstrate that fewer leafhopper pests settle on tomatoes grown on long-term organic farms (Fig. 1a) compared to conventionally grown plants. Previous studies have shown that differences in plant nutrient content can alter herbivore feeding preference and performance[14], however, there were no consistent differences in nutrient content between the organic and conventional fields across sites in our study (Supplementary Table 2). The largest differences in insect settling and insect populations were at Farm RR, where fewer leafhoppers settled and fewer insects were observed on plants grown organically compared to conventionally (Fig. 1a and Supplementary Fig. 2). No significant differences in carbon or C:N ratios were observed in these plants and, surprisingly, tomato leaves from the organic fields at Farm RR had higher nitrogen content compared to conventional plots (Supplementary Fig. 2). We show that organic soil management promoted SA accumulation, which influences plant–insect interactions (Fig. 1b–e). We demonstrate that changes in SA and insect preference are dependent on shifts in soil microbial communities associated with long-term organic management (Figs. 1–4) and that these findings may be applicable to multiple plant systems (Fig. 5). Although soil microbial effects on plant pathogens and soil-borne pests in agro-ecosystems are appreciated and relatively well-described, here we show that soil microbial communities probably play an unappreciated role in depressing insect pest populations through changes in plant resistance. These results suggest that more sustainable insect management strategies can be developed through soil health management.

Plants have evolved complex immune systems to protect themselves against pests and pathogens. Previous studies have identified SA in mediating plant defence responses to hemipterans[36–38], while changes in JA and ethylene have been largely connected to defences against chewing insects[30]. Consistent with this work, we observed an impact of organic soil management on plant resistance to multiple hemipterans (Figs. 1, 4 and 5) and no impact on the chewing

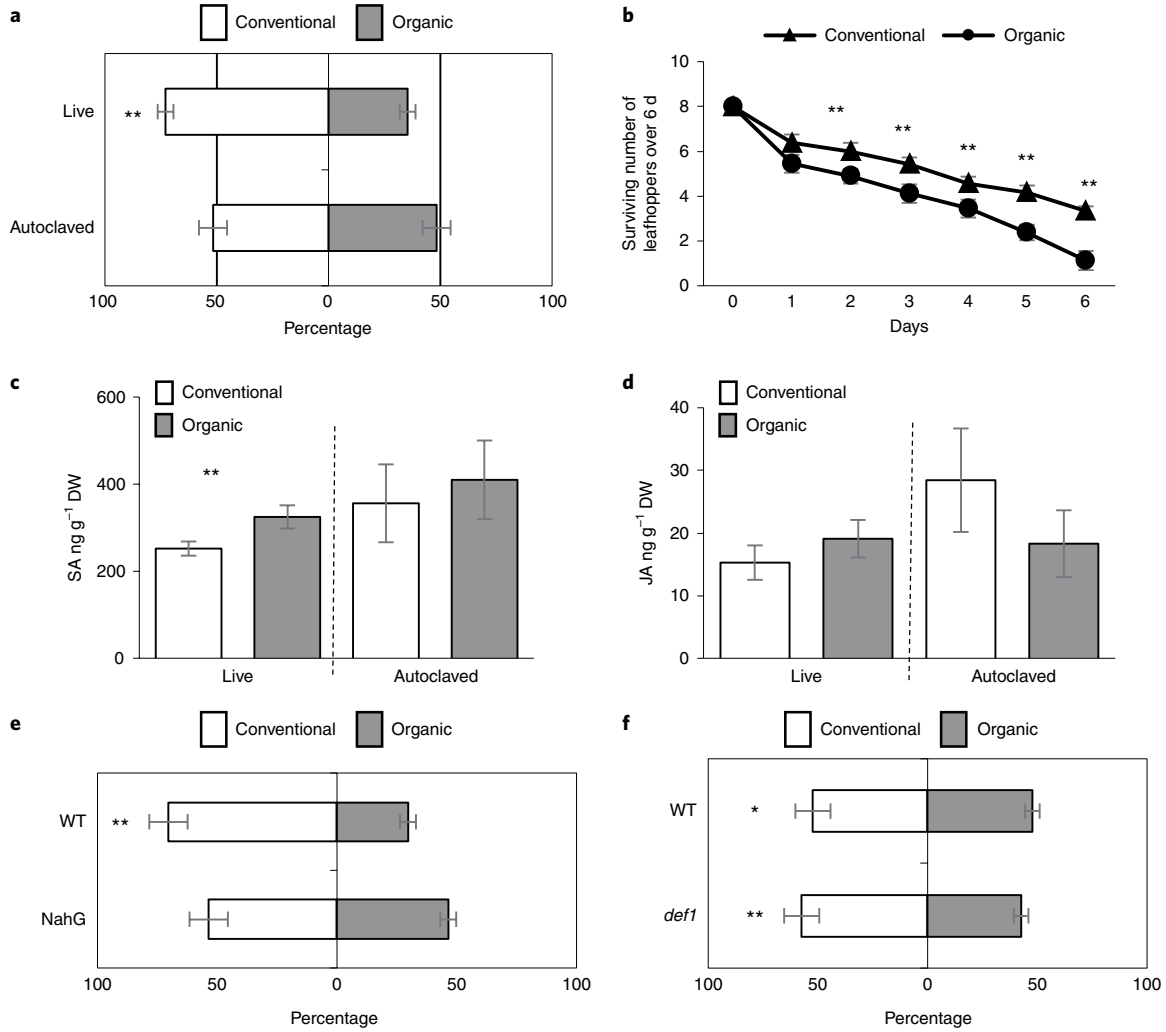

Fig. 4 | Soil biota drives differences in leafhopper populations, preference and plant resistance. a, Leafhopper settling preference for tomatoes grown with a soil slurry prepared from conventional and organic rhizosphere soil from Farm RR that was untreated (live) or autoclaved. **b**, Leafhopper survival on tomatoes grown with a soil slurry prepared from conventional and organic rhizosphere soil from Farm RR. **c**,**d**, SA (**c**) and JA (**d**) content of leaves from tomatoes grown with a soil slurry prepared from conventional and organic rhizosphere soil from Farm RR that was untreated or autoclaved. **e**,**f**, Leafhopper settling preference for leaves from WT moneymaker or NahG (**e**) and WT castlemart or *def1* (**f**) plants grown in conventional and organic soil slurries. Mean ± s.e.m.; $n = 36$ for **a**, $n = 9$ for **b**, $n = 6$–9 for **c** and **d**, and $n = 9$–12 for **e** and **f**. Binomial distribution test (**a**, **e** and **f**) and Student's *t*-test (unpaired and two-tailed) (**b**, **c** and **d**) were performed to determine significant differences. $^{*}P < 0.1$, $^{**}P < 0.05$.

caterpillar *M. sexta* (Fig. 5), when SA levels were elevated. Despite the induction by JA and SA of alternative resistance pathways, there is evidence to suggest that considerable crosstalk exists and that both can contribute to resistance against the same attacker. For example, aphids were shown to induce the JA pathway in addition to the SA pathway and to also be susceptible to JA-mediated plant defences[39–41]. We observed that treating plants with meJA repelled leafhoppers in laboratory bioassays (Fig. 1d), although there was no significant difference in JA levels in plants from Farm RR (Fig. 1b) or in plants inoculated with biologically active or inert slurries (Fig. 4d). Furthermore, leafhoppers were still repelled from JA-deficient plants grown in organic soil slurries as compared to slurries from conventionally managed soil (Fig. 4f). Together, these results suggest that changes in SA are primarily driving changes in leafhopper–plant interactions in our system.

Despite knowledge of the essential roles that microbe communities play in agro-ecosystems, we still have a limited understanding of the direct benefits that microbial diversity and composition provide in terms of plant health and resistance to insect pests. Organic sites in our study exhibited an over-representation of specific microbial taxa which are known to be involved in the induction of plant defences[41–43], including *Pseudomonas*, *Ochrobactrum*, *Glutamicibacter, Bacillus, Ralstonia* and others (Supplementary Table 4). Furthermore, microbial taxa from the bacterial order Micrococcales were positively associated with variation in plant SA concentrations in our field experiments (Fig. 3), while members of the Proteobacteria (orders Burkholderiales, Myxococcales and Sphingomonadales) were negatively associated with plant SA. The presence of these particular taxa may promote plant-induced resistance[44,25] although plant induction of SA, or changes in the soil environment may also modulate microbial interactions directly[45]. In our study, organically managed soils had higher organic matter and carbon, and reduced magnesium, compared to paired conventionally managed soils at three of the four sites (Supplementary Table 3). Changes in soil chemistry or nutrient availability in organic soils may contribute to enhanced plant defence responses through

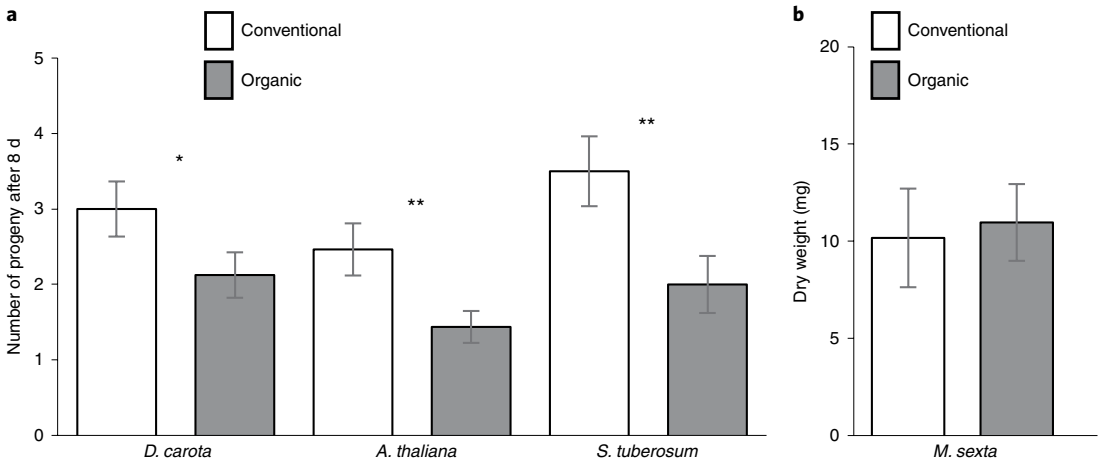

Fig. 5 | Soil biota drive differences in hemipteran population growth across plant species. a, *M. persicae* reproduction on carrot (*D. carota*), *Arabidopsis* (*A. thaliana*) and potato (*S. tuberosum*) inoculated with soil slurries prepared from conventional and organic rhizosphere soil at Farm RR. **b**, *M. sexta* dry weight when reared on tomatoes inoculated with soil slurries prepared from conventional and organic plots at RR. Mean ± s.e.m.; $n = 12$–18 for **a** and $n = 9$–13 for **b**. Student's *t*-test (unpaired and two-tailed) (**a**,**b**) was performed to determine significant differences. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

changes in the soil microbiome[46]. Although the particular microbial taxa or community composition underlying this effect are currently unknown, this study suggests that organic practices in agro-ecosystems can promote plant defences against insect pests through changes in soil microbiota.

While it is known that soil microbes can influence above-ground plant–insect interactions through changes in plant signalling and defence[47–50], the management techniques that promote beneficial microbial populations remain poorly understood. Our data demonstrate that organic management practices alter soil microbial communities, alter plant defence potentials through changes in SA and influence hemipteran settling and performance (Figs. 1–3). Although we cannot distinguish effects of diversity per se versus compositional changes or specific taxa underlying this effect, laboratory assays strongly implicate soil microbiota in plant protection (Fig. 4). Farm surveys support the hypothesis that organic practices can influence insect preference at large scales but also suggest that variation in practices or local conditions may moderate these results in some locations (Figs. 1 and 2 and Supplementary Fig. 1). Although further work is required to dissect the particular mechanisms involved, including investigation of microbial strains or signals, our results suggest that healthy soils cultivated using organic practices can promote sustainable and resilient yields in the face of hemipteran pest pressure. Organic agriculture therefore holds great potential to broadly improve the delivery of key ecosystem services critical for the sustainability of farming systems and the resilience of the food supply.

Methods

Field study sites. Field studies took place during the 2017 growing season at the organic and conventional long-term treatments of the century experiment established in 1993 at Farm RR (ref. [35]). Three additional field studies took place on commercial sites in Yolo County in 2017. In these studies, paired long-term organic and conventional processing tomato fields were compared. At Farm RR, paired site refers to both the organic and conventional replicated fields on the research farm. At Farm RR, each field was 0.4 ha and organized in a randomized block design[35]. We used three replicated fields for each treatment from this site. For the other farms, paired site refers to organic and conventional fields being managed by the same grower at the same site, and where tomato was sown at the same time. Details of field management strategies are available in Supplementary Table 1. At each field, 12 plants were collected in an 'M'-shaped sampling pattern for settling bioassays, phytohormone extraction, plant and rhizosphere soil nutrients and rhizosphere DNA amplicon sequencing. Details on soil chemistry for each site are available in Supplementary Table 3.

Insect sweepnet collections. Insect populations were sampled at the study sites described earlier, 3 weeks after transplanting. To standardize collections, six sweepnet collections were performed per field and each collection consisted of ten sweeps up and down the field within an eight-row boundary along the transect. Samples were bagged and frozen until insects were counted and sorted to order.

Plants and growth conditions. Moneymaker cultivar tomato, castlemart cultivar tomato, transgenic NahG tomato in the moneymaker background[51] and the JA-deficient *def1* mutant tomato in the castlemart background[52] were used in laboratory studies, while Heinz 8504 cultivar tomato was used for all Russell Ranch experiments. For commercial farms, tomato cultivar varied by site (Supplementary Table 1). For *Arabidopsis*, potato and carrot experiments, Col-0, and Desiree cultivars and Sativus subspecies were used respectively. For controlled experiments, plants were grown in Conviron growth chambers under 25/20 °C day/night with a photoperiod of 16/8 h day/night at a relative humidity of 50% and a light intensity of 200 mmol m^{-2} s^{-1}. The same growth conditions were used in all subsequent experiments.

Insects. Avirulent beet leafhoppers, *C. tenellus* were reared on beet (*Beta vulgaris*) under controlled conditions (28/24 °C day/night with a photoperiod of 16/8 h day/night). Aphids (*M. persicae*) were reared on potato under controlled conditions (28/24 °C day/night with a photoperiod of 16/8 h day/night). *M. sexta* eggs were ordered from Carolina Biological Supply and held at room temperature until hatching. Neonates were immediately used in bioassays under controlled conditions and not reared.

Settling bioassays from the field. Tomato branches were collected from the conventional and organic fields mentioned earlier, 3 weeks after transplanting and immediately used for settling bioassays. Avirulent beet leafhoppers were collected and starved for 2 h before the experiment. A cage was constructed that allowed an organic tomato leaf to be sealed at one end and a conventional leaf at the other (Supplementary Fig. 1). Developmentally similar leaves were selected to standardize the assay. Five avirulent beet leafhoppers were introduced in the centre of the cage equidistant to both leaves. Leafhopper position was recorded 2 h after release. This time was chosen based on preliminary experiments where leafhopper settling was measured at multiple time points over 24 h. The settling bioassays were conducted in the dark so leafhoppers could not make a settling based on visual cues. Each experiment was repeated using 18 independent branch pairs from each site (organic versus conventional). See Supplementary Fig. 1 for experimental design of the settling experiment.

Phytohormone extraction and liquid chromatography tandem-mass spectrometry (LC–MS/MS/MS) analysis. During sweepnet collections, developmentally similar true leaves from 12 separate 3-week-old tomato plants in each field were removed and immediately frozen in liquid nitrogen. For laboratory experiments, developmentally similar true leaves were removed from tomato plants 3 weeks post-emergence and immediately frozen in liquid nitrogen. Samples were stored at −80 °C until they were lyophilized. Subsequent tissue was then weighed, ground in a Harbil paintshaker and extracted according to Casteel et al.[53]. Samples were run on an Agilent 6420A Triple-quadrupole MS with an Infinity II HPLC

(Agilent Technologies). Quantification was based on an isotopically labelled internal standard that was spiked in each sample before the extraction. At least nine samples were measured for each treatment. For phytohormone quantification no insects were used, which means our data represent 'constitutive levels'; however, all field samples have some level of damage.

Settling bioassays with hormone-induced plants. Tomatoes were treated 3 weeks after emergence. For SA induction, 2 g of SA was dissolved in 250 ml of H_2O containing 0.01% TWEEN 20 and sprayed on plants until run off. For JA induction, a solution of meJA (0.45 mM meJA with 0.01% TWEEN 20) was used. Control plants were treated with H_2O containing 0.01% TWEEN 20. All settling bioassays were conducted as described above and 24 h after chemical treatment. Each experiment was repeated 10–15 times. See Supplementary Fig. 1 for experimental design of the settling experiment.

Plant, soil and soil slurry nutrient analysis. Composited dried and homogenized soil and plant samples were analysed for total nitrogen (N) and carbon (C) via combustion analysis[54]. Soil nitrate was measured using a flow injection analyser[55]. Soil extractable phosphorus (P) was determined according to Olsen and Page[56]. Soil organic matter content was determined via the loss-on-ignition method[57]. Soil pH was measured using a saturated paste extract. Soil slurries and plant nutrients were measured using inductively coupled plasma atomic emission spectroscopy or ICP-AES (ref. [58]) at the UC Davis and University of Pennsylvania analytical laboratories, respectively.

Rhizosphere DNA extraction and amplicon sequencing. During sweepnet collections, 12 plants were excavated from each field 3 weeks after transplanting as described earlier. In the laboratory, roots from each plant were pooled into six subsamples. Root fragment subsamples were shaken briefly to remove adhering soil, then shaken for 90 min in 0.9% NaCl and 0.01% TWEEN 80, then extracted using the MoBio PowerSoil Kit (Qiagen). At least 100 ng of rhizosphere DNA from each sample was sent for library preparation and sequencing using MiSeq at Dalhousie Integrated Microbiome Resource (IMR) facility. The V4–V5 region of the 16S ribosomal RNA region was sequenced to characterize bacterial communities and the internal transcribed spacer (ITS) region of the rRNA gene was sequenced to characterize fungal communities[59]. Negative controls from the extraction buffer and kit materials were also submitted but no reads were recovered. Reads were error-corrected and assembled into amplicon sequence variants (ASVs) using DADA2 v.1.8 (ref. [60]) and assigned taxonomy using SILVA v.128 for bacteria[61] and UNITE database (2017 release) for fungi[62]. Taxa without a taxonomic assignment, or assigned to archaea, mitochondria or chloroplasts, were removed from datasets. Those not assigned to the kingdom Fungi were removed from the fungal dataset. Sequence abundance was rarefied to 15,310 sequences per sample for bacteria and 13,000 per sample for fungi and all sampling curves approached saturation.

Settling bioassays with soil slurries. Rhizosphere soil was collected from the replicated conventional and organic fields at Farm RR. We chose to focus on Farm RR as a source of soils for our slurry experiment because: (1) results were most contrasting at this site while being representative of other farms and (2) it consists of three replicated fields for each management regime with consistent management for the last 25 yr (ref. [35]). Soil slurries were prepared by mixing sampled soil with ¼ strength Hoagland's nutrient solution at 1 g soil to 5 ml solution for 1 h at 350 r.p.m. The solution was then left to settle for 1 h at room temperature and centrifuged at 500 r.p.m. for 5 min. After centrifuging, the supernatant was removed and either autoclaved at 120 °C for 30 min three times or left untreated. The soil slurries were added at the time of sowing to sterilized soil at a rate of 15 ml twice per week until the settling, reproduction or survival experiments were performed 3 weeks after seedling emergence. This methodology was used for all plant species.

Survival and reproduction bioassays. Tomatoes were grown in sterile University of California potting mix supplemented with soil slurries as described above. Three weeks after tomato emergence, eight adult *C. tenellus* were installed on a single leaf and survival was recorded daily over 6 d. Each experiment was repeated at least twice. For reproduction bioassays *D. carota, A. thaliana* and *S. tuberosum* were grown in sterile soil supplemented with soil slurries as described above. At 3 weeks post-emergence, one adult *M. persicae* aphid was placed on a leaf. After 24 h, all aphids except one nymph were removed. After 9 d, the progeny of the founder nymph, which was now an adult, were counted to determine reproduction. Each experiment contained at least six replicates and was repeated at least two separate times.

***M. sexta* weight gain.** After *M. sexta* emerged from eggs, neonate larvae were immediately moved to cages with a paintbrush. Cages were installed on 3-week-old tomatoes, post-emergence, that were grown in sterile soil supplemented with soil slurry twice as described above. One week later all caterpillars were removed, freeze dried, and weighed. Each experiment was repeated at least twice with at least nine replicates each.

Statistical analysis. All statistics were conducted using R (v.3.2.2) (ref. [63]). Assumptions of homogeneity and normal distribution of residuals were checked and data were transformed when appropriate to improve homoscedasticity or non-parametric tests were used.

Insect counts from sweepnets, soil properties, plant chemistry, insect settling, insect reproduction and insect survival. A normal distribution could not be achieved for the insect count data so the more conservative Wilcoxon–Mann–Whitney tests were used to determine the impact of farm management on total number of Arthropods collected in sweepnets. One-way analyses of variance using Tukey's honestly significant difference post hoc tests were used to determine the impact of management on soil properties at each paired site. For data gathered in a nested fashion (multiple replicates from plots within a site) we used a generalized mixed model using linear regression in lme4 with plot nested within management and site as a random effect[64]. Specifically, a glmm was used to assess the impact of management on phytohormone levels and plant nutrition, with predictors indicated above. Insect settling data were analysed with binomial regression to determine the impact of soil management, chemical treatment and mutants on insect settling. Student's *t*-tests (unpaired and two-tailed) were performed to determine the impact of farm management on insect reproduction and survival in soil slurry experiments in the laboratory. Statistical differences were determined for settling assays using a binomial test assuming the null hypothesis of no difference between the treatments.

Correlations among plant, soil and microbial variables. Mantel tests were conducted to identify Pearson correlations among plant, soil and microbial variables. Plant variables included shoot and root dry weight, foliar nutrient concentrations (Supplementary Table 2) and log-transformed SA and JA concentrations. Soil variables included all measured soil nutrients (Supplementary Table 3). Bray–Curtis dissimilarity matrices were calculated separately for bacterial and fungal ASV tables. Samples within each farm were used as replicates ($n = 12$ samples/site, with $n = 6$ samples per field). Scaled Euclidean distance matrices were calculated for plant and soil variables. Correlations between all pairs of matrices were tested for significance using permutation (mantel() function of vegan package[65]. Partial Mantel tests were conducted for plant, soil and bacterial matrices and plant, soil and fungal matrices to determine whether plant or soil variables predicted microbial community composition if the other category of variables was held constant (mantel.partial() function of vegan package).

Differential abundance and indicator species analysis. We used differential abundance analysis (DESeq2 package)[66] to examine if the relative abundance of any bacterial and fungal orders varied among plants with different SA concentrations. Order-level data were used because relative abundance at lower taxonomic ranks was characterized by absence of taxa across sites. To control for variation in SA among sites, we calculated residuals with site only as a predictor. SA residuals were log transformed and used as continuous predictors in the DESeq2 analysis. Orders whose abundance varied significantly ($P < 0.05$) were identified using the Wald test. All mixed models, multivariate analyses including non-metric multidimensional scaling (NMDS), RDA and Mantel tests, and differential abundance analyses were conducted using R (v.3.2.2) and implemented in RStudio[67].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data that support these findings are available from C.L.C., A.G. and R.L.V. upon request. The raw sequencing dataset is available at the NCBI SRA data repository under the project accession number PRJNA539989.

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Author contributions

R.B., A.L.C., J.E.S, C.L.C, R.L.V. and A.I. conducted most of the experiments and analysis. C.L.C., A.G. and R.L.V. designed all experiments and directed the project. R.B., C.L.C., A.G. and R.L.V. wrote the paper with comments and input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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