



Solid vermicompost and its liquid derivative exhibit strong biocontrol properties against *Myzus persicae* aphids on sweet pepper

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Abstract

Vermicomposting is a biotechnique that relies on earthworms to convert organic waste into a humus-like material, rich in nutrients, plant growth stimulants and beneficial microbes, known as vermicompost. As part of a policy of recycling organic waste, vermicomposting is increasingly practiced on a large scale around the world, becoming a promising economic sector in the move towards more sustainable agricultural practices. In addition to improving soil fertility, vermicompost may have the potential to protect plants against disease and pests, but this issue has been addressed only superficially. In this study, we addressed this issue by testing the biocontrol properties of solid and liquid forms of vermicompost on the green peach aphid *Myzus persicae* feeding on sweet pepper. Our results show that vermicompost treatment has a range of adverse effects on aphids, including reduced survival and fecundity rates, as well as repellent activity. Treatment with vermicompost tends to reduce the growth of aphid populations and improve the growth of the plants that are attacked. We chemically mapped liquid vermicompost and found it to be rich in antioxidants and phytohormones likely to improve plant health. Using a metabarcoding approach, we found that both solid and liquid vermicompost exhibit rich bacterial and fungal communities, but with a few dominant taxa that could contribute to vermicompost's biocontrol properties. Overall, our study shows that different forms of vermicompost can be effective aphid control agents and paves the way for investigating the modes of action and optimizing the use of vermicompost according to the diversity of agricultural practices.

Keywords Earthworms · Vermicomposting · Organic fertilizer · Pest control · *Myzus persicae* · Waste management

Introduction

The increase in food demand and consumption due to global population growth generates huge quantities of organic waste (food waste, livestock products, paper and wood waste, etc.), which can have adverse environmental, social and economic

consequences if not properly treated (Papargyropoulou et al. 2014). At the same time, global population growth requires an increase in agricultural production, which in turn is a source of significant organic waste streams (Davis et al. 2016). To meet this dual challenge, waste management methods must therefore evolve to enter a more virtuous circle. Given that organic waste is an abundant reservoir of valuable organic matter and plant nutrients, one strategy is to integrate it into a sustainable circular management system in order to transform it into high-value materials for agriculture (Rosemarin et al. 2020). In this context, biological processes such as composting and vermicomposting are now widely recognized as effective ways of converting organic waste into nutrient-rich fertilizers and soil conditioners (Zhou et al. 2022). Both are aerobic processes, in which organic waste is biologically degraded by indigenous microorganisms and transformed into a stabilized and sanitized humus-like material (Partanen et al. 2010). Vermicomposting specifically involves earthworms interacting with microorganisms for the

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production of a fairly homogenous, humus-like final product called vermicompost (Fornes et al. 2012; Lim et al. 2015). Both practices offer environmental and economic benefits such as reduced greenhouse gas emissions, land conservation through improved biodiversity and soil fertility, and reduced use of chemical fertilizers (Sharma et al. 2019). However, compared to compost, vermicompost is considered more cost-effective as it can be produced in less time, is more nutritious (e.g. richer in nitrogen, potassium and calcium), has lower electrical conductivity (EC) and phytotoxicity, contains more microorganisms and phytohormones, contains fewer pathogens and heavy metals, and contributes to greater plant growth and yield (Yatoo et al. 2021). In addition, vermicompost can be used in solid (vermicast) or liquid form (e. g. vermicompost extract, vermicompost teas and vermiwash depending on the manufacturing process): while solid vermicompost is a nutrient-rich manure that acts as a biofertilizer, restoring soil nutrients, stabilizing the soil and improving its long-term fertility, liquid derivatives act more as biostimulants concentrated in microorganisms and plant hormones that promote crop growth (Kiyasudeen S et al. 2016; Rehman et al. 2023). These different forms offer a range of applications tailored to the type of agricultural practice targeted (e.g. open field versus greenhouse cultivation, soil/in-ground versus soilless) (Lim et al. 2015; Arancon et al. 2019).

Because of its benefits for a more sustainable agriculture, vermicompost is increasingly used, particularly in organic farming, and vermicomposting is now practiced on a large scale around the world, becoming a promising economic sector (Dey Chowdhury et al. 2023; Kavitha 2023). However, a growing number of studies suggest that the benefits of vermicompost are not limited to its nutritional dimension. Indeed, it has a wide range of indirect effects on plant growth, including the control or suppression of diseases, parasitic nematodes and other pests (Simsek-Ersahin 2011; Yatoo et al. 2021). For example, it was reported over twenty years ago that vermicompost can significantly inhibit infection of tomato plants by *Fusarium oxysporum* f. sp. *Lycopersici*, with the protective effect increasing in proportion to the rate of vermicompost application (Szczech 1999). Foliar spraying of vermicompost extracts tends to reduce *Phytophthora infestans* infection of tomato plant leaves, stems and fruit (Zaller 2006) and vermicompost application tends to suppress fusarium root rot in American ginseng (Tian et al. 2021). It is assumed that the microbial dimension of vermicompost play a pivotal role in its biocontrol capacities. This hypothesis is supported by the fact that vermicompost enriched with microorganisms tends to have enhanced biocontrol capabilities, whereas sterilized vermicompost tends to lose its ability to control plant pathogens (Chaoui et al. 2002; Rao et al. 2017; dos Santos Pereira et al. 2020). Vermicompost treatment has also been shown to control

parasitic nematodes and arthropod pests in field and greenhouse crops, including root-knot nematodes of the genus *Meloidogyne*, caterpillar and beetle pests, spider mites, aphids and mealybugs (Arancon et al. 2007; Edwards et al. 2010b; Xiao et al. 2016). It is assumed that these biocontrol properties result from a boost to plant defenses by vermicompost, but the exact modes of action are still unknown and, in general, the biocontrol properties of vermicompost have only been touched upon.

One of the difficulties in testing the properties of vermicompost is to work with a product whose composition tends to remain stable over time: this is a sine qua non for effective use in agriculture, but also for conducting sound experiments. Strict control of environmental parameters, combined with the use of a continuous-flow system and a specific composition of raw materials, is necessary to guarantee consistent vermicompost quality over time. The importance of well-controlled conditions in vermicomposting has been particularly emphasized by Edwards et al. (2010a, b, c), who noted that the quality of vermicompost, not only in terms of nutritional profile, but also in terms of physical characteristics and microbial activity, can be significantly influenced by the composition of the raw material and the environmental conditions of production (Edwards et al. 2010a). This is an important point to emphasize because, in addition to nutrient supply, the physical and biological characteristics (associated microorganisms) of vermicompost play a key role in its effectiveness, influencing plant growth and development. For example, a controlled environment during vermicomposting tends to promote microbial activity and the production of plant hormones produced by the microorganisms thriving in the vermicompost, such as auxins (Arancon et al. 2004).

Aphids are among the most destructive insect pests of indoor and outdoor crops, sucking nutrients from the phloem and transmitting viruses to plants (Matthews 2017). Some species are particularly destructive to global agriculture. This is the case of the green peach aphid *Myzus persicae*, which is particularly destructive worldwide as it can colonize over 400 plant species from 50 different families, including many cultivated species, and is the vector of over 100 different plant viruses (Blackman and Eastop 2000; Schoonhoven et al. 2005). With the banning of certain effective pesticides to control these pests, a major challenge is to find alternative control solutions that fit in with more sustainable and healthier agricultural practices, and that can improve plants' defenses against pests whose resistance to insecticides is evolving particularly rapidly (Silva et al. 2012; Epstein et al. 2022). Vermicompost treatment could be one such solution. However, research into the antagonistic effects of solid and liquid vermicompost on aphids is currently rather limited (Arancon et al. 2005; Edwards et al. 2010b; Razmjou et al. 2011, 2012), hence

the interest in better understanding the biocontrol properties of vermicompost and the underlying modes of action.

In this study, we investigated the biocontrol properties of vermicompost against aphids. More specifically, we tested the effect of solid vermicompost and a liquid derivative, produced industrially under standardized conditions, on the life cycle characteristics and population growth of *M. persicae* aphids on sweet bell pepper. We also tested the repellent effects of the liquid form on aphids. Overall, our results show that both forms of vermicompost are effective aphid control agents. We discuss modes of action in the light of detailed compositional mapping of solid and liquid forms of vermicompost, paying particular attention to microbial composition. Our study paves the way for the study of modes of action and the targeted, optimized application of different forms of vermicompost according to agricultural practices.

Materials and methods

Vermicomposting set-up

To conduct the experiments, we used the vermicompost industrially produced by PUR VER SA (Belgium). This vermicompost is produced in continuous flow under extremely controlled conditions: a temperature of $25\text{ °C} \pm 2\text{ °C}$ and a relative humidity of $75\% \text{ RH} \pm 5\%$. The *Eisenia fetida* worms are fed exclusively with controlled organic matter of plant origin (brewers' spent grains and corn silage). The result is a vermicompost (PUR VER® vermicompost) that is consistent in terms of nutritional and microbial composition, making it particularly suitable for experimental purposes aimed at determining its biocontrol properties on plant pests. The liquid derivative (Green Booster®) is obtained by soaking the solid vermicompost in water, allowing the water-soluble nutrients and bioactive compounds to leach out. This solution is then filtered to remove solid particles, resulting in a purified liquid. Filtration is performed in aerobic conditions, while conditioning is carried out in anaerobic conditions.

This liquid vermicompost creation process ensures that the composition of the extract remains consistent and concentrated, providing a stable form of liquid vermicompost. This liquid vermicompost is a type of vermicompost tea and is therefore different from vermiwash, a liquid filtered from the aqueous washing of earthworms (Naidoo et al. 2017).

Effects of vermicompost treatment on life history traits, offspring size and aphid population

Insects, plants and general treatments

The *Myzus persicae* clone used for the experiments was obtained from Viridaxis SA (Charleroi, Belgium). It was

reared on sweet pepper (*Capsicum annuum*; var. Zamboni RZ provided by Rijk Zwaan SA) in wooden cages (0.3 m^3) under long-day conditions (16 h L: 8 h D) at 20 °C and 60% relative humidity (RH). To obtain age synchronized individuals, patches of 10 adults from stock rearing were placed on an artificial diet device (Cambier et al. 2001). The feeding device consisted of 600 μl of the solution deposited on the surface of a small, sterilized plastic Petri dish ($\text{Ø } 5\text{ cm}$) covered with a piece of stretched parafilm to create a thin membrane through which the aphids can feed. After 10 h, the adults were removed, and the laid nymphs were reared on the same artificial diet (changed every two days to ensure diet freshness) at 20 °C . Adults were obtained after ten days. 24 h old adults were used for the experiments. All the experiments were conducted in an air-conditioned room, at a temperature of $20 \pm 2\text{ °C}$, a relative humidity of $40 \pm 5\%$, and under long-day conditions (16 h L: 8 h D).

Capsicum annuum (var. Zamboni RZ) plants were grown in a growth chamber under long-day conditions (16 h L: 8 h D) at $22\text{ °C}/20\text{ °C}$ (day/night) and 60% relative humidity (RH). Seeds were germinated on unsterilized peat compost. They were covered with a glass plate and regularly moistened to stimulate germination. After two weeks, the plants reached approximately 5 cm and were individually transferred to 10 cm diameter pots containing: (1) only unsterilized peat compost (CTL), (2) 70% (of the total volume) unsterilized peat compost and 30% of solid vermicompost (SOL), (3) unsterilized peat compost treated with 5 ml of liquid vermicompost once a week (LIQ). The liquid vermicompost treatment was applied once a week from potting until the end of the experiment, while the solid vermicompost treatment was applied once (at the time of potting). All plants were watered (200 ml) every two days. For the LIQ treatment, liquid vermicompost was applied every two days (on days when plants were not watered).

The plants used for all experiments were at the 10–12 leaf stage (35 days) and the same treatment was maintained for all experiments. Treated plants infested with aphids are termed SOL+ and LIQ+ (for solid and liquid vermicompost, respectively). Untreated, aphid-infested plants are referred to as CLT+.

Effects of vermicompost treatment on aphids' life history traits

To obtain synchronize first-instar nymphs on plants, one 24-h-old female *M. persicae* was placed per pepper plant (CTL, SOL and LIQ; $N = 15$). After 24 h, a single larvae per plant was kept in a clip cage (15 replicates per treatment) to assess the effect of treatment on different life-history traits, including development time, survival rate, daily fecundity and longevity. Clip cages were monitored daily to record the date at which the nymph became adult and produced its

first offspring (development time). Every 24 h the number of nymphs produced per female was recorded, and the nymphs subsequently removed. Biological parameters such as maturity time (age at first reproduction, development time in days), daily fecundity and total fecundity per female aphid, aphid survival rate and average longevity were determined. Life tables were computed based on the data collected according to (Carey 1993) as used for *M. persicae* in Ali et al. (2021). The intrinsic rate of increase (r_m) denotes the growth rate of a population under ideal environmental conditions, with stable biological and abiotic factors, in which the influence of other species is entirely excluded. It (r_m) is calculated by solving numerically the Birch's approximation of Lotka's equation (Birch 1948; Carey 1993):

$$1 = \sum_0^K e^{-r_m x} l_x m_x$$

where: x is the age, K is the maximum age reached, l_x the daily survival and m_x the daily fecundity.

The net reproductive rate (R_0) represents the total number of offspring produced by an individual after one generation and is computed according to Carey (1993) using the following formula:

$$R_0 = \sum l_x m_x,$$

The mean generation time T indicates the time required for the population to increase to R_0 times of its original size when the population age structure shows a stable distribution. It is calculated using the following formula according to Carey (1993):

$$T = \ln R_0 / r_m$$

The doubling time (DT) which is the time required in days for the population to double is calculated using the following formula:

$$DT = \ln 2 / r$$

The finite rate of increase (λ) refers to the total growth rate within a certain period and is calculated as follows: $\lambda = e^r$.

Effects of vermicompost treatment on aphid's offspring size

The plants (CTL, SOL and LIQ; $N = 15$) were infested by one apterous synchronized female 24-h-old of peach aphid. After 24 h, the female was removed. After four weeks of population growth for each treatment, 30 adults were removed from the plant and their right hind tibia was measured with a micrometric scale under a microscope (6.39 magnification) for 30 apterous individuals per treatment. Tibia length is recognized as a reliable morphometric

indicator of aphid size (Honěk 1993; Vorburger and Ramsauer 2008; Tian et al. 2018).

Effects of vermicompost treatment on growth of aphid populations and on growth parameters of sweet pepper *C. annuum*

To assess the effect of vermicompost treatment on population growth, fifty apterous synchronized female 24-h-old of *M. persicae* were placed on sweet pepper plants (CTL, LIQ and SOL; $N = 15$). Two weeks later, the total number of aphids was counted. Untreated plants without aphids (CTL-) were kept as a positive control ($N = 15$). The effect of aphids on all plants categories (LIQ+, SOL+, CLT+ and CTL-) was evaluated through morphological indicators. Plant length and number of leaves were measured before and two weeks after infestation.

Two weeks after infestation, all leaves were scanned and the leaf area assessed using the Image J data processing program (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, MD, USA, <https://imagej.net/ij/>, 1997–2008). Different parts of the plant (roots, leaves, and stem) were dried for 3 days at 60 °C in an air oven and weighed using an electronic balance (Denver APX-200) to measure the dry mass. The specific leaf area was calculated using the following formula:

Leaf area/leaf's dry weight

Statistical analysis

The pre-adult duration (developmental time) was analyzed using an ANOVA and a Tukey test. To analyze daily fecundity differences in aphids, we fitted a generalized mixed effect model (GLMM) with a Poisson family and a log-link function to the data, using the glmmTMB package in R (Brooks et al. 2017). As fixed effect terms in the model, we used the treatment (4 levels) in interaction with the number of days after the start of analysis (quadratic covariate to account for increasing and decreasing fecundity slopes). We fitted a Cox survival model to the data to analyze aphid longevity (survival probability) on each treatment (Cox 1972). Adult longevity was analyzed with an ANOVA test. The fundamental life table parameters, including, intrinsic rate of increase (r_m), reproductive rate (R_0), finite rate of increase (λ), mean generation time (T), and doubling time (DT) were analyzed using the software program TWOSEX-MS Chart (Chi et al. 2020). Population parameters (r_m , R_0 , λ , T , and DT) were compared using a quick paired bootstrapping technique. The bootstrapping technique in the program with 100,000 random samplings was used for calculating the SE for the population. The effect of treatment in posterior tibia

length was analyzed using ANOVA with a Tukey test. A linear model followed by an ANOVA and a Tukey test were performed to test the effect of treatment on aphid's densities and physiological parameters of plants. Statistical analyses and charts were all done on R v4.0 (R Core Team 2022).

Repellent activity of liquid vermicompost on aphids

Olfactory bioassay in a glass tube olfactometer

To test the response of aphids to the odor of liquid vermicompost (LIQ) and its repellent effects, a glass tube olfactometer was used. Two glass closed bells (\varnothing 3.5 cm) were connected to each front arm of the olfactometer: one containing 1 ml of odor sources (liquid vermicompost or nettle manure) and the other containing 1 ml of water. Nettle manure (NET) is a liquid derived from the fermentation of nettle leaves (*Urtica* sp.), known for its aphid-repellent properties (Wulf et al. 2023; Toffolatti et al. 2023), and was used here as a positive control. The organic nettle manure used in the experiments was obtained from Agri Pur SA (Belgium).

A constant airflow of 60 ml per minute with a pressure of 970–1014 hPa was maintained through the chamber. Experiments were conducted between 10:00 and 18:00 h, under 7500 lx artificial light. Each test was repeated 30 times with a single aphid individual and with a group of ten individuals aged 24–48 h, placed in the olfactometer's central neutral chamber and observed for 15 min. The olfactometry bioassays were performed on a single insect as well as on groups of 10 individuals for a simulation closer to natural conditions that considers the aggregative behavior of aphids. To avoid any asymmetrical bias, the position of the products (LIQ and NET) was alternated after each replication to prevent variation.

For single aphid tests, we considered that one individual aphid had made a choice between one of two sources of odors when it passed the 3 cm mark of the tube connecting the neutral chamber to one of two olfactory. For tests with 10 aphids, the number of aphids passing the 3 cm mark of the tube connecting the neutral chamber to one of two olfactory sources were counted after 15 min. To ensure that no odor residues remained from one experiment (or repetition) to the next, the pots containing the extracts were emptied and the olfactometer was washed and sterilized with 70% ethanol, then dried for five minutes before used again.

Behavioral response of aphids on treated leaves

A piece of bean leaf (76×26 mm) measuring $\approx 19.72 \text{ cm}^2$ was used for this experiment. Half of the leaf piece was treated with 10 ml of odor source as described in the previous experiment. The behaviors of apterous adult aphids aged of 24–48 h (N=40 and 39 respectively for NET and LIQ),

were observed under a light of $30 \mu\text{mol/m}^2/\text{sec}$. Females were individually placed on the vertical central line of the piece of bean, in the center of a 9 cm diameter Petri dish filled with water to prevent aphids from escaping. For each female (i.e., for each behavioral trial), the time spent was recorded on each part of the bean leaf using the Cheese software (V.334.0). The maximum observation time was 15 min, and an individual was considered to have made no choice if it spent more than 15 min on the central line of the bean leaf. The data were analyzed using Behavioral Observation Research Interactive Software (BORIS) and the final position (choice) observed at the end of the experiment was scored.

Dual choice test on whole plant

Ten ml of liquid vermicompost or nettle manure were applied on a sweet pepper plant using an air atomizing nozzle attached to an air compressor at 1.4 bar in a Burgerjon spray tower (Burgerjon, 1956) (Demeter et al. 2021). To test the repellent potential of the two products (liquid vermicompost and nettle manure), one treated and one untreated plant at the second-leaf stage were placed in a wooden cage (40×40×45 cm). Twenty alatae aphids per cage were then placed in an open Petri dish on the other side of the cage and at the same distance from the two plants ($\approx 15 \text{ cm}$) to test their choice between the two odors sources. Aphid choice was assessed by counting the number of aphids found on each of the two plant types twenty-four hours after being placed in the cage, and each choice experiment was repeated twenty-five times (Safari Murhububa et al. 2021).

Statistical analysis

Generalized linear models (GLMs) were used to analyze the repellent activity of the nettle and the vermicompost (olfactometry bioassay and behavior assessment). The data of choice assay were transformed to proportions. Proportions were calculated as the number of aphids choosing a treatment divided by the total number of aphids that made a choice, excluding individuals making no choice for clearer interpretation. GLMs was assessed using the ANOVA function. Statistical analyses and charts were all done with R v4.0 (R Core Team 2022).

Analysis of vermicompost composition

Physico-chemical analysis of liquid vermicompost

The pH and the electrical conductivity (EC) of the liquid vermicompost was determined using a digital pH meter (Mettler Toledo, FE20/EL20) and a conductimeter (WTW LF92 + probe Tetracon 96), respectively. Density was

determined by weighing 1 ml of liquid vermicompost. Residual dry matter (expressed in %) was assessed after incubation in an oven at 70 °C during 48 h.

Biochemical and mineral analysis methods for liquid vermicompost

To determine the biochemical and mineral composition of liquid vermicompost, three 1 ml samples were analyzed.

Phytohormonal profile The phytohormonal profile and composition of the liquid vermicompost were established by considering major hormones and their metabolites, including abscisic acid (ABA), auxins, salicylic acid (SA), jasmonates (JA), brassinosteroids (BR), benzoic acid (BzA), and cytokinins (CK). They were extracted and quantified following the methods of Ivanov Dobrev and Kamínek (2002) and Dobrev and Vankova (2012). A fresh 1 ml sample was mixed with 0.5 ml of an extraction mixture (methanol: formic acid: water, 15:1:4 by volume) and kept at –20 °C. The following internal standards (10 pmol per sample) were added: $^{13}\text{C}_6$ -indole-3-acetic acid (IAA; Cambridge Isotope Laboratories), $^2\text{H}_4$ -SA (Sigma-Aldrich), $^2\text{H}_6$ -ABA (NRC-PBI), $^2\text{H}_3$ -phaseic acid (PA; NRC-PBI), $^2\text{H}_5$ -JA (C-D-N Isotopes Inc.), $^2\text{H}_5$ -*trans*Z, $^2\text{H}_5$ -*trans*ZR, $^2\text{H}_5$ -*trans*Z7G, $^2\text{H}_5$ -*trans*Z9G, $^2\text{H}_5$ -*trans*ZOG, $^2\text{H}_5$ -*trans*ZROG, $^2\text{H}_5$ -*trans*ZRMP, $^2\text{H}_3$ -DHZ, $^2\text{H}_3$ -DHZR, $^2\text{H}_3$ -DHZ9G, $^2\text{H}_6$ -iP, $^2\text{H}_6$ -iPR, $^2\text{H}_6$ -iP7G, $^2\text{H}_6$ -iP9G, $^2\text{H}_6$ -iPRMP (all CK standards are from Olchemim; the system of CK abbreviations used according to (Kamínek et al. 2000)), $^2\text{H}_3$ -castasterone, $^2\text{H}_3$ -epibrassinolide, $^2\text{H}_2$ -GA1 $^2\text{H}_2$ -GA4 $^2\text{H}_2$ -GA7 $^2\text{H}_2$ -GA8, $^2\text{H}_2$ -GA19 and $^2\text{H}_2$ -GA20 (all BRs and GA standards are from Olchemim). After 1 h extraction at –20 °C, the pellets were separated by centrifugation (15,000 g, 15 min) and re-extracted for 30 min at –20 °C with 5 mL of the same extraction solvent. The combined supernatants were purified using the dual-mode solid-phase method (Ivanov Dobrev and Kamínek 2002). Two phytohormone fractions were obtained: fraction A—containing acidic and neutral compounds (auxins, GAs, BRs, ABA, SA, JA), and fraction B—containing basic compounds (CKs). Hormonal quantification was performed by HPLC (Ultimate 3000, Dionex) coupled to a hybrid triple quadrupole/linear ion trap mass spectrometer (3200 Q TRAP; Applied Biosystems) as described previously (Djilianov et al. 2013) using isotope dilution method with multilevel calibration curves ($r^2 > 0.99$). Data processing was carried out using Analyst 1.5 software (Applied Biosystems).

Mineral composition The following nutrients were quantified in the liquid vermicompost: Na, Ca, K, Fe, Zn, Mg, Cu, P, As, B. To this end, samples (1 ml) of liquid vermicompost were digested in 4 ml of HNO_3 (35%) and evaporated to dry-

ness on a sand bath at 80 °C. The resulting minerals were incubated with a mixture of 37% HCl and HNO_3 (3:1, v/v). This mixture was gently evaporated for a few minutes until the residues were completely dissolved in 10 ml HCl 0.1N. The samples were then filtrated on a Whatman N° 2 filter paper. Elements were quantified by inductively coupled plasma-optical emission spectroscopy (type MPX; Varian). Blank controls were prepared following the same procedure, but without liquid vermicompost. The concentrations of ions were expressed in mg/L of liquid vermicompost.

Total nitrate was quantified colorimetrically according to Cataldo et al. (1975) using nitration of salicylic acid. Ammonium quantification was performed using the phenol-hypochlorite reaction as detailed by Weatherburn (1967). Total nitrogen quantification was performed with the kit LCK 138 (1–16 mg/L TN) (Hach Lange).

Antioxidant, total protein and polyamine content Total glutathione was determined according to Cereser et al. (2001) and total ascorbate was assessed according to Kampfenkel et al. (1995). Proline concentrations was estimated by the acid ninhydrin method (Bates et al. 1973). Free polyamines were extracted with 10% perchloric acid and quantified by HPLC as detailed in Quinet et al. (2010). Total soluble sugars were quantified using the anthrone test (Yemm and Willis 1954). Total soluble protein concentration was estimated according to Bradford (1976). Total phenolic concentration was assayed using the Folin-Ciocalteu reagent according to Singleton and Rossi (1965) while flavonoids concentration was measured using the colorimetric assay developed by Dewanto et al. (2002).

Determination of the microbial communities of solid and liquid vermicomposts

DNA extraction The microbial community composition of solid and liquid vermicompost was studied using a metabarcoding approach. To ensure optimal extraction, the solid vermicompost was first homogenized and sieved through a 2 mm mesh. For the liquid vermicompost, a high-speed centrifugation step (21,000 g) for 5 min was performed to obtain a pellet of at least 250 mg. DNA extraction was then performed from 250 mg of homogenized solid vermicompost or 250 mg of liquid vermicompost (pellet), using the DNeasy PowerSoil Pro Kit (Qiagen), following the manufacturer's instructions. An additional homogenization step was conducted using the Precellys Evolution (Bertin Technologies). Genomic DNA concentration was measured with a NanoDrop 3300 Fluorospectrometer (Thermo Fisher Scientific), using the Pico Green dye. The analyses were carried out in 4 replicates for solid vermicompost and in 2 replicates for liquid vermicompost.

PCR and sequencing Sequencing libraries were prepared according to the Illumina MiSeq system protocol. For the study of the bacterial communities, the V3–V4 variable regions of the 16S rRNA gene were amplified using the primers 16S_341FF (5'-CCTACGGGNGGCWGCAG-3') and 16S_805R (5'-GACTACHVGGGTATCTAATCC-3'). For the study of the fungal communities, the Internal Transcribed Spacer 2 (ITS2) region was targeted with the primers ITS3_KYO1 (5'-AHCATGAAGAACYAG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3'). The PCR step was performed using the ready-to-use 2× mixture Phusion Plus PCR Master Mix (Thermo Fisher Scientific), following the supplier's recommendations. Briefly, 3 µl of genomic DNA were amplified in a PCR reaction volume of 20 µL containing 10 µL 2× Phusion Plus Master Mix, 5 µL PCR-grade water, and 1 µL of each primer (at 10 µM). The cycling conditions were: 30 s at 98 °C for initial denaturation, followed by 25 cycles of 10 s at 98 °C, 30 s at 60 °C, and 30 s at 72 °C, with a final elongation step of 10 min at 72 °C. All PCR products were purified using the Spar Q Pure Mag Beads purification kit (Quantabio) prior to the next step. The expected size of PCR products is around 615 bp for the bacterial 16S rRNA gene and 400–450 bp for the fungal ITS2 region.

The library preparation workflow continued using the Phusion Plus PCR Master Mix (Thermo Fisher Scientific) and the Nextera XT Index Kit v2 Set A (Illumina) according to the manufacturer's instructions. The final steps of library preparation involved purification using Spar Q Pure Mag Beads (Quantabio). The size of the libraries was then checked with a bioanalyzer (Tape Station 4150, Agilent Technologies) using D1000 Screen Tape. The concentration of the libraries was measured with the NanoDrop 3300 Fluorospectrometer as described above. Finally, the pooled libraries were analyzed by the Mi Seq system using the Illumina Mi Seq Reagent Kits v3, based on a paired-end approach for sequencing 2×300 bp. The Mi Seq software generates FASTQ files for each sample (demultiplexed). The raw sequences contained in these files were then analyzed in a bioinformatics pipeline as described in the following section.

Data analysis Bioinformatics analysis was performed using an in-house pipeline, which enables taxonomic assignment of the sequences obtained, and sequence counting for each sample. Our in-house pipeline incorporates various bioinformatics tools such as Cutadapt, Pear, DADA2, and UCHIME, and uses BLAST against NCBI databases for taxonomic assignments. The pipeline includes the following major steps to generate a csv file:

- Primers Cutting with Cutadapt and Pre-assembly of Reads with Pear.
- Sequence Analysis using the DADA2 package, which is based on Amplicon Sequence Variant analysis of demultiplexed reads. This includes several features: (I) Filter And Trim, (II) Learn Errors, (III) Derep Fastq (ITS), (IV) Dada, and (V) an additional step of dechimerization with UCHIME from the USEARCH package.
- Taxonomic Assignment using BLAST against NCBI databases and determination of functional aspects with FAPROTAX for bacteria (Louca et al. 2016) and Fun-Guild for fungi (Nguyen et al. 2016).

Taxonomic data were filtered and normalized according to relative abundance for each sample. Principal coordinate analysis (PcoA, Bray-Cutis distance) and diversity index of microbial data were performed using PAST v4.09 (Hammer et al. 2001).

Results

Vermicompost treatment alters aphid survival, reproduction and population growth

The duration of the pre-adult period (development time) did not vary according to plant treatment ($df=2$, $F=0.784$, $p=0.463$) (Fig. S1). Mean aphid development times were 9.68 ± 0.47 , 10.71 ± 0.61 and 9.33 ± 2.63 days on CLT+, SOL+ and LIQ+, plants respectively.

Aphid survival was significantly lower on treated plants (Cox: $coef=1.7253$, $z=4.306$, $p=1.66e-05$ ***; Cox: $coef=1.5477$, $z=3.955$, $p=7.67e-05$ ***; for SOL+ and LIQ+, respectively) than on untreated plants. Survival rates were similar when plants were treated with liquid or solid vermicompost ($p=0.96$) (Fig. 1).

Daily fecundity per female varied with treatment (GLMM: $z=-3.476$, $p=0.00051$ ***; $z=-2.226$, $p=0.02600$ * for SOL+ and LIQ+, respectively) and with time (days) (GLMM: $z=-23.289$, $p<2e-16$ ***). No interaction effect was observed between the day and the treatment ($p>0.1$). Fecundity was higher for aphids reared on control plants than on treated plants. The lowest fecundity was recorded for aphids reared on plants treated with liquid vermicompost (Fig. 1).

Adult longevity was affected by plant treatment ($df=2$, $F=30.07$, $p=7.84e-09$ ***) (Fig. 2). Treatment of sweet pepper with vermicompost decreased the longevity of adults (Tukey test: $p=0$; $p=9e-07$ *** for SOL+ and LIQ+, respectively). The two vermicompost treatments (SOL+ and LIQ+) had a similar effect on aphid longevity (Tukey test: $p=0.499$).

The intrinsic rate of increase (r_m) and the finite rate of increase (λ) did not vary with treatment (paired bootstrap test, $p>0.1$ for aphids reared on CTL vs aphids reared on

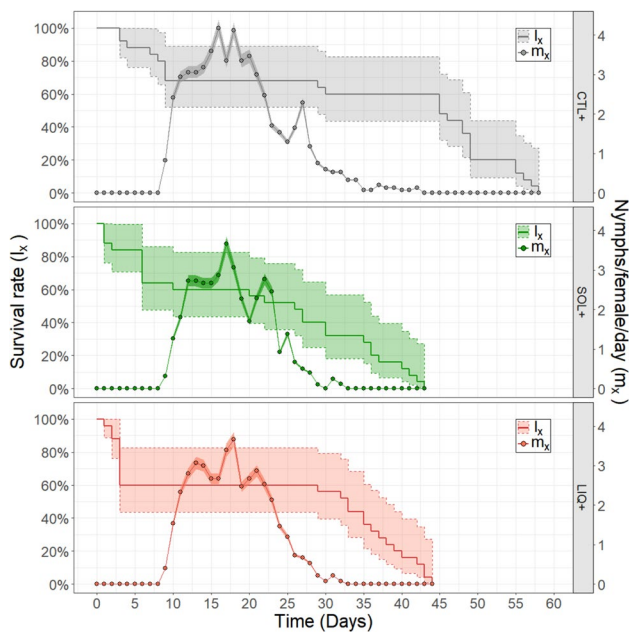


Fig. 1 Daily survival rate l_x (the proportion of individuals surviving to age x) and daily fecundity of aphids m_x (the average number of offspring produced per individual at age x) reared on treated plants and untreated plants ($N=25$). CTL+, SOL+ and LIQ+ indicate infested untreated plants, infested solid vermicompost-treated plants, and infested liquid vermicompost-treated plants, respectively

LIQ; $p > 0.1$ for aphids reared on SOL+ vs aphids reared on LIQ; $p > 0.05$ for aphids reared on CTL vs aphids reared on SOL) (Table 1).

The net reproductive rate (R_0) was higher on untreated plants than on plants treated with solid vermicompost (paired bootstrap test, $p=0.0321^*$). Aphids reared on plants treated with liquid vermicompost exhibited a net reproductive rate that was not significantly different from aphids reared on untreated plants (paired bootstrap test, $p=0.1139$). The net reproductive rate of aphids reared on plants treated with solid vermicompost or liquid vermicompost was similar (paired bootstrap test, $p=0.6253$). Aphids' populations increased less rapidly on treated plants than on untreated plants (Table 1).

Generation time (T) did not vary with treatment (paired bootstrap test, $p > 0.1$) and the doubling time (DT) was also the same for aphids exposed to the three treatments (paired bootstrap test $p > 0.05$ for aphids reared on CTL plants vs aphids reared on SOL plants; $p > 0.1$ for the two other comparisons) (Table 1).

Treatment with vermicompost influenced the size (tibia length) of aphid's offsprings ($p=0.0028^{**}$) (Fig. 3A). Treatment of sweet pepper with either liquid or solid vermicompost reduced adult size (Tukey Test: $p=0.0047^{**}$; $p=0.0140^*$, for SOL+ and LIQ+, respectively). Liquid and solid vermicompost had the same effect on aphids' size

(Tukey test: $p=0.927$). Mean tibia was 1.03 ± 0.12 mm for aphids reared on untreated plants, 0.95 ± 0.08 mm and 0.96 ± 0.08 mm for aphids reared on plants treated with solid vermicompost and liquid vermicompost, respectively.

The treatment had a significant effect on the aphid population ($df=2$, $F=44.011$, $p=4.942e-11^{***}$) (Fig. 3B). Aphid population growth was significantly reduced on plants treated with vermicompost compared with untreated and LIQ plants (Tukey Test: $p < 0.0001^{***}$). Compared with the control, a reduction in the aphid population was observed on plants treated with solid vermicompost (Tukey test: $p < 0.0001^{***}$) and liquid vermicompost (Tukey test: $p=0.0013^{**}$). After three weeks, we counted an average of 6542 ± 1013 ; 3058.5 ± 581 and 5123.7 ± 1303 aphids on CTL, SOL and LIQ plants, respectively. We noted a 53.24% and 21.69% reduction in the average number of aphids when the insects were developed on SOL and LIQ plants, respectively.

Vermicompost treatments had no significant effect on the relative increase of leaf numbers (Fig. 4A) and on the relative increase of plant length when plants were infested with aphids ($p > 0.9$ for the two parameters) (Fig. 4B). We found that untreated plants without aphids (CTRL-) had the most important increase of leaf numbers and relative increase of plant length compared with treated plants infested with aphids (Tukey-test: $p < 0.0001^{***}$).

With regard to dry weight, this growth parameter was different for the four treatments (CTRL-, CTRL+, SOL+ and LIQ+) ($df=3$, $F=9.3911$, $p=4.006e-05^{***}$) (Fig. 5A) and that this trend was the same for specific leaf

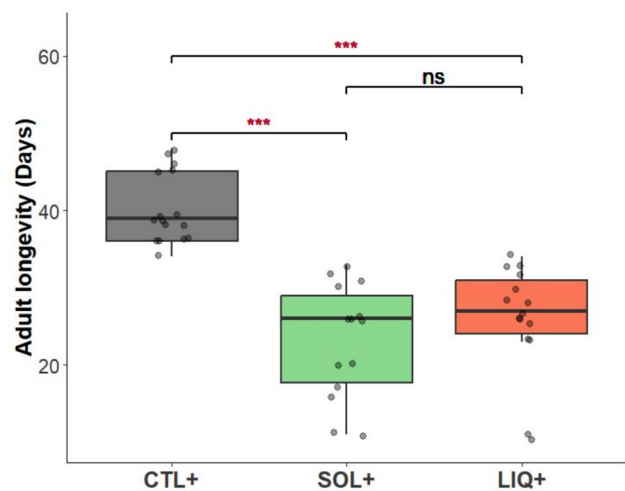


Fig. 2 Effect of vermicompost treatment on aphid's longevity. NS indicate non-significant results ($p > 0.05$), (***) indicate significant differences ($p < 0.001$). CTL+, SOL+ and LIQ+ indicate infested untreated plants, infested solid vermicompost-treated plants, and infested liquid vermicompost-treated plants, respectively

Table 1 Effect of vermicompost treatment on life table indices of *M. persicae* aphids reared on sweet pepper plants

Treatment	Intrinsic rate of increase (r_m)	Net Reproductive rate (Ro)	Finite rate of increase (λ)	Generation time (T)	Doubling time (DT)
CTL	0.21	38.20 (a)	1.24	16.70	3.17
SOL	0.18	22.64 (b)	1.20	16.65	3.70
LIQ	0.19	26.00 (a)	1.21	16.72	3.55

area ($df = 3$, $F = 5.9229$, $p = 0.001391^{**}$) (Fig. 5B). The dry weight of LIQ + plants was higher than that of CTL – plants ($p < 0.0001^{***}$) and CTL + ($p = 0.0063^{**}$). Plants treated with liquid vermicompost (LIQ +) had a higher dry weight than those treated with solid vermicompost (SOL +) ($p = 0.0211^*$). Untreated plants (CTL – and CTL +) showed a very similar dry weight, regardless of their infestation status ($p = 0.2814$) (Fig. 5A). The results indicate that treatment tends to influence the specific leaf area ($df = 3$, $F = 5.9229$, $p = 0.001391^{**}$). Infested plants treated by solid vermicompost (SOL +) had a more important leaf surface area than untreated plant without aphids (CTL –) ($p = 0.0035^{**}$). In the case of untreated plants, plants infested with aphids had a greater leaf area than non-infested plants ($p = 0.0031$) (Fig. 5B).

Liquid vermicompost has repellent effects

For both modalities tested (a single aphid versus a population of ten aphids), liquid vermicompost and nettle manure were found to be repellent against aphids ($p = 0.0334^*$ for test with one aphid (Fig. 6A); $p = 0.00467^{**}$ and $p = 83e-05^{***}$, respectively for vermicompost extract and nettle manure for the test with ten aphids (Fig. 6B)) and had similar effects against apterous aphids ($p > 0.05^*$ and $p = 0.1130$, respectively for the test with one aphid and the test with ten aphids).

Spraying nettle manure or the liquid vermicompost on the leaves reduced aphid residence time ($p = 0.0327^*$, $p = 0.000365^{***}$ for NET and LIQ, respectively) (Fig. 7). NET (Fig. 7A) and LIQ (Fig. 7B) treatments had similar effects on aphid residence time ($p = 0.202$).

Furthermore, for the final choice recorded on leaf parts, the nettle manure treatments appear to be repellent ($p = 0.0141^*$), but this is not the case for liquid vermicompost ($p = 0.153$). The final choice of aphids was not significantly different between the two treatments ($p = 0.4288$) (Fig. 8).

Regarding dual choice test on whole caged plants, nettle manure and liquid vermicompost were not significantly repellent to aphids ($p = 0.37$ and $p = 0.696$ for NET and LIQ, respectively) and had similar effects ($F = 0.842$, $p = 0.363$) (Fig. S2).

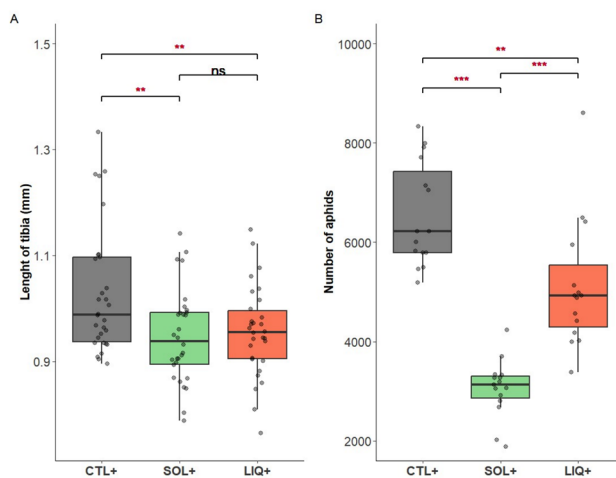


Fig. 3 Effect of vermicompost treatment on aphid size and population size. **A:** Effect of treatment on aphid size by measurement of the right hind tibia length. **B:** Effect of treatment on aphid population. NS indicates non-significant results ($p > 0.05$), (**) and (***) indicate significant differences ($p < 0.01$ and $p < 0.001$, respectively). CTL +, SOL + and LIQ + indicate infested untreated plants, infested solid vermicompost-treated plants and infested liquid vermicompost-treated plants, respectively

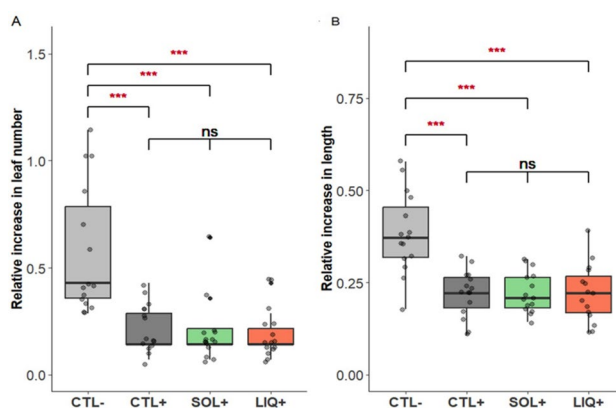


Fig. 4 Effect of vermicompost treatment on leaf number and plant length. **A:** Effect of treatment on the relative increase of leaf numbers. **B:** Effect of treatment on relative increase of plant length. NS indicates non-significant results ($p > 0.05$) and (***) indicate significant differences ($p < 0.001$ respectively). CTL -, SOL + and LIQ + indicate infested untreated plants, infested solid vermicompost-treated plants and infested liquid vermicompost-treated plants, respectively

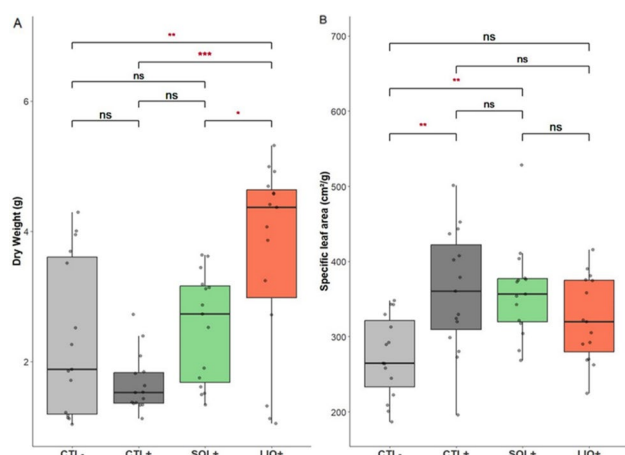


Fig. 5 Effect of treatment on growth parameters—dry weight (**A**) and specific leaf area (**B**)—of sweet pepper (with and without aphids). NS indicates non-significant results ($p > 0.05$), (*), (**) and (***) indicate significant differences ($p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively). CTL-, CTL+, SOL+ and LIQ+ indicate aphid-free untreated plants, infested untreated plants, infested solid vermicompost-treated plants and infested liquid vermicompost-treated plants, respectively

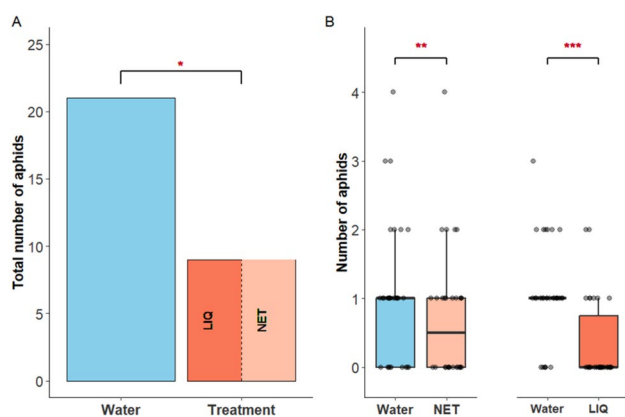


Fig. 6 Repellent activity of liquid vermicompost on aphids. **A**: Repellent activity of liquid vermicompost (LIQ) and nettle manure (NET) on one aphid. **B**: Repellent activity of nettle manure and liquid vermicompost (proportion of aphids making a choice) on ten aphids. (*), (**) and (***) indicate significant differences ($p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively)

Physico-chemical parameters, mineral and biochemical composition and phytohormonal profile of liquid vermicompost

Table S1 summarizes the compounds identified in the liquid vermicompost. The pH is nearly neutral, and the main ions detected are potassium (K^+), calcium (Ca^{2+}), sodium (Na^+), and sulfur (S^{2-}). Nitrogen is primarily present in the form of nitrate (NO_3^-). The liquid vermicompost contains proline, a well-known osmoprotectant. It also contains significant amounts of antioxidants such as phenolics, flavonoids,

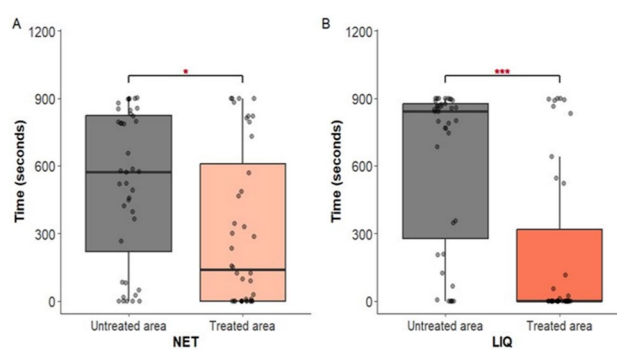


Fig. 7 Aphid behavior on vermicompost-treated leaves. **A**: Effect of nettle manure treatment (NET) on aphid behavior (residence time in each part of leaf). **B**: Effect of liquid vermicompost treatment (LIQ) on aphid behavior (residence time in each leaf area). (*) and (***) indicate significant differences ($p < 0.05$ and $p < 0.001$, respectively)

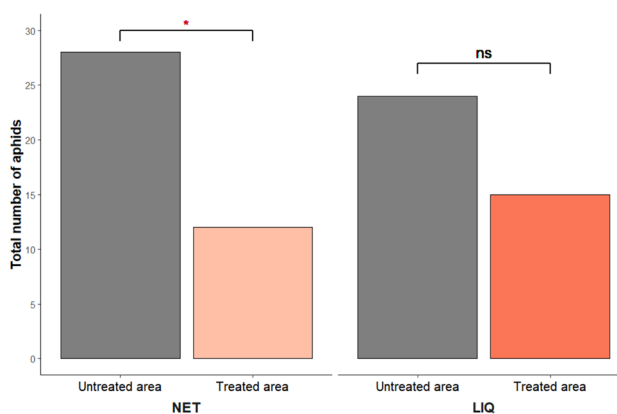


Fig. 8 Effect of liquid vermicompost (LIQ) and nettle manure (NET) treatments on aphid behavior. NS indicates non-significant results ($p > 0.05$) and (***) indicate significant differences ($p < 0.05$), respectively

anthocyanins, glutathione, and ascorbate. Sugars and proteins are also present in high concentrations.

The main phytohormone classes, except for gibberellins, were identified in the liquid vermicompost. Total cytokinins (CK) exceeded 20 pmol/ml (Table S1), with *trans*-zeatin and *trans*-zeatin-riboside accounting for 43.5%. The dihydrozeatin and *cis*-zeatin types were found in similar concentrations, while the concentration of the biologically low-active *cis*-zeatin form reached at 1.63 pmol/ml and that of the isopen-tenyl free form (iP) was less than 0.8 pmol/ml (Table S2). Various conjugated forms of CKs, including glucosides and ribosides, were detected (Table S2).

Abscisic acid (ABA) was present in significant amounts (> 3 pmol/ml), and its oxidation products were even higher (Table S2). Benzoic acid (BzA) and salicylic acid (SA) were extremely high, whereas jasmonic acid (JA) and jasmonic acid -Isolecine were low (Table S1).

Concerning total auxin, free indole acetic acid reached a concentration close to 10 pmol/ml., but its conjugated forms were low (Table S2). The concentration of the ethylene precursor, 1-aminocyclopropane-1-carboxylic acid, was low, and its malonyl form was undetectable (Table S2).

Vermicompost, whether solid or liquid, is rich in bacteria and fungi

Using the Illumina sequencing approach, we established a microbiological map—bacterial and fungal communities—of the solid and liquid forms of vermicompost. Paired sequence assembly yielded consensus sequences which, after quality-based filtering, resulted in 2,099,442 high-quality sequences (Table S3). ASVs were agglomerated at phylum and genus levels (Tables S4 &). It should be noted that a large proportion of the reads could not be identified taxonomically, and that most of the genera identified are present in very low proportions. α -diversity indexes (number of ASVs, number of genera, Shannon and Simpson indices) were assessed (Fig. S3 & as well as β -diversity (Figs. S5–S8): Principal Coordinates Analysis (PCoA) shows that solid and liquid vermicompost are grouped in distinct clusters at the ASV and genus level.

Together, solid and liquid vermicomposts home a bacterial community that comprises 40 phyla, most of which are shared between the two forms of vermicompost, and consists mainly of Bacillota, Actinomycetota, Pseudomonadota, Bacteroidota, Planctomycetota and Myxococcota (Table S4 and Figs. S9 & S10). A total of 1104 bacterial genera were identified in all phyla combined. 32% of bacterial genera were specific to solid vermicompost, 16% to liquid vermicompost and 52% were common to both (Fig. S11). Although bacterial communities of solid and liquid vermicomposts appear to be highly diverse, it should be noted that most genera are in fact poorly represented (Table S4). For discussion purposes, only the 10 most abundant genera in each type of vermicompost were examined in more detail (Fig. 9 for relative abundance and Fig. S12 for absolute abundance). *Actinomarinicola*, *Ilumatobacter*, *Planifilum*, *Chryseolinea*, *Bacillus* and *Sphaerobacter* were the most abundant genera shared by solid and liquid vermicomposts. Although present in solid vermicompost, the genera *Bythopirellula*, *Hydrogenispora*, *Rubinisphaera* and *Vicinamibacter* are among the most abundant genera in liquid vermicompost. Based on these results and the literature, Table 2 lists the main characteristics of these top 10 bacterial genera, to serve as a basis for further discussion.

Regarding the fungal community, solid and liquid vermicomposts together comprise 7 phyla, most of which are shared between the two forms of vermicompost, and consists mainly of Ascomycota, Basidiomycota and Mucoromycota

(Table S5 and Figs. S13 & S14). A total of 345 fungal genera were identified, across all phyla. 42% of fungal genera were specific to liquid vermicompost, 29% to solid vermicompost and 29% were common to both (Fig. S11). As with bacterial communities, most fungal genera are in fact poorly represented (Table S3). As with bacterial communities, only the 10 most abundant fungal genera in each vermicompost type were examined in detail (Fig. 10 for relative abundance and Fig. S15 for absolute abundance). Both forms of vermicompost showed a high abundance of the genera *Thermomyces*, *Scedosporium*, *Parascedosporium*, *Mortierella* and *Enterocarpus*. Interestingly, some of the most abundant genera in solid vermicompost were not found in liquid vermicompost: *Derxomyces*, *Lomentospora*, *Paratracharina* and *Tulosesus*. Others, such as *Apiotrichum*, are marginally present in liquid vermicompost, whereas they are superabundant in solid vermicompost. Based on these results and the literature, we have compiled a table (Table 3) showing the main characteristics of these different genera, to serve as a basis for further discussion.

Using the FAPROTAX database, we established the top 10 functional characteristics of bacterial communities present in solid and liquid vermicompost (Fig. S16). Chemoheterotrophy, aerobic chemoheterotrophy, nitrate reduction and hydrocarbon degradation are the most represented metabolic traits. Remarkably, the functional data show a high degree of similarity between solid and liquid vermicompost samples. FUNGuild was used to establish the top 10 functional traits associated with the fungal community (Fig. S17). Interestingly, the results suggest that a significant proportion of fungal diversity is associated with endophytic traits.

Discussion

In our study, we tested the ability of solid and liquid forms of vermicompost to control *M. persicae*, one of the world's most damaging aphids to crops. We also examined the influence of these biological amendments on growth parameters of infested sweet pepper plants. Overall, our results show that vermicompost has powerful biocontrol properties against aphids. By acting on the plant, it indirectly alters the survival and reproduction of aphids, resulting in a reduction in the growth of the aphid population (a form of antibiosis). Our results also highlight the strong repellent action of liquid vermicompost (antixenosis). These two properties highlight the potential of this type of extract in biological control. Analysis of the microbial composition of solid and liquid vermicomposts and the chemical composition of the liquid form has shed light on potential underlying modes of action. To our knowledge, our study is the most comprehensive to date assessing the biocontrol properties of different forms of vermicompost on aphids. It represents a step towards

exploring its use in controlling other insect pests through its effects on the plant, as well as towards studying its underlying modes of action.

Our results show that vermicompost, whether applied in solid or liquid form to sweet pepper plant, has an impact on a range of life-history traits of *M. persicae* aphids, reducing aphid survival, longevity, daily fecundity and size. This translates into a significant reduction in aphid populations on treated plants, a result particularly marked for solid vermicompost, since its application for two weeks results in a reduction of over 50% in aphid populations compared with untreated plants. *M. persicae* life table parameters revealed no significant differences in intrinsic growth rate (r_m), despite slightly lower values in treated plants. This result is not surprising, as r_m considers factors such as development time, which remained unchanged across the treatments. Notably, r_m reflects population growth once a stable age structure has been reached (Carey 1993), which is not the case when starting with a few individuals of the same age. However, the net reproductive rate (R_0) is significantly lower on treated plants. Our results are in line with those reported in Polat Akköprü (2021) who showed that liquid vermicompost negatively impacts on *M. persicae* reproduction parameters and population growth.

Overall, our results demonstrate that vermicompost has powerful biocontrol properties against aphids. The biocontrol qualities of vermicompost against phytophagous pests have already been documented in a few studies, but despite the growing interest in vermicompost in recent years, very few studies have tackled the topic comprehensively, particularly with regard to understanding its modes of action. For example, greenhouse experiments have shown that the application of vermicompost (in both solid and liquid forms) tends to reduce populations and damage caused by various pests (mealybugs, spider mites and aphids) on artificially infested plants (Arancon et al. 2005, 2007; Edwards et al. 2010b). Similarly, vermicompost has also been reported to significantly suppress the population of cucumber beetles (*Diabrotica undecimpunctata* and *Acalymma vittatum*) on cucumber plants, and to reduce plant damage (Yardim et al. 2006). Vermicompost treatments have also been shown to reduce populations of the aphid *Aphis gossypii* in cucumber crops (Razmjou et al. 2011, 2012). However, with the exception of Polat Akköprü (2021), little attention was paid to pest life history traits, and the modes of action of vermicompost remain poorly documented. Interestingly, Little et al. (2011) reported that vermicompost treatment affected the preference and performance of aphids on plants, demonstrating the bottom-up effects of vermicompost. By applying different doses of (solid) vermicompost to cabbage, they showed that this amendment tended to reduce the colonization capacity of *M. persicae*, and that aphids on treated plants showed reduced weight and fewer nymphs produced. Our results

point in the same direction, highlighting the repellent activity of liquid extracts of vermicompost. This repellent effect on aphids is similar to that of aqueous nettle extract, known for its insecticidal properties (Wulf et al. 2023; Toffolatti et al. 2023). Although research on the repellent effect of vermicompost is limited, some studies indicate that humic acid extract from vermicompost can repel crickets (Khiew et al. 2020). In our study, spraying liquid vermicompost on plant leaves significantly reduced the residence time of aphids, which tend to leave treated areas. Therefore, its use as a preventive spray to repel insect pests is an interesting prospect. The feeding behavior of the psyllid *Diaphorina citri* Kuwayama was also found to be affected by vermicompost amendments, with a reduction in sap ingestion and, consequently, in the transmission of the bacteria responsible for Huanglongbing (HLB) disease (Tao et al. 2023). It has been suggested that the repellent effect and reduced plant palatability are likely due to phenolic compounds released by plant growth-promoting microorganisms that develop in vermicompost (Wallis and Galarneau 2020; Rehman et al. 2023).

A striking result of our study is that vermicompost treatment has a transgenerational effect. Indeed, our results show that second-generation adults exposed to both solid and liquid forms of vermicompost have a reduced body size compared with aphids from control plants (reflected by a reduction in tibia length). This result is important, because although we did not follow pest population dynamics throughout the plant cycle, it suggests that in the field, there may be an amplification of aphid quality alteration from generation to generation on the scale of the plant life cycle, and thus perhaps much greater deleterious effects on aphid populations than those observed during the duration of the experiment. Extended experiments over the entire plant cycle would enable this hypothesis to be tested.

The modes of action of vermicompost have been little studied and are still widely unknown. Yet identifying them is an important step in tailoring the application of vermicompost to specific crops, target pests, and particular agricultural practices. In this study, we conducted a comprehensive analysis of the chemical composition (for liquid vermicompost) and microbiological composition (for solid and liquid vermicomposts) in order to deduce the underlying modes of action. The composition of liquid vermicompost (or vermicompost tea) varies depending on several factors, such as the organic materials used, the vermicomposting process and the additives used (Fritz et al. 2012). However, in general, liquid vermicompost tends to exhibit a neutral pH, a similar composition in terms of major mineral elements (Fritz et al. 2012; Kim et al. 2015; Zarei et al. 2018) and to contain various phytohormones (Wong et al. 2020). The liquid fraction used in our study is no exception to this trend. The products contained in vermicompost tend to promote

seed germination, seedling growth and crop growth, both in soil and under hydroponic conditions (Arancon et al. 2007; Lazcano et al. 2010; Joshi et al. 2015; Blouin et al. 2019; Jiang et al. 2023). In our study, treatment with liquid vermicompost increased the dry weight and leaf area of peppers infested with aphids, similar to the effects observed on cucumbers and tomatoes attacked by beetles and aphids (Edwards et al. 2010b, c). Our hypothesis is that these beneficial effects on the plant may largely be attributed to the chemical composition of vermicompost. For example, potassium and calcium, found in high concentration in liquid vermicompost, tend to boost plant resistance and resilience by promoting the development of thicker cell walls, helping plants to resist pest attack and disease. Indeed, potassium activates defense-related enzymes and promotes the synthesis of secondary metabolites that prevent aphids from feeding (Amtmann et al. 2008). Calcium acts as a secondary messenger in plant defense mechanisms (Lecourieux et al. 2006). Biochemical elements present in liquid vermicompost, such as soluble sugars, can act as signaling molecules that trigger defense responses in plants, leading to the synthesis of secondary metabolites that deter herbivores (Neilson et al. 2013; Divekar et al. 2022). Proline is amino acid acting as an osmoprotectant: it stabilizes cell structures, mitigates the effects of stress and facilitates recovery processes (Szabados and Savouré 2010). Glutathione, an antioxidant found in high concentration in liquid vermicompost, activates genes related to defense pathways (Zechmann 2014) and helps detoxify reactive oxygen species (ROS) produced in response to pathogen attacks, protecting cellular structures and maintaining cellular integrity (Noctor et al. 2012). Liquid vermicompost is also rich in benzoic acid, which is essential for plant defense, as it serves as precursor for a variety of compounds important for plant health (Widhalm and Dudareva 2015). For example, benzoic acid is a precursor of salicylic acid (also present in large quantities in vermicompost), which is considered to be one of the main endogenous signals involved in the activation of the defense response and an important signaling molecule for triggering responses to several abiotic stresses (Dempsey et al. 2011; Widhalm and Dudareva 2015). Benzoic acid also contributes to the synthesis of secondary metabolites such as lignin and flavonoids, which strengthen plant cell walls and improve their defense against pathogens (Rashad et al. 2020). Aromatic cytokinins, also derived from benzoic acid, promote root and shoot formation and delay leaf senescence in many species (Mutui et al. 2012; Vylčílová et al. 2016). Our study shows that liquid vermicompost is extremely rich in a variety of inorganic and organic components that may have benefits for plants and suggests that this soil amendment could serve as a valuable resource for the isolation of compounds of interest.

Vermicompost is not an inert soil amendment: it is also teeming with microorganisms that may also be involved in the modes of action underlying biological control of insects. In recent years, there has been growing evidence that soil-dwelling microbes can help plants cope with insect pests (bottom-up effect) (Pineda et al. 2010; Jaber and Ownley 2018; Syed Ab Rahman et al. 2018; Ciancio et al. 2019; Francis et al. 2020; Elnahal et al. 2022; Lee et al. 2022; Álvarez-Pérez et al. 2024). In practice, only a few studies have examined the microbial composition of vermicompost, either in solid or liquid form (Domínguez et al. 2019, 2021; Srivastava et al. 2021; Pérez-Losada et al. 2022). In line with these studies, our metabarcoding approach reveals that both solid and liquid vermicompost are extremely rich in bacteria and fungi. Our study presents the first comparative map of the microbial communities present in solid vermicompost versus its liquid derivative. Interestingly, while many of these microbes are common to both forms of vermicompost, some microbes that are very abundant in solid vermicompost are lost in the liquid derivative. This means that there is a loss of microorganisms during the soaking and filtration process and a general modulation of the microbiota, with the two types of vermicompost having a different microbial composition and, undoubtedly, distinct microbiological properties. Although microbial diversity is high in both solid and liquid vermicompost, this diversity is in fact confined to a few dominant genera whose proportion exceeds 1%, and most genera are present in residual amounts. With regard to bacteria, most of the abundant genera identified thrive in soil and sediment (e. g. *Actinomarinicola*, *Ilumatobacter*, *Sphaerobacter* and *Planifilum*). Unfortunately, these abundant genera are generally poorly described, with little information available on their biology and interaction with other organisms, so it is hard to speculate on how they might contribute to the biocontrol properties of vermicompost. *Calderihibitans* is an intriguing case, as this genus is only present in solid vermicompost and the only known species is *Calderihibitans maritimus*, found in marine sediments (Omae et al. 2017). The only genus for which it is possible to make assumptions is *Bacillus*, a large genus that includes a diverse set of species well known to be rhizosphere-associated (Zeigler and Perkins 2021; Lengrand et al. 2024). In addition, some *Bacillus* species and strains have already shown biocontrol properties against insect pests. For example, *Bacillus pumilus* has negative effects on whiteflies and the cucumber beetle (Zehnder et al. 1997; Murphy et al. 2000) and *Bacillus subtilis* and *Bacillus amyloliquefaciens* increase fruit yield in sweet peppers infested by *M. persicae* (Herman et al. 2008). This suggests that the *Bacillus* genus has great potential for biocontrol of insects, and that vermicompost can be a reservoir of these bacteria for plants. The results are easier to interpret when it comes to fungal diversity, as many of the genera identified are better described and

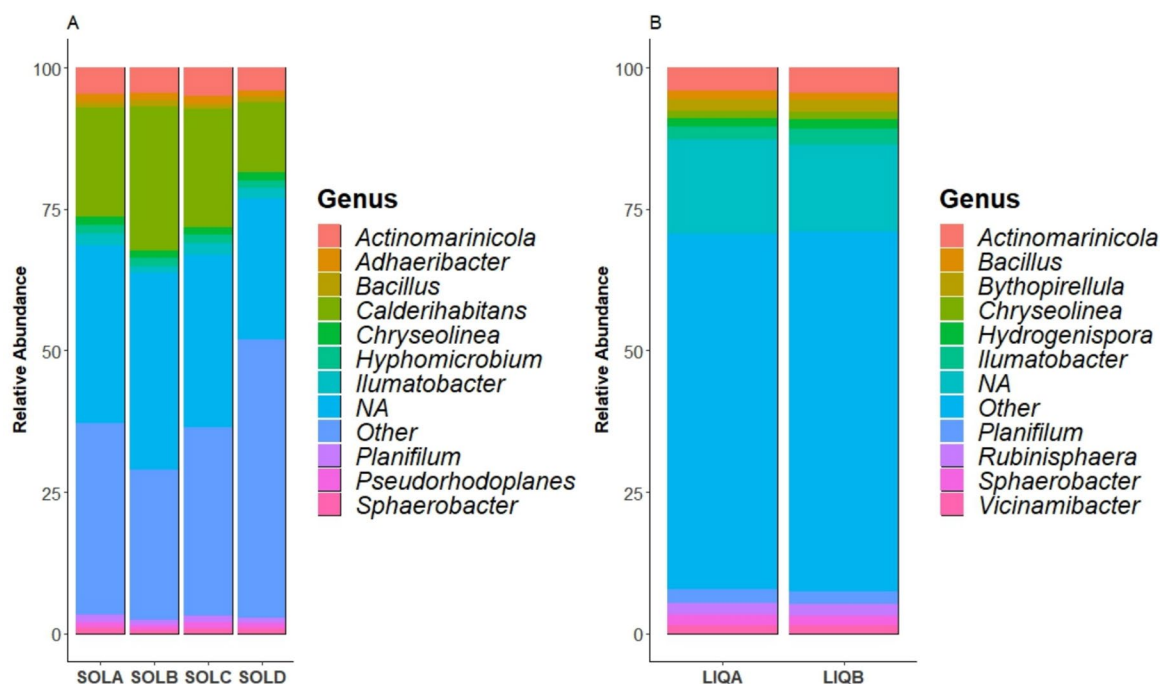


Fig. 9 Relative abundance of top 10 bacterial genera in solid (A) and liquid (B) vermicompost. The respective percentages of the top 10 genera are displayed in a bar chart for solid and liquid vermicompost.

SOLA, SOLB, SOLC, SOLD, and LIQA, LIQB refer to the four replicates for solid vermicompost and the two replicates for liquid vermicompost, respectively

include growth-promoting fungi. For example, members of the *Tulosesus* genus (only present in solid vermicompost) promote seed development (Pan et al. 2024). Members of the *Mortierella* genus are phosphate-solubilizing fungi that promotes the plant growth and phosphate uptake (Li et al. 2018; Zhang et al. 2020; Ozimek and Hanaka 2021). In addition, they tend to enhance the development of arbuscular mycorrhizae (AM) (Zhang et al. 2011; Tamayo-Velez and Osorio 2017). The genus *Aspergillus* is also of interest as it includes many species that can benefit the plant in a number of ways, for example by solubilizing phosphate and producing phytohormones (Bennett 2007; Chuang et al. 2007; Hung and Lee Rutgers 2016; Park et al. 2017). Members of the *Cephalotrichum* genus, which are abundant in liquid vermicompost (over 9% of relative abundance), are known to produce a range of secondary metabolites that may have antibacterial activities (Zhu et al. 2019). Fungi are known to produce a variety of secondary metabolites that may have insecticidal properties (Keswani et al. 2019), and it would be valuable to examine whether vermicompost fungi have these properties. Thus, biocontrol properties may be due to the ability of microorganisms present in vermicompost to enhance plant growth through improved nutrient uptake (e. g. phosphate), the production of phytohormones, their ability to induce plant resistance in systemic tissues, and the release of secondary metabolites and volatiles (Pineda et al. 2010). Although it highlights target microbial taxa, the limitation of

our study is that it remains descriptive and is based on short-read DNA sequencing, which offers limited resolution in the identification of microbial taxa. Long-read DNA sequencing, isolation and culture of these microorganisms, along with genome sequencing and in vivo experiments on plants and insects are necessary approaches to take this research a step further and unravel the role of these microbes in the biocontrol properties of vermicompost.

In conclusion, as the world faces the dual challenge of preserving the environment and producing enough food for a growing global population, there is a need to shift toward more natural pest control methods. Vermicompost and its liquid derivatives offer exceptional prospects and complements the range of environmentally friendly solutions such as the use of organic fertilizers (e. g. hoof, horn and chicken manure) and essential and mineral oils, which have also proven effective in controlling aphid populations (Garratt et al. 2010; Luo et al. 2022; Denoirjean et al. 2023). They could replace chemical fertilizers while helping to control insect pests and improve plant health. Moreover, by embracing an upcycling approach to organic matter, vermicompost and liquid derivatives not only reuse biological waste, but also improve soil structure, enrich the soil microbiota and strengthen the resistance of crops to abiotic stress. The use of these new biofertilizers is still in its infancy, and the study of application methods and modes of action is an essential step towards optimizing

Table 2 Characteristics of the main bacterial genera present in solid and liquid vermicompost

Bacterial genus	Sol	Liq	Characteristics	References
<i>Actinomarinicola</i>	+	+	A little-described, recently discovered genus, it grows in aerobic environments and is often associated with sulfur and iron biomining processes	He et al. (2020), Ayaz et al. (2024)
<i>Ilumatobacter</i>	+	+	A poorly know genus whose members thrive in sediments	Matsumoto et al. (2009, 2013)
<i>Planifilum</i>	+	+	A genus comprising thermophilic and aerobic members regularly found in compost and thermophilic sludge	Hatayama et al. (2005), Han et al. (2013), Yu et al. (2015), Zhang et al. (2021), Tseng et al. (2024)
<i>Chryseolinea</i>	+	+	A genus whose members are frequently isolated from the soil	Kim et al. (2013), Wang et al. (2018), Lee et al. (2019)
<i>Bacillus</i>	+	+	A large genus comprising an extensive and diverse set of species, some of which are rhizosphere-associated	Zeigler and Perkins (2021), Lengrand et al. (2024)
<i>Sphaerobacter</i>	+	+	A poorly described genus whose members have been isolated from thermophilically treated sewage sludge	Hensel et al. (1989)
<i>Calderihabitans</i>	+	-	A little-known genus: the only known species is <i>Calderihabitans maritimus</i> , a thermophilic, hydrogenogenic and carboxydophilic bacterium isolated from marine sediments	Omae et al. (2017)
<i>Adhaeribacter</i>	+	+	A genus whose members are generally found in the soil	Zhang et al. (2009), Elderiny et al. (2017), Kim et al. (2018), Chhetri et al. (2020)
<i>Hyphomicrobium</i>	+	+	Bacteria ubiquitous in water and soil and known for their denitrification capacities	Kloos et al. (1995)
<i>Pseudorhodoplanes</i>	+	+	A poorly described genus whose members have been reported to live in the soil	Tirandaz et al. (2015)
<i>Bythopirellula</i>	+	+	A poorly documented genus whose members are found in low temperature iron-hydroxide deposits	Storesund and Øvreås (2013)
<i>Hydrogenispora</i>	+	+	Anaerobic carbohydrate-fermenting bacteria found in anaerobic sludge	Liu et al. (2014)
<i>Rubinisphaera</i>	+	+	A poorly described genus that includes members isolated from sediments	Vitorino et al. (2022)
<i>Vicinamibacter</i>	+	+	A poorly described genus including soil bacteria	Huber et al. (2016)

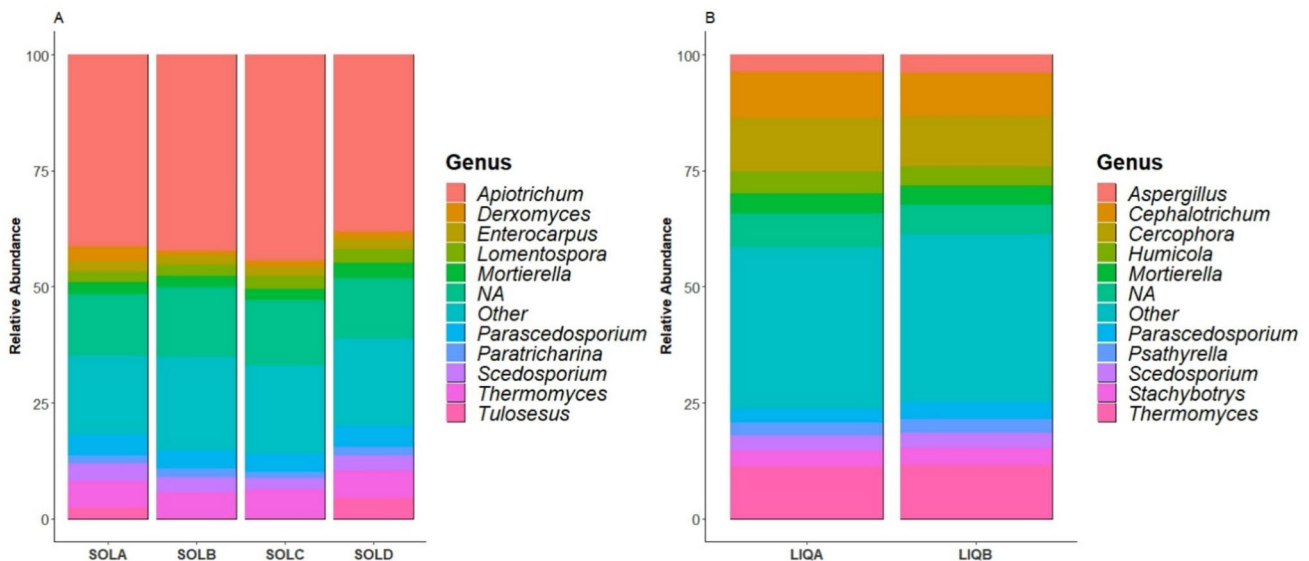


Fig. 10 Relative abundance of top 10 fungal genera in solid (A) and liquid (B) vermicompost. The respective percentages of the top 10 genera are displayed in a bar chart for solid and liquid vermicompost.

SOLA, SOLB, SOLC, SOLD, and LIQA, LIQB refer to the four replicates for solid vermicompost and the two replicates for liquid vermicompost, respectively

Table 3 Characteristics of the main fungal genera present in solid and liquid vermicompost

Fungal genus	Sol	Liq	Characteristics	References
<i>Thermomyces</i>	+	+	Widespread and frequently isolated thermophilic fungus known to produce high levels of cellulase, hemicellulase and chitinase. <i>Thermomyces lanuginosus</i> is the dominant fungus in maize straw composts. Some members increase the heat stress tolerance of associated plants	Singh et al. (2003) Fernandez-Lafuente (2010), Khan et al. (2015), Zhang et al. (2015); Ali et al. (2018, 2019)
<i>Parascedosporium</i>	+	+	A genus whose members are known for their lignocellulose-degrading properties	Lackner and de Hoog (2011), Oates et al. (2021)
<i>Scedosporium</i>	+	+	Filamentous fungi that are considered as emerging opportunists and are found in a variety of environments (usually rich in nutrients)	Kaltseis et al. (2009), Rougeron et al. (2018), Ramirez-Garcia et al. (2018)
<i>Mortierella</i>	+	+	Some strains are plant growth-promoting fungi (PGPF), notably by increasing biomass	Li et al. (2018), (2020), Zhang et al. (2020), Ozimek and Hanaka (2021)
<i>Apiotrichum</i>	+	+	Yeasts associated with decaying plant matter and rotting wood. Some species are known to produce high levels of microbial lipids	Cadete et al. (2017), Qian et al. (2021), Smáros et al. (2025)
<i>Dexomyces</i>	+	-	Poorly described genus that includes endophytic members	Wang and Bai (2008, Liu et al. (2012), Cui et al. (2021)
<i>Enterocarpus</i>	+	+	Poorly described genus found in soil	Jin et al. (2022)
<i>Lomentospora</i>	+	-	A genus that includes soil fungi, some members of which are considered emerging opportunistic pathogens	Konsoula et al. (2022)
<i>Paratricharina</i>	+	-	Poorly described Ascomycota	Van Vooren et al. (2015)
<i>Tulosesus</i>	+	-	A recently established genus. Some of its members have been found to induce seed germination and promote seed development	Pan et al. (2024)
<i>Aspergillus</i>	+	+	This is a highly diverse genus comprising over 300 species that can colonize a wide variety of environments. <i>Aspergillus</i> spp. benefit plants in several ways (e.g., phosphate solubilization and phytohormone production)	Bennett (2007), Chuang et al. (2007), Hung and Lee Rutgers (2016; Park et al. 2017)
<i>Cephalotrichum</i>	+	+	The genus includes fungi isolated from the rhizosphere soil. Some members are known to produce secondary metabolites with antibacterial and antitumoral activities	Zhu et al. (2019)
<i>Cercophora</i>	+	+	A little-described genus whose members thrive in the rhizosphere	Zhou et al. (2024), Li et al. (2024)
<i>Psathyrella</i>	+	+	<i>Psathyrella</i> is an important but relatively little-studied genus of basidiomycetes, which colonizes a variety of environments and is found in abundance in sewage sludge, for example	Padamsee et al. (2008), Petkova and Shilev (2023)
<i>Humicola</i>	+	+	A genus whose members thrive in the soil and are known to produce various molecules (enzymes, secondary metabolites) of pharmaceutical interest	Ibrahim et al. (2021, Chen et al. (2024)
<i>Stachybotrys</i>	+	+	A genus inhabiting cellulose-rich substrates. Many members of the genus are responsible for respiratory disorders in humans	Wang et al. (2015), Dyląg et al. (2022)

and generalizing their use. While our study demonstrates the biocontrol properties of solid and liquid forms of vermicompost on a cosmopolitan crop pest, it only scratches the surface of the study of modes of action, and future studies will need to demonstrate that these biocontrol effects can be generalized to other plants and pests. Our study was conducted under highly controlled conditions,

but field studies are needed to determine the benefits of vermicompost under more natural and challenging conditions. In terms of modes of action, vermicompost and its derivatives could induce systemic resistance in plants, i.e. the strengthening of their innate defense mechanisms to resist pathogens and parasites—a promising avenue for plant protection. However, much remains to be done to

understand the exact effects of the chemical or microbiological composition of these composts on plant health. Multiple interactions are possible, with additive or synergistic effects depending on the characteristics of the environment, soils and climatic components. To ensure a consistent effect, it is essential to standardize production processes and provide detailed information on the composition of the compost, to reduce variability and enhance reliability in agricultural applications. The study of microbiota using culture-dependent approaches is also an important step towards effectively deciphering the underlying effects linked to associated microorganisms. Our study points to genera of interest to target for isolation for plant trials. Overall, vermicompost constitutes an exceptional technological reservoir, with chemical and biological elements that could be diverted for agronomic purposes in the context of an agriculture seeking sustainable solutions.

Author contributions

MJE, GS, FR, MQ, SL and TH designed the study. MJE, JR, LGD, MA and DL performed the experiments. MJE, JR, DL and SB analyzed the obtained data. MJE and FR wrote the first draft of the manuscript. All authors contributed to the final draft of the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest GS, while continuing to teach at the ULB Faculty of Medicine, is partly in charge of the research and development department of PUR VER SA.

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