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Crop domestication reduces root volatile organic compounds diversity and abundance across species

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Abstract

Background and aims

: Plant domestication has been a long coevolutionary process with humans, profoundly shaping plant chemical traits. Secondary metabolites involved in plant interactions, such as volatile organic compounds (VOCs), may have been reduced in domesticates compared with crop wild relatives (CWRs), with possible effects on root-associated bacterial communities and crop resilience. However, the effects of domestication in root VOCs and the implications of such changes remain unknown.

Methods

We conducted a greenhouse experiment with eight crops (barley, beet, broad bean, cucumber, sunflower and tomato), comparing landraces and CWRs. Root VOCs were collected with SPME fibres and analysed by GC–MS; root-associated bacterial diversity was also characterized.

Results

Domesticated plants emitted almost three times less total root VOCs and had lower compound diversity than CWRs. Total net depletion of VOCs was also reduced in domesticates. Chemical composition was more dependent on crop identity than on domestication status, although for broad bean and barley an effect of the latter was seen. VOC diversity was negatively related to bacterial diversity, and VOC profiles explained bacterial and part of fungal composition.

Conclusions

In summary, domestication has reduced the quantity and diversity of root VOCs, potentially impairing chemical communication and response to soil biota; CWRs emerge as reservoirs of chemical and genetic traits essential for restoring crop resilience and sustainability.

1. Introduction

For most of human history, food came from wild plants and animals, until independent agricultural origins ~ 10,000 years ago initiated crop domestication (Alger et al., 2023; Crittenden & Schnorr, 2017; Diamond, 2002; Fuller et al., 2011, 2023; Gowdy & Krall, 2014; Zeder, 2015). This was a long and intense coevolutionary process between humans and some plant species that were able to thrive in nutrient-rich, emergent anthropogenic soils (Jones et al., 2021; Smith, 2007; Zeder, 2016). This potentially unintentional selection began around 10,000 years ago in multiple locations (Fuller et al., 2023) where some species could thrive in a progressively more controlled habitat. Later, it is believed that selective breeding promoted yield-enhancing traits in the domesticated lineages derived from wild relatives

(Purugganan, 2022). As a result, modern domesticated crops show many common traits that can be defined as the domestication syndrome. This includes several morphological and physiological traits such as taller growth, increased apical dominance, larger organs, synchronized flowering, reduced seed shattering, and a loss of dispersal mechanisms and defences (Doebley et al., 2006; Meyer & Purugganan, 2013). However, belowground domestication traits relating to plant-soil interactions are far less well documented.

Although domestication supported larger human populations, it also contributed to a reduction in genetic, agroecosystem and dietary diversity (Krug et al., 2023). Consequently, some crops may present a loss of resilience to stress factors such as drought and salinity (Roy et al., 2011). Furthermore, it has also altered plant ecological traits and interactions with other plants, herbivores and natural enemies (Milla et al., 2015), through changes in morphology and secondary metabolism that ultimately led to plant vulnerability (Chen et al., 2015). For instance, it has been seen that high fertilization regimes can contribute to changes in plant-microbe interactions decreasing mycorrhizal colonization efficiency in crops compared to CWRs (Martín-Robles et al., 2018). Moreover, maize (*Zea mays* L.) resistance to Western corn rootworm has declined through breeding under pesticide-intensive regimes (Bernal & Medina, 2018).

The interactions between plants and other organisms are universally mediated by volatile organic compounds (VOCs; Peñuelas et al., 2014), a diverse group of secondary metabolites, such as terpenes, methanol and aldehydes, involved in defence, communication and pollination (Abbas et al., 2022). Furthermore, VOCs also participate in plant-environment interactions, as increasing atmospheric CO_2 might lead to the synthesis of some allelopathic terpenoids (Bae et al., 2019). Not only this, but VOCs can directly affect atmospheric chemistry by participating in ozone and secondary organic aerosols formation (Wang et al., 2024). VOCs are produced across various plant organs, including leaves, flowers, and roots. Within these tissues, VOCs can be stored in specialized secretory structures to form internal reservoirs, emitted constitutively as background fluxes, or actively induced in response to environmental stressors (Peñuelas et al., 2014). By releasing these volatiles, plants significantly influence their surrounding ecosystems, such as by triggering defensive responses in neighbouring plants and altering herbivore distribution (Bergman et al., 2025). However, the emission amount and the VOC profile show a high amount of variability explained by taxa, physiological state, plant tissue or sampling method (Liu et al., 2023).

Like aboveground emissions, root VOCs mediate signalling, defence, and regulation of plant-microbe interactions (Delory et al., 2016; Karban et al., 2014 Insam & Seewald, 2010). Roots have been reported to emit a greater abundance and diversity of VOCs than leaves, including compounds such as glucosinolates and terpenoids (Bourtsoukidis et al., 2018; Van Dam et al., 2016). In barley, it has been seen that constitutively emitted VOCs from roots are dominated by fatty acid derivatives, similarly to aboveground emissions (A. Gfeller et al., 2013). The same study showed that compound detection was broadly affected by the media in which roots were exposed. Also, maize varieties with less infestation by wireworms showed higher and more diverse radicular VOC emissions than the more affected varieties,

highlighting a possible function of these blends to repel herbivores (la Forgia et al., 2020). Root emissions are also affected by their relationship with other organisms, such as mycorrhizal fungi. Species-specific profiles were seen in sorghum mycorrhized roots, exhibiting more alcohols, alkenes, ethers and acids, and less linear alkanes, than non-colonized plants (Sun & Tang, 2013).

Roots are not the sole source of belowground VOCs (Peñuelas et al., 2014). These compounds can also be synthesized or transformed by soil microbes(Del Giudice et al., 2008) or released abiotically through degradation of organic matter and soil solutions, especially for VOCs such as methanol and terpenes (Gray et al., 2010; Schade & Custer, 2004). Soils can both emit and absorb volatiles(Peñuelas et al., 2014) through microbial metabolism, diffusion and adsorption, in addition to previously mentioned passive root uptake (Jiao et al., 2023; Yang et al., 2024). Moreover, soil VOCs can influence biogeochemical processes by stimulating microbial respiration and altering nitrogen and methane dynamics (Amaral et al., 1998; Ramirez et al., 2010; Smolander et al., 2006). Despite their ecological importance, belowground VOCs remain understudied compared with those from aboveground tissues, as they present methodological challenges associated with sampling under non-induced stress conditions (Dicke & Baldwin, 2010).

Domestication has likely reshaped plant biochemical pathways, altering secondary metabolite profiles between crops and wild relatives (Meyer et al., 2012). Selection for yield and palatability often reduced pest resistance and chemical diversity, including defensive VOCs (Doebley et al., 2006; Milla et al., 2015; Whitehead et al., 2016). For instance, β-caryophyllene root emissions, which attracts entomopathogenic nematodes, are lower in domesticated maize compared to wild relatives (Bernal et al., 2023). Additionally, VOC diversity in maize and cranberry (*Vaccinium macrocarpon* Aiton) domesticates is reduced under herbivory (Rodriguez-Saona et al., 2011; Rowen & Kaplan, 2016). While leaf VOC changes under domestication are well documented, root VOC dynamics remain largely unexplored despite their role in ecologically important processes such as microbiome assembly, plant defence and signalling. Identifying differences between crops and their wild relatives could reveal new strategies to enhance beneficial soil interactions that may have been altered or lost during domestication. Ultimately, improved understanding of these patterns may contribute to improved crop resilience and fostering food security under current global change scenarios (Preece & Peñuelas, 2020).

Here we provide, to our knowledge, the first comparative assessment across six crops and their wild relatives (CWRs or wild relatives, from now on) on how domestication has shaped belowground VOC emissions, uptake, composition, and diversity. By simultaneously quantifying both VOC exchange and root-associated microbiome diversity, this study tests whether domestication-driven shifts in belowground chemical profiles are linked to microbial assemblage. We hypothesize that domesticated plants – which have an evolutionary history related to highly controlled conditions for food production – would have lost some secondary metabolites responsible for interactive functions. As a result, we expect that VOC emissions and uptakes in soil related to their root activity will be fewer and less diverse than in CWRs (H1). Additionally, because VOCs influence soil microbiota, we further expect that VOC

profiles correlate with root-associated microbiome diversity, linking chemical composition with microbiome assemblage (H2).

2. Methods

2.1 Plant material and growth conditions

We selected six annual crops representing six different families (Table 1). The chosen crops were barley, beet, broad bean, cucumber, sunflower and tomato, each with two levels of domestication: the landrace varieties (domesticated lineage, without modern breeding) and its closest wild relative. Seeds were obtained from the IPK Liebniz-Institut (GBIS, last updated August 13, 2025) and USDA Germplasm Resources Information Network (GRIN, last updated February 24, 2025) seed banks. Seeds were selected from origins close to the known domestication site whenever it was possible to minimize confounding effects of geographic adaptation.

Table 1
Crops used in this study, indicating the binomial name for both the domesticated plant and the wild relatives, and its botanic family. Between 3 and 5 different seed accessions (table S1) were used for each species depending on availability.

Crop	Domesticated species	Wild relative	Family
Barley	*Hordeum vulgare* L. subsp. *vulgare* cv.	*Hordeum vulgare* L. subsp. *spontaneum*	Poaceae
Beet	*Beta vulgaris* L. subsp. *vulgaris* cv.	*Beta maritima* L.	Amaranthaceae
Broad bean	*Vicia faba* L. cv.	*Vicia narbonensis* L.	Fabaceae
Cucumber	*Cucumis sativus* L. var. *sativus* cv.	*Cucumis sativus* var. *hardwickii* (Royle) Alef.	Cucurbitaceae
Sunflower	*Helianthus annuus* L. cv.	*Helianthus annuus* L.	Asteraceae
Tomato	*Solanum lycopersicum* L. cv.	*Solanum pimpinellifolium* L.	Solanaceae

Seeds were directly germinated in 7 L pots (20 cm × 20 cm × 25 cm) filled with a substrate consisting of washed river sand (maximum particle size of 4 mm), compost and field soil following a 5:4:1 proportion, respectively. The compost component consisted of a peat-free universal substrate (Geolia Universal Substrate; 70% bark and wood fibre, 20% coconut fibre, 5% perlite, 5% seaweed humus) (Geolia Universal Substrate). The field soil was obtained from the top 20 cm of a one-year fallowed field at the experimental fields of the Autonomous University of Barcelona and was described as loamy Typic Calcixerept soil. All three components were mixed until homogenous.

2.2 Experimental design

The experiment was conducted during spring–summer (from March to August) 2022 in a greenhouse at the Autonomous University of Barcelona (Bellaterra, northeastern Iberian Peninsula). Mean daytime temperature and relative humidity were 31.9 ± 8.2°C and 46.8 ± 23.4%, respectively, while mean nighttime temperature and relative humidity were 19.1 ± 4.9°C and 81.9 ± 13.5%, respectively. Each species was initially represented by ten replicate pots (one plant per pot). Accessions were used to maximize variability not accounted for by domestication and were therefore treated as independent replicates within treatments. However, accession availability was limited, so the number varied between species. Due to aphid and mite infestations during the growing season, affected plants were excluded from the analysis and final replication varied between four and nine individuals per species and domestication status (see Table S1). Pots were evenly distributed across four tables. Within each table, pot positions were randomly assigned at the beginning, and air temperature and relative humidity were continuously monitored (Lascar EasyLog EL-USB-2 data loggers).

All pots were irrigated via drip system under identical conditions, with watering volume adjusted to plant growth. Each table also included two bare-soil control pots receiving the same irrigation regime. Soil moisture was measured weekly in all pots using a Delta-T ML3 probe. Mean soil moisture during plant growth was of 14.7 ± 4.7%.

2.3 VOCs sampling using SPME

Belowground VOCs were sampled from a subset of aphid-free plants (n = 67), representing the six crop species and two domestication levels. Sampling occurred once plants had reached maturity, being at maximum vegetative size and having started fruit or grain production. This timing was assessed on an individual plant basis, so that the phenological stage of individual plants was comparable at the time of sampling (Table S2). At the time of sampling, most plants were reaching full maturity and starting to show the expected signs of leaf senescence typical of annuals. Beta vulgaris individuals did not reach full reproductive maturity, likely reflecting their facultative biennial growth habit. Samplings were conducted between 10:00 and 14:00 from June to August to ensure similar physiological conditions. We used solid phase microextraction (SPME) fibres (100 µm polydimethylsiloxane, Torion Technologies Inc., Utah, USA) directly inserted into the soil to passively adsorb VOCs emitted under natural, non-induced conditions (Tholl et al., 2021). Before sampling, fibres were preconditioned at 250ºC for 20 minutes under helium flow rate of 100 ml min^{-1} and preserved in glass tubes sealed with a Teflon-coated cap. A small hole (~ 2 mm diameter, 10 cm depth) was made in the soil adjacent to the plant stem using a sterilized stainless-steel rod. A pipette tip was gently inserted to hold the fibre in place, and the SPME fibre was exposed to the soil atmosphere for 20 min. The fibre exposure time was based on pilot tests to avoid saturation. Control samples included bare soil controls (1–3 per sampling day), air controls (1–2 per day), and blank fibres that were transported to the field but not exposed, to detect possible contamination. After sampling, SPME fibres were returned to the glass tubes and stored at 4ºC until laboratory analysis.

2.3.1 GC-MS analysis

The VOCs sampled with SPME fibres were analysed using a 7890A gas chromatograph coupled to a 5975C mass spectrometer inert 154 MSD/DS Performance Turbo EI System (Agilent Technologies, Santa Clara, USA) equipped with a HP5MS capillary column (30 m × 0.25 mm × 0.25 µm; Agilent J&W) using a transfer line at 250 ºC. VOCs were thermally desorbed from the SPME fibres in the injector port at 250°C in splitless mode. Analyses were conducted in full-scan mode, ranging from 35 to 350 m/z. For the chromatographic analysis, helium was used as the carrier gas with a column flow of 1 mL min^{-1}. Oven temperature was programmed from 35°C (5 min hold) to 150°C at 15°C min^{-1} (5 min hold), then to 250°C at 15°C min^{-1} (3 min hold), and finally to 280°C at 30°C min^{-1} (5 min hold).

Chromatograms analyses were conducted using Enhanced ChemStation software (Agilent Technologies). Each peak was assigned a compound using mass spectra contrasted in the NIST 05a and Wiley 275 mass spectral data and PARADISe software. Compounds were identified by comparing mass spectra with the NIST 05a and Wiley 275 libraries using PARADISe software. The criterion to select which compounds were retained is further explained later in the section 2.6.1. When available, retention indices were compared with literature values for confirmation (Johnsen et al., 2017). Mean blank values were subtracted from all samples to remove background signals. Air control data were available for one sampling date and applied as correction factors across all measurements, since variation among days was negligible. Mean peak areas from bare-soil controls were subtracted from plant samples to isolate VOCs of root and rhizosphere origin.

Quantification was based on calibration curves obtained from external pure standard solutions of 3-hexen-1-ol (RT 7.98), α-pinene (9.18), myrcene (10.01), 3-carene (10.29), limonene (10.53), dodecane (12.40), and α-humulene (15.30), prepared in hexane at different dilution factors and analysed under the same conditions as the experimental samples (Llusià et al., 2022; Yang et al., 2024). Calibration curves ($R^2 > 0.95$) slopes were used to calculate an empirical response factor (RF) using a reference value (S_{ref}) for to approximately represent each compound class (non-terpenoid, monoterpene, sesquiterpene) and sampling date. However, these were not specific calibration factors for each compound and RFs included a marked variability (Table S9). Therefore, quantification must be taken as an approximation based on the representativeness of standard solutions for found root volatiles. VOC blends of multiple compounds are difficult to quantify simultaneously, supposing a limitation of this type of studies(A. Gfeller et al., 2013) .

The VOC quantity (µg g^{-1} root L^{-1} soil) for each compound was estimated as described in (1).

$$Q = \frac{S_{obs} \times RF}{S_{ref} \times M_{root} \times V_{soil}}$$

(1)

where *Sobs* is the observed peak area (a.u.), *RF* the response factor (µg), S_{ref} the reference area (a.u.), M_{root} the root mass (g), and V_{soil} is the soil volume (L). For V_{soil}, we considered pot volume to facilitate the comparison between pots, as all sources of soilborne VOCs must come at most from all soil within

the pot once excluded the controls. Therefore, the amount of VOCs must be considered as apparent amount. We used the SPME fibres as an approximation of the whole soil system due to experimental limitation, although less mobile particles might tend to be underestimated compared to the highly diffusive ones (Degtyarenko et al., 2008). Positive values obtained after air and soil control corrections represent a mixture of plant, microbial, and abiotic VOCs influenced by root activity in the headspace surrounding the SPME fibre, which we collectively interpret as net root-associated emissions. Conversely, negative values after control corrections may be caused by many different factors, including root uptake, microbial consumption, soil adsorption and subtraction artifacts among others. Henceforth, these values will be referred to as net depleted VOCs.

2.4 Root and microbial sampling and sequencing

Plants were harvested approximately one week after VOC sampling. Roots were gently shaken and rinsed with sterile distilled water to remove loosely adhering soil. Root-associated microbial communities were sampled by collecting 5–10 fine root fragments per individual (≥ 0.25 g fresh weight). Samples were immediately stored at − 20°C, ground in liquid nitrogen, and transferred to sterile Eppendorf tubes at − 80°C until DNA extraction. Microbial DNA was extracted using the DNeasy PowerSoil Pro Kit (Qiagen) following the manufacturer's protocol. Extraction blanks were included to monitor potential contamination.

Amplification and sequencing were conducted at the University of Antwerp following Radujković et al. (2025). Briefly, the bacterial 16S rRNA (V4) gene region was amplified using the 515F–806R primer pair (Caporaso et al., 2011), and the fungal ITS1 region using the ITS1–ITS2 primers (Stoeck et al., 2010). PCR reactions (25 µL total volume) contained 1 µL of DNA template, 0.5 µM of each primer, 1× PCR buffer, 200 µM dNTPs, and 1 U of Phusion High-Fidelity DNA polymerase (New England Biolabs, Ipswich, MA, USA). PCR conditions for 16s and ITS region were as follows: initial denaturation at 98°C for 60 s, followed by 25 (30 for fungi) cycles of: denaturation at 98°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 30 s; and an additional extension of 72°C for 10 min. The success of amplification was tested with electrophoresis on 1.5% agarose gel, where it was confirmed that negative controls remained empty otherwise PCR was repeated. PCR products were diluted 50-fold and a second PCR was performed using dual barcoded primers with Illumina adapters (2 × 300 bp paired-end) and amplicons were pooled in equimolar concentrations into a single library. The library was purified using the QIAquick Gel Extraction Kit (Qiagen, Venlo, the Netherlands) and quantified using qPCR (KAPA Library Quantification Kits, Kapa Biosystems, Wilmington, MA, USA).

The FASTQ files were cleaned, merged and filtered using the R package dada2 (v.1.16.0). In summary, first primers were removed, by length for 16S, and using Cutadapt (v3.7) for ITS. Trimming and filtering criteria were chosen based on the analysis of the decline of Q scores along the length of the sequences, considering the total length of the sequence (e.g. relatively short length of 16s V4 region allows large merging overlap as an additional quality control). Truncation was set to F = 270, R = 200, for 16s; F = 250, whereas ITS was truncated using truncQ = 2 and trimRight = 50. Quality filtering was set with maxEE = 2 for 16s and maxEE_F = 3 and R = 5 for ITS. Merging minimal overlap was set to 50 bp for 16s and kept

the default for ITS. The resulting output was an amplicon sequence variant (ASV) table for prokaryotes and fungi. Taxonomic assignment of prokaryotic ASVs (composed predominantly of bacteria) was performed against the SILVA database (version 138.1; Quast et al., 2013), and fungal ASVs were assigned using the UNITE database (release April 2024; Kõljalg et al., 2005).

2.5 Plant biomass measurements

After microbial sampling, plants were separated into leaves, stems, roots, and reproductive structures. Each fraction was oven-dried at 60°C for three days and weighed to determine organ-specific and total dry biomass. These data were subsequently used for correlation analyses with VOC emissions and microbial community composition.

2.6 Data analysis

2.6.1 General data treatment

For VOC analyses, the dataset included all compounds detected per pot. Only compounds with a spectral match quality ≥ 90% (NIST library) were retained. Potential contaminants such as column siloxanes and phthalates were identified based on their occurrence in blanks and known artefact profiles and were excluded. This filtering yielded a final set of 52 compounds out of 310 initially detected (Table S3). For these compounds, additional detections with match quality between 80–90% were retained when supported by co-detection in other samples and bibliographical evidence of their presence as root VOCs (following standard practice in ecological VOC studies; Tholl et al., 2021). The resulting dataset was divided into emission and net depletion subsets by summing all positive and negative compound values per pot, respectively. Compounds that displayed both positive and negative values across samples were included in both subsets according to their direction per observation.

One sample (a domesticated cucumber) showing abnormally high total emission values -two orders of magnitude above the dataset mean - was identified as an outlier (exceeding the 99th percentile of total VOC emissions) and excluded from analyses.

All analyses were performed in R version 4.3.0 (R Core Team, 2025). Model diagnostics were evaluated using the DHARMa package (version 0.4.6; Hartig, 2024) and residuals were checked to ensure that there were no over-dispersion or zero-inflation. We compared models that potentially answered our hypotheses and selected those that show significance with the lowest AIC values that had a higher adjusted R2. We kept interaction terms whenever they were significant and met the above explained conditions

2.6.2 Total emission and net depletion concentrations

To evaluate differences in total VOC emission and net depletion, generalized linear models (GLMs) with a Gamma distribution and log link were used, given the strong right-skewness and heteroscedasticity of the data. Each model included domestication status and crop as fixed effects. Random effects for crop identity and table position were initially tested, but the models did not converge due to a not large

enough sample size and were therefore excluded. Model residuals and fitted value relationships were visually inspected to confirm the adequacy of the Gamma distribution. Models were fitted using the glmmTMB() function from the glmmTMB package (version 1.1.7; Brooks et al., 2025). Adjusted R^2 values were computed using the delta method (r.squaredGLMM() in MuMIn, version 1.48.4; Bartoń, 2024). Type II Wald χ^2 tests were applied to models without interaction terms, and Type III tests when interactions were present, using the car package (version 3.1-2; Fox et al., 2024). When significant interactions were detected, pairwise contrasts were performed with the emmeans package (version 1.8.8; Lenth, 2024).

Predicted means and 95% confidence intervals on the response scale were obtained using the ggpredict() function from ggeffects (version 2.3.0; Lüdecke, 2024). Observed and predicted values were visualized on log-transformed y-axes using ggplot2 (version 3.4.4; Wickham, 2016), with units expressed as $\mu g\ g^{-1}$ root L^{-1} soil.

2.6.3 Composition differences

Differences in VOC composition between domesticated crops and their wild relatives were explored separately for emissions and net depletion values using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities. Ordinations were computed with two dimensions and 1000 random starts using the metaMDS() function in the vegan package (version 2.6-4; Oksanen et al., 2024). Three pots without detected emissions and one pot without any detected net depletion were excluded. No additional data transformation was applied because VOC abundances were already standardized by root mass and soil volume, and preliminary analyses showed consistent ordination patterns with or without transformation. The final stress value was reported to assess ordination quality. Centroids were calculated as the mean NMDS scores for each domestication status within crop type.

To test for compositional differences, permutational multivariate analyses of variance (PERMANOVA) were performed using the adonis2() function (vegan) with 9999 permutations, including domestication status and crop type as predictors. Homogeneity of multivariate dispersions was assessed using the betadisper() function in vegan based on Bray–Curtis distances. No significant differences were found among groups ($p > 0.05$), indicating that the PERMANOVA assumptions were met. Separate analyses were run for emission and net depletion datasets. When overall effects were significant ($p < 0.05$), pairwise PERMANOVA comparisons for each crop were performed with the pairwiseAdonis package (version 0.4; Martinez Arbizu, 2017), applying false discovery rate (FDR) correction for multiple testing. For interaction effects, we applied adonis2() function to each crop to determine the significance of the domestication effect in the composition of VOCs.

To visualize the dominant contributors to observed differences, the five compounds with the highest mean emission or net depletion values were identified for each crop type and domestication level. These were represented using bar plots created with ggplot2. The same approach was applied to chemical groups classified by compound type (Table S3). These visualizations were intended to aid interpretation rather than to represent formal statistical significance.

2.6.4 Changes in VOC diversity

VOC alpha-diversity per pot was quantified using the Shannon index (H'), based on the relative abundance of detected compounds, calculated with the diversity() function in the vegan package. Shannon diversity was chosen because it integrates both compound richness and evenness, providing a robust representation of chemical complexity. Separate indices were calculated for emitted and net depleted VOC datasets.

Homoscedasticity was assessed using the Fligner–Killeen test ($p < 0.05$), and model residuals were visually inspected for normality. Linear models were fitted with domestication status and crop type as fixed predictors. Random effects for species and table position were initially tested but the models failed to converge due to a not large enough sample size and were therefore excluded. Type II Wald χ^2 tests were applied to models without interactions, and Type III tests when interactions were present, using the car package. Pairwise contrasts were performed with the emmeans package when significant interaction effects were detected. Eta squared (η^2) was obtain using eta_squared function in effect size (version 1.0.3; Ben-Shachar et al., 2020) to address the partial contribution to variance of each predictor.

Model predictions and 95% confidence intervals were obtained using the ggpredict() function in ggeffects. Observed and predicted values were plotted in the original diversity scale using ggplot2.

2.6.5 Root microbial diversity relationships with VOC diversity

The relationship between root VOC α-diversity (Shannon index) and the α-diversity of root-associated bacterial and fungal communities was evaluated using linear models. Bacterial and fungal Shannon diversity indices were computed with the diversity() function in the vegan package. Microbial data were previously rarefied to account for variation caused by unequal sequencing depth across samples, as explained in the next paragraph. One pot lacking microbial data due to sampling failure was excluded. Each model used bacterial or fungal diversity as predictor of VOC diversity, following the same procedures as described for VOC α-diversity analyses. Observed data and fitted regression lines with 95% confidence intervals were visualized using ggplot2.

To explore associations between VOC and microbial community composition, we tested if VOC composition could explain microbial assemblages. For this, non-target ASVs were eliminated and the resulting microbial ASV tables were rarefied to correct for amplification bias using the rrarefy() function, with depths of 10,000 reads for bacteria and 6,000 for fungi, chosen to retain over 90% of samples while minimizing loss of low-abundance ASVs. Bray–Curtis dissimilarity was used for both VOC and microbial matrices, as suitable for non-normal and zero-inflated ecological data. Then we performed distance-based redundancy analyses (dbRDA) using the capscale() function in vegan, with microbial community matrix as the response variable and VOC matrix as the explanatory variable. Variable selection for VOC compounds was performed with ordiR2step() (9999 permutations), and model significance and adjusted R^2 values were obtained via permutation ANOVA tests. When analyses were significant, sample distances correlated with several CAP axis that were further used for the ordination (as shown in Fig. 5).

Correlations between dissimilarity matrices of VOCs and microbial communities were further assessed using Mantel tests (Bray–Curtis distance, Spearman correlation, 9999 permutations) implemented in vegan. All analyses were conducted separately for bacterial and fungal datasets. Graphical representations of dbRDA ordinations were generated with ggplot2.

2.6.6 Effect of air temperature and humidity

To evaluate potential environmental influences on VOC fluxes, we tested whether total VOC emission and net depletion values correlated with ambient air temperature (°C) and relative humidity (%). Mean temperature and humidity values recorded during VOC sampling were used as predictors in quadratic models, with total VOC emission and net depletion concentrations as response variables. Models with just temperature as predictor were found significant (Table S8; Figure S2), although residual diagnostics (DHARMa adjusted quantile test, $p < 0.05$) indicated deviations from the expected distribution, suggesting violation of model assumptions. Adding the humidity factor enhanced the model fitting and exposed a significant interaction between these two factors. However, temperature and humidity measures were highly correlated in our data, therefore it was not biologically relevant and we did not further interpretate them (Figure S3). We treated air temperature and humidity as qualitative controls for greenhouse environmental conditions, because our experimental setup lacked the measurement of the main variables affecting VOCs behaviour in soil (i.e. soil temperature, moisture and structure; Peñuelas et al., 2014), Consequently, results must be interpreted cautiously.

3. Results

3.1 Total VOC emission and net depletion concentrations

Overall, domestication was associated with a reduction in total root VOC emissions across crop lineages (GLM, $\chi^2 = 8.56$, $p = 0.003$), with domesticated plants emitting less than their wild relatives. On average, CWRs emitted nearly three times more VOCs than domesticated plants (0.072 µg g^{-1} root L^{-1} soil vs. 0.022 µg g^{-1} root L^{-1} soil; $p < 0.01$). Crop type also had a significant effect (GLM, $\chi^2 = 20.10$, $p = 0.001$, $R^2 = 0.33$), indicating that total emissions differed among crop species (Fig. 1a). Wild relatives of cucumber, beet, and broad bean exhibited the highest mean emission levels (predicted means = 0.16, 0.15, and 0.11 µg g^{-1} root L^{-1} soil, respectively), whereas their domesticated counterparts showed consistently lower values (0.05, 0.05, and 0.03 µg g^{-1} root L^{-1} soil; Table S4). The interaction term was non-significant, suggesting that the domestication effect was generally consistent across crop types.

For VOC net depletion, domesticated plants showed overall lower values than CWRs among the different crops (GLM, $\chi^2 = 30.49$, $p < 0.0001$). Mean depletion values in CWRs were more than six times higher than those from domesticated plants (0.066 µg g^{-1} root L^{-1} soil vs. 0.011 µg g^{-1} root L^{-1} soil; $p < 0.0001$). Again, net depletion values changed for the different crops, showing a significant effect in the model (GLM, $\chi^2 = 25.24$, $p < 0.001$, $R^2 = 0.50$; Fig. 1b). Among all crops, wild varieties of cucumber and broad bean exhibited the highest predicted depletion values (predicted means = 0.22 and 0.10 µg g^{-1} root L^{-1}

soil, respectively), contrasting with lower values in their domesticates (0.03, and 0.02 μg g^{-1} root L^{-1} soil; Table S5).

3.2 VOC composition differences

The NMDS ordination of VOC emissions (2D stress = 0.199) showed no general separation according to domestication status, although a significant interaction effect between crop and domestication was found in the analyses (PERMANOVA, $p < 0.01$, pseudo-$R^2 = 0.09$). Broad bean showed a significant domestication effect in emitted VOC composition (Dom: n = 9, CWR: n = 4; $p < 0.001$), explaining a 27.9% of observed variance. Also, a marginal but non-significant effect was detected in barley ($p = 0.0661$, pseudo-$R^2 = 0.12$; Fig. 2a).

The same pattern was found for net depleted VOCs, where crop and domestication interaction was again significant (PERMANOVA, $p < 0.05$, pseudo-$R^2 = 0.09$), as seen in Fig. 2b (stress = 0.205). In this case, barley was the only crop that showed a significant distinction in composition of net depleted VOCs between CWR and domesticate samples ($p < 0.01$, pseudo-$R^2 = 0.24$).

Analysis of the top five emitted compounds per crop and domestication status revealed pronounced variation among species and domestication status (Figure S1). Members of the Asteraceae family (lettuce and sunflower) displayed particularly similar emission profiles across domesticated and wild forms, dominated by 2-methoxy-[1]benzothieno[2,3-c]quinolin-6(5H)-one and 1,1,2-trifluoro-2,5-bis(trifluoromethyl)-hexane. In contrast, other crops showed divergent profiles between domesticated and wild relatives, although no consistent directionality was observed across species.

Net depletion profiles showed greater overlap between domesticated and wild plants (Figure S1). For example, three compounds were detected in both wild and domesticated cucumber (nonanal, benzothiazole, and salicylaldehyde) and in wild and domesticated broad bean (pentane, hexane, and β-ionone epoxide). Benzothiazole (detected in six of eight crops) and nonanal (five of eight) were among the most frequently detected depleted compounds across species.

When VOCs were grouped by chemical family, several crop-specific trends in relation to domestication emerged (Fig. 3). Sunflower (Asteraceae) was dominated by heterocyclic and halogenated compounds in both domesticated and wild forms. Although these compound classes were also abundant in barley, they decreased in the domesticated variety. Cucumber wild relatives emitted high levels of terpenoids that were qualitatively lower in domesticated forms, where heterocyclic compounds became relatively more abundant. In broad bean, reduced total emissions in domesticated plants were primarily driven by lower fatty acid derivatives.

For net depletion, patterns by chemical class were largely consistent across crops and domestication statuses, with a few notable exceptions. Broad bean wild relatives showed a qualitatively higher terpenoid depletion than their domesticated counterparts, which lacked detectable heterocyclic

compounds. In tomato, while the relative proportions of compound classes were similar, total VOC net depletion was lower in domesticated individuals.

3.3 Diversity of VOC profiles

The diversity of emitted VOCs, calculated using the Shannon index, was significantly positively correlated with both crop type ($p < 0.001$, $\eta^2 = 0.40$) and domestication status ($p < 0.05$, $\eta^2 = 0.05$) in a linear model (adjusted-R^2 = 0.39). Wild relatives consistently exhibited higher chemical diversity in their emitted VOC profiles (mean H' = 1.27 ± 0.10) compared to domesticated varieties (H' = 0.94 ± 0.11). The interaction between crop type and domestication status was not significant, indicating that the domestication effect was consistent across species (Fig. 4a). Among individual crops, tomato showed the highest VOC emission diversity overall, with mean H' values of 2.21 for wild and 1.88 for domesticated individuals, followed by sunflower (1.31 and 0.99, respectively) and beet (1.28 and 0.96; Table S6).

In contrast, diversity of net depleted VOCs was significantly explained by the interaction between crop type and domestication status ($p < 0.001$, adjusted $R^2 = 0.57$; Fig. 4b). This indicates that domestication correlation with net depleted VOC diversity was species-specific. Barley showed a significant reduction in diversity in domesticated plants compared with their wild relatives (mean H' = 1.99 vs 0.90, respectively; $p < 0.0001$). Aversely, beet domesticates followed the opposite trend, showing significant higher diversity values (2.03) than their wild relatives (1.51). For the remaining crops, no consistent or significant domestication trend was detected. Despite a significant overall domestication effect in the model ($p < 0.0001$), the strong interaction with crop type underscores the variable impact of domestication across species. The highest mean net depletion diversity was observed in domesticated sunflower (mean H' = 2.07), followed by domesticated beet (2.03) and cucumber (1.98), while the lowest diversity occurred in the broad bean domesticates (H' = 0.63; Table S7).

3.4 Root microbiota relationship with VOCs

Microbial analyses resulted in 1,277,970 bacterial and 1,237,591 fungal sequences from chosen samples. For bacteria, we detected an average of 19,661 reads (12,725 min. – 27,101 max.), consisting of 3029 ASVs. Rarefaction at 10,000 samples let 2,966 ASVs with which we conducted the analyses. Also, the mean fungal reads detected per sample was 22,502 (6,758 min. – 50,550 max.) for a total of 984 ASVs. Data was rarefied at 6,000 samples, which excluded no samples. The resulting dataset consisted of 902 ASVs. PERMANOVA analyses showed that bacterial composition was correlated with domestication in barley ($p < 0.05$) and broad bean ($p < 0.01$), after finding a significant interaction between crop and domestication status ($p < 0.05$, adjusted-$R_2 = 0.076$). Beta dispersion was found significant for crop ($p < 0.01$), but not for domestication status ($p = 0.25$). The ordination plot (Figure S5a) indicates that both location and dispersion effect might be happening at the same time. However, crop type was generally correlated with fungal communities' composition ($p = 0.0001$), while no tendency was detected according to domestication status ($p = 0.26$). Dispersion was also found to be significantly

different among crops ($p < 0.0001$) and for domestication status ($p < 0.05$), thus results must be interpreted carefully (Figure S5b).

Linear models linking VOC and microbial α-diversity revealed a significant negative relationship between the Shannon diversity of emitted VOCs and bacterial diversity (β = − 0.50, $p < 0.001$; Figure S3a), whereas no relationship was detected for fungal diversity (β = − 0.07, $p = 0.53$; adjusted $R^2 = 0.16$; Figure S3b). A similar pattern was observed for net depletion of VOCs, which showed a negative association with bacterial diversity (β = − 0.29, $p < 0.05$; Figure S3c), but not with fungal diversity (β = − 0.14, $p = 0.13$; adjusted $R^2 = 0.08$; Figure S3d). These results indicate that higher bacterial α-diversity was generally linked to lower VOC diversity, while fungal α-diversity appeared unrelated to root VOC richness.

Multivariate analyses further demonstrated that root VOC composition significantly correlated with bacterial community composition. A dbRDA based on emitted VOCs explained a considerable proportion of bacterial compositional variance (adjusted $R^2 = 0.147$, $p = 0.001$; Mantel test $p < 0.01$; Fig. 5a). The main compounds driving this relationship were 2,2,4,6,6-pentamethyl-Heptane (PMH cpd, $p = 0.001$), 1,1,2-Trifluoro-2,5-bis(trifluoromethyl)hexane (F_3-hex$(CF_3)_2$, $p = 0.001$), 1-Acetyl-6-(acetylamino)-5-methyl-1H-indazole (Ac-NHAc-Me-indaz, $p < 0.05$), tribromo methane ($p < 0.05$), β-bisabolene ($p < 0.05$), 4-(benzoyloxy)-2H-pyran-3-one (BzO-Pyranone, $p < 0.05$) and 1-methyl-6-(1-oxoethyl)-3-oxo-4-prop-2-ylidene-cyclononene (Me-Ac-oxo-C_9 ylid, $p < 0.05$). Net depleted VOCs also accounted for significant variation in bacterial composition (adjusted $R^2 = 0.117$, $p = 0.001$; Mantel $p < 0.001$; Fig. 5b), mainly explained by β-ionone-epoxide ($p = 0.001$), l-α-pinene ($p = 0.001$), β-bisabolene ($p < 0.01$) and Me-tetracycloheptane ($p < 0.01$).

In contrast, no clear relationship was detected between VOC composition and fungal community structure (Mantel $p = 0.07$). However, dbRDA models significantly related fungal composition with three emitted compounds (adjusted $R^2 = 0.075$, $p = 0.001$; Fig. 5c), namely PMH cpd ($p = 0.001$), 7,8-Dimethoxy-1,2,4,5,10a,10b-hexahydrobenzo[de]pyrrolo[3,2,1-ij]quinoline (DM-HPQ, $p < 0.01$) and β-bisabolene ($p < 0.05$). Reversely, net depleted VOC composition correlated with fungal communities (mantel $p < 0.001$), although no specific VOC explained this relation (dbRDA $p > 0.05$). This means that samples that differ in fungal composition also differ in net depleted VOC blends, while there is no lineal structure remaining after the dimension reduction.

4. Discussion

Belowground volatile organic compounds (VOCs) play a central role in mediating plant–soil interactions, influencing root–microbe communication, allelopathy, and plant responses to environmental cues (Delory et al., 2016; Jiao et al., 2023). The domestication process, by selecting for traits related to yield and productivity, may have unintentionally reduced plants' investment in chemical signalling. In this study, we examined how domestication shaped root VOC emission and net depletion across six major crops and their wild relatives, aiming to determine whether these changes could have altered the chemical interface between roots and their environment.

4.1 Total VOC emission and net depletion concentrations

Our results provide the first evidence of a consistent, cross-species reduction in root VOC emissions associated with domestication, with potential consequences for both biotic and abiotic interactions in the rhizosphere (Fig. 1a). These findings align with the generalized loss of defences during domestication, caused by the trade-off between the selection for yield and secondary metabolite production (Meyer et al. 2012). The intensive modification of agricultural environments seems to have caused crops to rely more on management activities rather than ecological signalling for resource acquisition or defence (Milla et al., 2015). Root VOC emission mechanisms remain poorly understood, as roots lack both cuticular barriers and stomatal structures that modulate volatile fluxes aboveground (Bergman et al., 2025). Moreover, rhizosphere microbes also contribute substantially to total VOC emissions (Chowdhury et al., 2019), further complicating the interpretation of plant versus microbial sources. Thus, the biochemical and ecological processes underlying the observed reductions remain to be fully resolved.

Significative differences in emission rates were also observed among the six studied species, likely reflecting species-specific physiological or morphological traits. Because emission rates were normalized to root mass rather than surface area, variation in root architecture could have influenced apparent emission intensity. Nevertheless, emission rate does not appear to be a phylogenetically conserved trait, as even closely related species within the same genus (e.g., *Centaurea* L.) exhibit contrasting sesquiterpene emission profiles (V. Gfeller et al., 2019).

Patterns of net depleted VOCs followed a similar trend (Fig. 1b); different values among crops but a general reduction in domesticates. There is evidence that a loss of signal perception capacity could reduce defence priming (Brosset & Blande, 2021). While this aligns with our results, careful interpretation of net depletion reduction must be done as it can be attributable to several soil factors. Differences in root-associated microbiota may also contribute, since microbial metabolism can serve as a major sink for soil-borne VOCs (Jiao et al., 2023). Furthermore, while aboveground absorption occurs mainly via stomata, the mechanisms enabling VOC uptake by roots remain largely unknown (Matsui, 2016). Future work integrating microbial community composition with plant physiological traits will be crucial to disentangle these processes and assess whether VOC exchange capacity represents an overlooked component of crop functional diversity.

4.2 Compositional changes in VOC profiles

The plants studied exhibited a wide diversity of compounds in their root VOC profiles, both for emission and net depletion. Contrary to expectations, no consistent domestication effect was associated with specific compositional changes. Instead, domestication effect was crop-specific for both emitted and depleted volatile blends, showing effects just for two species (Fig. 2). This pattern suggests that root VOC composition may be shaped by phylogenetic constraints rather than domestication. Thompson et al., 2024), discussed that pathways underlying secondary metabolite synthesis could have been already fixed within each lineage prior to agricultural selection pressures, thus resulting in more similar blends

between domesticates and CWRs. Also, root architecture and physiology should be considered potential drivers of interspecific diversity, possibly masking domestication patterns in these blends (Wen et al., 2019). The expected difference was seen for broad bean (regarding emitted compounds) and barley (both for net depleted and emitted, marginally). These findings align with the hypothesis that VOC compositional shifts would reflect adaptive responses to the functional and environmental differences between wild and cultivated habitats (Bernal et al., 2023), although only for some species.

A domestication-related shift in compound chemical families was observed in broad bean, where emissions of fatty acid derivatives qualitatively decreased compared with its wild relative (Fig. 3). These compounds, commonly detected in root VOC blends (Peñuelas et al., 2014), are linked to 13-lipoxygenase activity and are central to defence-related signalling against both biotic and abiotic stress (Van Dam et al., 2016). Their reduction in domesticated broad bean may therefore indicate a diminished capacity for belowground chemical defence.

Among net depleted VOCs, two compounds—nonanal and benzothiazole—were nearly ubiquitous across all species (Figure S1). Nonanal, a hydrophobic fatty acid–derived aldehyde, plays a well-established role in plant defence signalling during fungal infection (Brambilla et al., 2022; Li et al., 2021), yet it is also emitted constitutively under unstressed conditions (Wildt et al., 2003). Exposure to nonanal has been shown to trigger bacterial and fungal resistance responses in diverse crops (Girón-Calva et al., 2012; Sharifi et al., 2022) and has recently been proposed as a sustainable elicitor to enhance yield and seed quality in common bean (Razo-Belmán et al., 2024). In our study, domesticated barley and beet showed reduced nonanal net depletion compared to their wild relatives. As mentioned before, this can be the result of compound factors, including plant uptake, soil adsorption and microbial activity, among others (Jiao et al., 2023). Nevertheless, a lower capacity to respond to defensive cues would potentially reduce the resilience to soil-borne pathogens (Brosset & Blande, 2021), highlighting the importance of disentangling the processes beneath the observed patterns. Similarly, β-ionone-epoxide —a defence-related apocarotenoid (Brambilla et al., 2022)— showed lower depletion values in domesticated broad bean. Conversely, depletion of nonanal remained comparable between sunflower, and cucumber, underscoring the species-specific nature of VOC net depletion profiles.

The dynamics of nonanal in soil further explain part of this variability. Its moderate hydrophobicity (log Kow ≈ 3.5–3.6) promotes adsorption to soil organic matter and root surfaces, increasing local availability while limiting volatilization (Degtyarenko et al., 2008). Moreover, aldehydes such as nonanal are rapidly metabolized by soil microbes or oxidized to nonanoic acid and can also react with root exudates (Jiao et al., 2023). Thus, both chemical reactivity and microbial degradation likely contribute to species-specific depletion patterns.

Benzothiazole was another compound widely present in net depletion values. It is of particular interest because it can originate from both microbial activity and anthropogenic pollution (e.g., tyre additives). It is commonly reported as an antibacterial VOC (Rani et al., 2023) and has been shown to be absorbed and metabolized by carrot roots (Wu et al., 2024). Other less abundant depleted compounds, including 2-

ethyl-1-hexanol (Y. Zhang et al., 2024) and tridecane (Lee et al., 2012), also exhibit antipathogenic properties. The widespread presence of these volatiles in agricultural soils could suggest that plants may have evolved conserved uptake mechanisms to detect and metabolize stress-related or contaminant VOCs, a capacity that could be adaptive in anthropogenically altered environments (Oikawa & Lerdau, 2013).

A small number of halogenated compounds were detected in both the emitted and depleted profiles (Fig. 3). Because terrestrial plants are not known to synthesize these specific halogenated phytochemicals, their presence is highly likely derived from exogenous sources, such as greenhouse background air, soil legacy contamination, or analytical artifacts. We retained these compounds in our untargeted pipeline to accurately reflect the total chemical environment the roots and microbiome were exposed to, but they should not be interpreted as plant-derived metabolites. Interestingly, the observed net depletion of some of these synthetic compounds suggests potential absorption or degradation by the root-microbiome complex, a phenomenon previously noted in studies of halogenated contaminant uptake (Fan et al., 2020), though this remains outside the primary ecological scope of this study and no causation can be established.

Overall, compositional analyses indicate that root VOC chemistry is mainly constrained by phylogeny, with domestication producing functionally relevant modifications in specific crops and compound classes, that may be linked to defence and pollutant metabolism.

4.3 Emitted and net depleted VOC diversity

In line with total emission trends, the diversity of emitted VOCs was consistently lower in domesticated varieties compared with their wild relatives (Fig. 4). This finding suggests that domestication might have reduced the chemical complexity of root volatile blends. Interestingly, this pattern contrasts with reports in other systems. For example, the diversity of herbivory-induced volatiles increased in six Cucurbitaceae species following domestication, although it was also observed that prolonged coexistence with herbivores reduced root volatile diversity (Thompson et al. 2024). Similarly, the increased diversity of maize root VOCs found in domesticates influenced herbivore preference (Bernal et al. 2023). These discrepancies suggest that the direction of domestication effects on chemical diversity may depend on the ecological context and plant compartment studied. Aboveground tissues, which are directly exposed to herbivory and pollination pressures, may have experienced selective maintenance or enhancement of chemical diversity, whereas belowground tissues, under the protection of managed soils and reduced biotic stress, may have undergone relaxed selection for secondary metabolite variability (Gaillard et al., 2018).

The observed skewed relative abundances could result from metabolic canalization, where specific biosynthetic pathways become upregulated or fixed during domestication at the expense of others, because of different adaptation strategies (Lemoine et al., 2023). This narrowing of chemical profiles may have consequences for ecological interactions in the rhizosphere, potentially reducing the range of microbial or signalling partners that plants can effectively engage with.

4.4 Microbial diversity relationship with compound diversity

VOC alpha diversity, both for emitted and net depleted compounds, was negatively correlated with bacterial alpha diversity but showed no significant relationship with fungal alpha diversity (Figure S3). This suggests that plants hosting more diverse bacterial communities tend to show less chemically diverse sets of emitted and depleted VOCs. To explain this relationship, carbon consumption and antimicrobial activity should be considered. On the one hand, VOC production correlates with pathogen suppression activities, limiting the growth of some sensitive bacterial species and impoverishing their communities (Raza et al., 2020). On the other hand, a more diverse bacterial community may be able to metabolize or transform a broader range of volatile compounds, thereby reducing the observable diversity of VOCs in the rhizosphere (Raza et al., 2021). Competitive use of VOC-derived carbon sources and co-metabolic degradation could also contribute to this pattern. The absence of a similar relationship for fungi might reflect the generally slower metabolic response and lower catabolic diversity of fungal communities toward volatiles, or a lesser role of VOCs as signalling cues in fungal recruitment.

Evidence from other systems supports this interpretation. In wheat (*Triticum durum* Deff.), domesticated varieties exhibited reduced VOC diversity but higher root endophytic bacterial diversity, although with lower functional diversity compared to their wild relatives (Deng et al., 2024). This suggests that domestication may have promoted more taxonomically diverse but functionally convergent microbial assemblages, potentially linked to simplified VOC emission patterns.

It is important to note that the use of Shannon diversity indices may mask more specific associations between individual VOCs and microbial taxa. Indeed, several emitted (n = 7) and net depleted (n = 4) compounds were significantly associated with bacterial and three with fungal community composition (Fig. 5). This finding supports the idea that plant-specific metabolic traits influencing VOC synthesis and uptake pathways can shape the establishment of distinct bacterial communities during coevolution (Sharifi et al., 2022).

However, not all found correlated VOCs can be unequivocally assigned to plant production, as the interplay between VOCs and microbiota is highly reciprocal. Plants can use VOCs to recruit or stabilize specific microbial partners, as shown in tomato, where root-associated bacterial inoculation induced leaf emissions of β-caryophyllene that, in turn, promoted microbiome similarity among neighbouring plants (Kong et al., 2021). Conversely, microbes can modulate plant VOC metabolism, altering plant–plant and plant–herbivore interactions (Russo et al., 2022). Genetic and functional shifts in microbiomes under domestication further illustrate this bidirectional relationship: wild rice relatives harbour microbiomes richer in nitrogen-fixation genes (Chang et al., 2025), while bacterial taxa specific to certain cultivars may alter VOC emission or uptake patterns (Kumar et al., 2024). Such effects would remain undetected when relying solely on diversity indices, highlighting the need for integrative approaches combining metabolomic, genomic, and network-based analyses.

Overall, our findings suggest that domestication may have decoupled the diversity of root-emitted VOCs from microbial community complexity. This chemical–microbial imbalance could have consequences for soil communication networks, nutrient cycling, and the resilience of cultivated plants to environmental stress.

4.5 Limitations and future perspectives

Measurements of VOCs are highly sensitive to sampling methods. In this exploratory study, we selected direct SPME fibre injection because it enables minimally invasive detection of root emissions and soil net depletion under non-induced stress conditions (Tholl et al., 2021). However, SPME adsorption efficiency is strongly affected by fibre coating chemistry, temperature, and humidity (Fontez et al., 2025), and soil matrices can substantially reduce VOC recovery by adsorption and diffusion limitations (Voyard et al., 2024). These factors may have biased absolute flux estimates, particularly for low-molecular-weight or highly polar compounds, which could partially explain the lower emission values recorded in some species. Standardizing exposure times and using the same fibre type across all samples minimized comparability issues, but complementary quantitative methods such as Proton Transfer Reaction–Time of Flight–Mass Spectrometry (PTR-ToF-MS) would provide real-time dynamic measurements to refine flux estimates when combined with SPME (Brennan et al., 2022). Also, choosing sampling date according to phenological stage suppose a methodological trade-off, as chronological exposure time to the soil environment could influence the cumulative microbial recruitment and subsequent VOC profiles.

Although ambient air temperature correlated with VOC emissions and net depletion concentrations (Figure S2), other missing variables, like soil temperature, structure and moisture, are known to be the key modulators of VOC synthesis and volatility (Jiao et al., 2023). Future work should include the monitoring of these variables to reduce microclimatic bias. Given that VOC responses to temperature often display nonlinear or threshold behaviour, such high-resolution measurements may reveal subtle treatment effects masked in this study.

The present study includes an unequal distribution of accession number among crops, which may cause within-crop diversity to be overlooked and could affect the general interpretation of the results. However, at least three different accessions were present for each factor. Also, here we compared landraces and their wild relatives, thereby focusing on early domestication effects. However, most modern cultivars have experienced additional selective pressures due to intensive breeding for yield and the chronic use of fertilizers and pesticides (Krug et al., 2023). Including modern varieties would allow discrimination between initial domestication changes and more recent agroecological adaptations. Wild relatives often display greater resistance to abiotic and biotic stress and harbour valuable genetic diversity for crop improvement (F. Zhang & Batley, 2020). Understanding how domestication has altered belowground chemical and microbial traits could therefore inform breeding programs aimed at restoring lost functional diversity (Preece & Peñuelas, 2020).

Finally, belowground VOCs remain poorly integrated into terrestrial carbon and signalling models. Incorporating soil and root VOC fluxes into atmospheric carbon budgets could improve predictions of ecosystem feedbacks, as these compounds represent an overlooked yet potentially significant carbon source (Isidorov & Zaitsev, 2022).

In conclusion, by demonstrating that domestication consistently reduced root VOC diversity and emission fluxes, this study highlights belowground chemical diversity as a potentially eroded functional trait. Moreover, differences among crops underscore the need to understand the crop-specific patterns in belowground traits that may shape distinct interactions and physiological pathways. Further research into how these changes affect microbial recruitment, nutrient cycling, and plant resilience will be essential for developing more sustainable and self-regulating crop systems in the face of global environmental change.

Declarations

5.3 Competing interests

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

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5.2 Author contributions

(CRediT)

5.4 Data availability

The data that support the findings of this study, sequencing data and the scripts used to treat them will be published in an online repository upon the acceptance of this manuscript.

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Figures

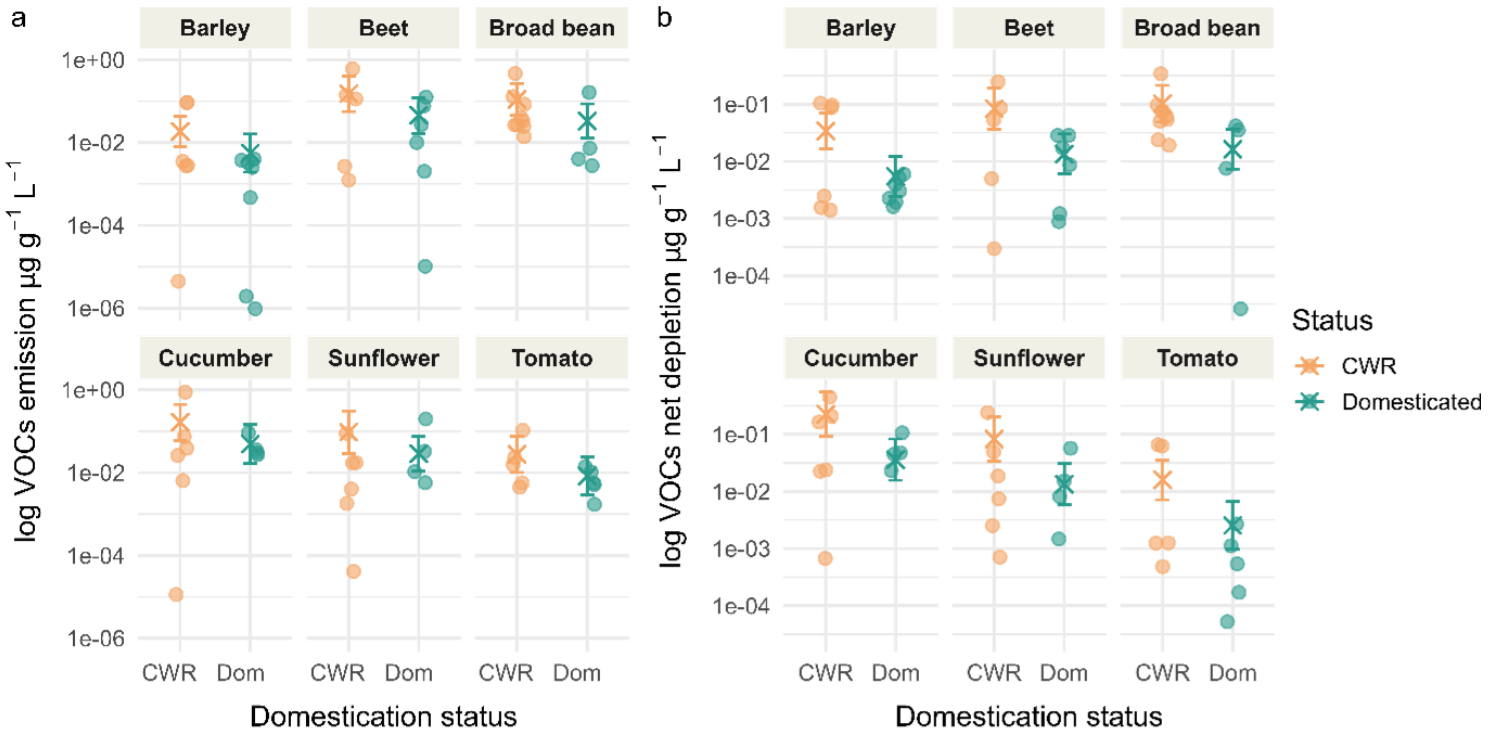


Figure 1

VOC emissions (a) and net depletion concentration (b) per gram of root and litre of soil (on a natural log scale) for crop wild relatives (CWR, in orange) and domesticated (Dom, in green) of the eight studied species. Each point represents a plant pot. Mean predicted values with its 95% IC from the GLM are represented with a cross and whiskers, respectively. Asterisks show significant differences (·, $p < 0.06$; *, $p < 0.05$; ***, $p < 0.001$) from emmeans.

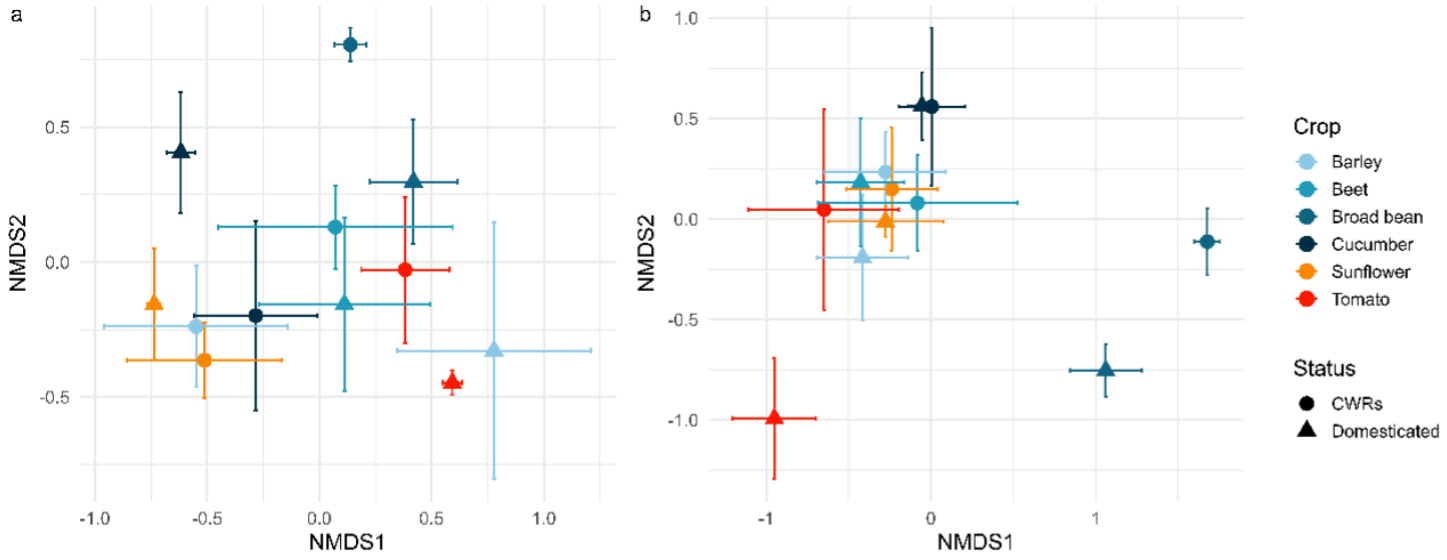


Figure 2

Plot of the scores of the NMDS conducted with the emitted (a) and net depleted (b) VOC composition (mean ± SE; n = 67) with stress = 0.199 and stress = 0.205, respectively. Colour grading is attributed by crop species. Domestication status is indicated by shape; circle for crop wild relatives (CWRs) and triangle for domesticates.

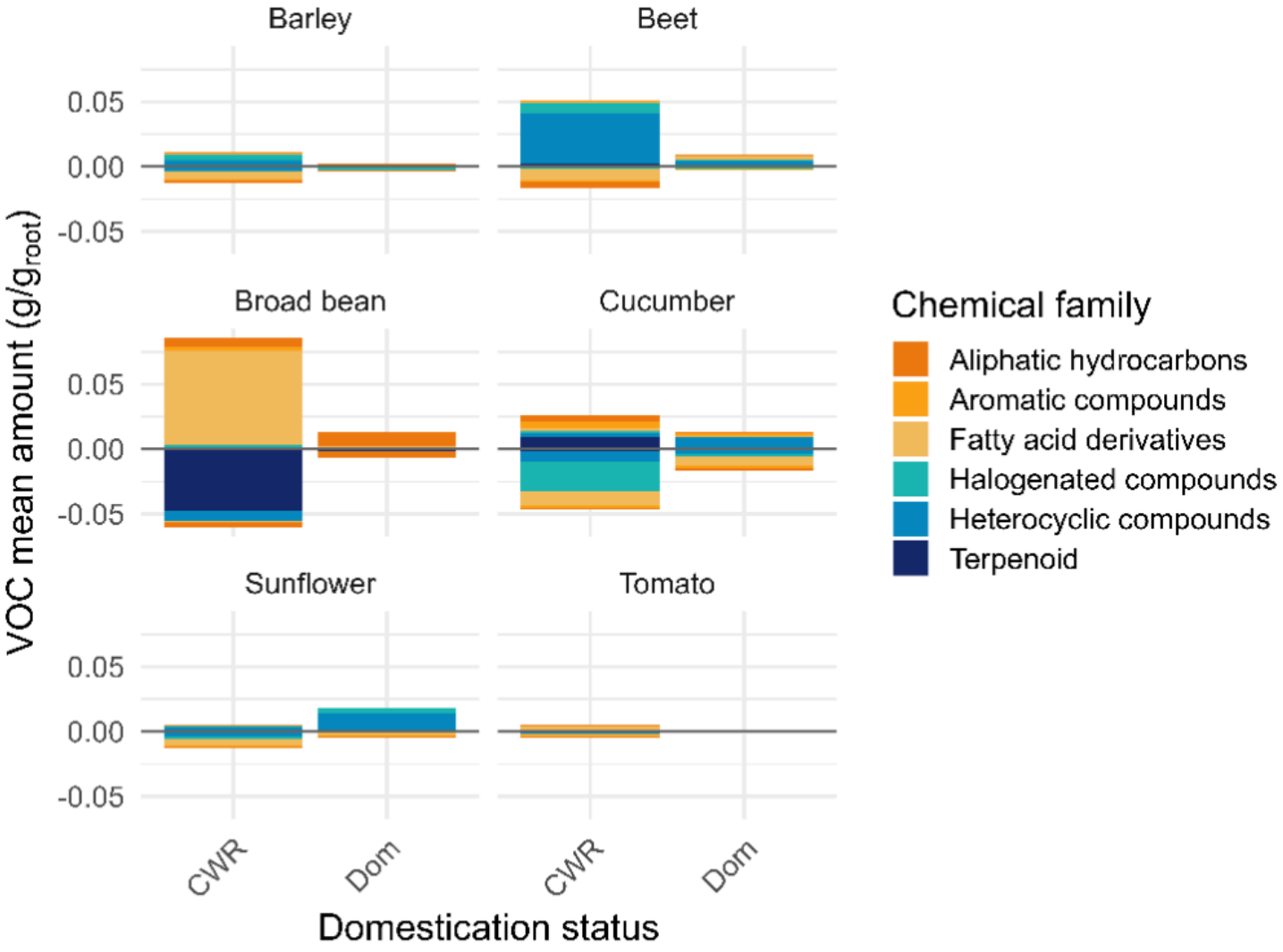


Figure 3

Mean of the emitted and net depleted chemical groups of all compounds per gram of root and litre of soil for each species and domestication status (n = 67). Each chemical family is represented as a coloured bar as listed in the legend on the right side: aliphatic hydrocarbons (orange), fatty acid derivatives (light orange), aromatic (amber), halogenated (teal), heterocyclic compounds (cyan-blue) and terpenoids (navy blue).

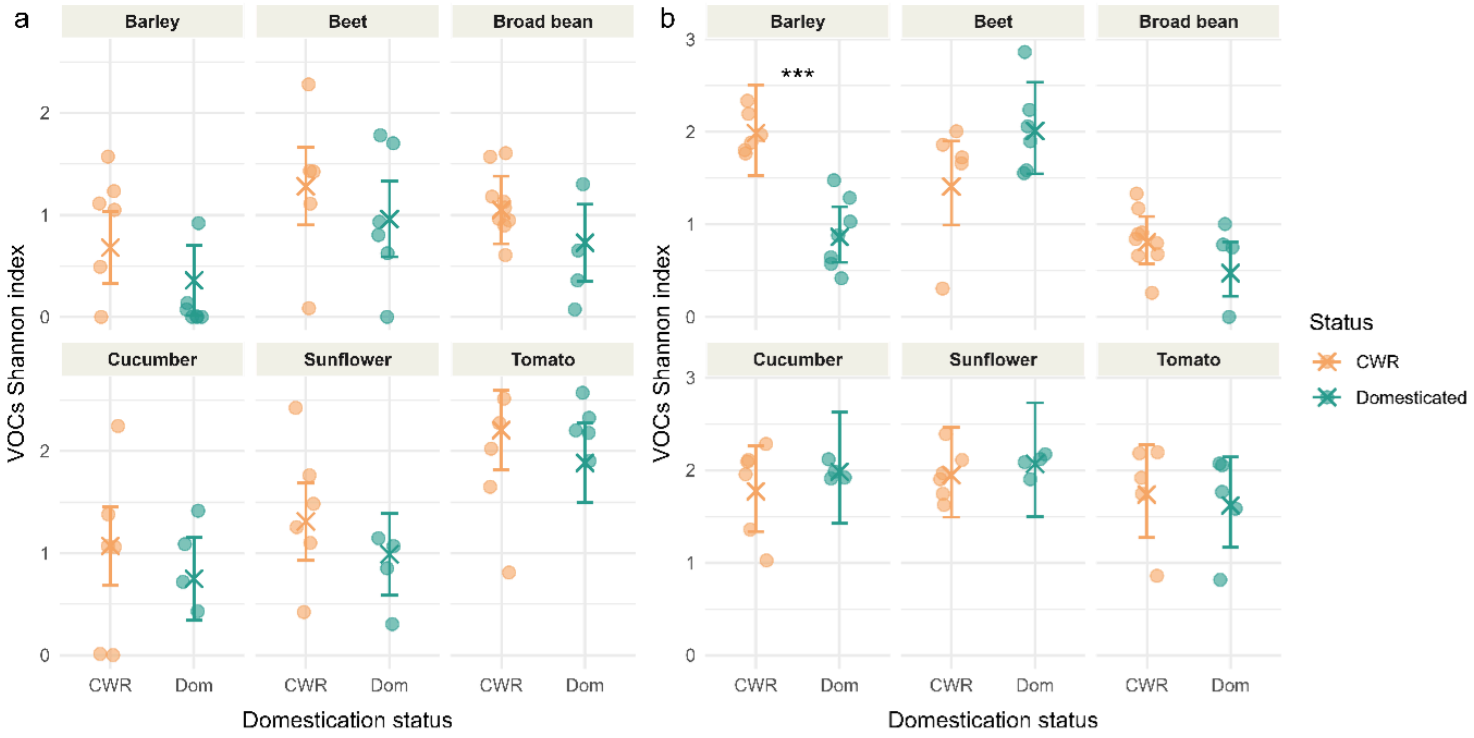


Figure 4

Alpha diversity of VOCs emitted (a) and net depleted (b) VOCs in Shannon index for crop wild relatives (CWR, in orange) and domesticated (Dom, in green) of the eight studied species. Each point represents a plant pot. Mean predicted values with its 95% IC from the linear model are represented with a cross and whiskers, respectively. Asterisks show significant differences (***, $p < 0.001$; *, $p < 0.05$) from emmeans.



Figure 5

dbRDA with bacterial composition explained by root emitted (a, n = 65) and net depleted (b, n = 65) VOCs and fungal composition explained by root emitted VOCs (c, n = 55). Each point represents a plant pot, colour indicates crop species and shape indicates the domestication status. Significant compound relations to the CAP axis are shown in blue arrows with the compound name on its tip. The cumulative proportion of squared Bray distance for CAP1 and CAP2 axis are of 0.15 for emissions, 0.14 for net depletion concentrations and 0.10 for fungi and emissions.

Supplementary Files

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