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Joint effects of inter-specific and intra-specific diversity of tomato volatile profiles on antixenosis against *Tuta absoluta*

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With 4 figures and 1 table

Abstract: Since volatile organic compounds (VOCs) shape plant defenses against pests, ecologists strive to understand their sources of variation. The worldwide distribution of tomato offers an ideal system to explore the ecological diversity of VOCs produced by plants supporting a large range of local adaptations. In this study, we analyzed the diversity of VOC profiles released by 29 accessions of tomato belonging to five species with different natural histories and including domesticated plants and wild relatives. In addition, olfactometer assays were performed on 10 accessions characterized by strong differences in VOC emissions to test the consequences on host-plant location by a major pest specialized on solanaceous plants, *Tuta absoluta*. Based on 77 VOCs detected, our results suggest that the large diversity of volatile profiles reflect different biogeographic areas. A phylogenetic tree was constructed to test phylogenetic drivers in VOC emissions. The richness of volatile profiles and sesquiterpenoid emissions were relatively high in ancestral branches and decreased exponentially with evolution according to early-burst patterns. In olfactometer assays, we identified four repellent accessions belonging to *S. pennellii*, *S. habrochaites* and *S. cheesmaniae*. This study points out the importance of inter- and intra-specific diversity of VOCs in antixenosis. Further, our results suggest that methyl salicylate, β -myrcene and sesquiterpenoids such as (3E,7E)-4,8,12-trimethyltrideca-1,3,7,11-tetraene or α -curcumene could serve as repellents against *T. absoluta*. In a greenhouse, we confirmed the biological relevance of agroecological research interested in screening repellent plants. Bridging chemical ecology with phylogenetic approaches helps to better understand the evolution of mechanisms supporting anti-herbivore plant defenses.

Keywords: biodiversity; phylogeny; evolution; volatile organic compound; plant-insect interactions; South American tomato pinworm

1 Introduction

While up to a third of carbon assimilated by plants is converted into volatile organic compounds (VOCs), these emissions are assumed to be under selective pressure since ecologists suggested their roles in plant fitness. A large body of knowledge show that VOCs convey information governing plant defenses against insects. More particularly, these

compounds are considered key features of antixenosis, i.e. plant characteristics that reduce the location or the acceptance by herbivore insects. So far, research on antixenosis, as well as other plant defense categories, has been pivotal to understand plant-insect interactions albeit much more remains to be done to integrate evolutionary questions into ecological approach. For example, while abiotic factors can also result in changes in VOC, it is reasonable to assume that

local adaptations to complex environments including different biophysical parameters can influence antixenosis. In this context, we took advantage of the worldwide diversity of tomato to explore variations of VOCs released by plant lineages spanning a vast range of biogeographical and environmental adaptations. In turn, we investigated the mechanistic consequences on plant defenses against pests. From an agroecological perspective, because these defenses operate before pest damages, they offer a sound strategy to screen plants of interest to develop cropping systems less reliant on insecticides.

In the tomato clade (*Solanum* sect. *Lycopersicon*), although phylogenetic approaches have brought insights to understand how rapid adaptive variations have facilitated the colonization of various environments (Pease et al. 2016), research addressing adaptive sources of phenotypic variations has long revolved around morphological traits related to fruit architecture and mating systems underlying the diverse degree of gametophytic compatibility (Moyle 2008). However, phylogenetically explicit analyses are also powerful to track biochemical variations related to plant defenses. In wild lineages like milkweeds, evolutionary models based on trait distribution over phylogenetic trees have provided important milestones to understand variations of non-volatile compounds involved in plant defenses against insects (Agrawal et al. 2009). For agronomic plants like tomato, comparative approaches between modern cultivars and wild relatives are generally used to study how plant traits related to anti-herbivore defenses have evolved during the domestication process (Ferrero et al. 2020). To date, even if outstanding studies have compared the diversity of morphological traits like trichome density (Lucatti et al. 2013) or the production of phenolic compounds (Paudel et al. 2019) between cultivated tomato and wild relatives, they generally do not encompass more than one or two genotypes per species. As a corollary, these typological approaches assume that few phenotypes mirror vast categories of clades that have been subjected to different selective pressures resulting in various domestication syndromes and local adaptations. While only few comparative studies have addressed VOCs emissions in tomato and wild relatives (Paudel et al. 2019), to our knowledge, none of them have wrapped variations of volatile profiles with a phylogenetically-explicit framework across clade-wide investigations. This line of research could provide an interesting compass to seek for genetic resources supporting antixenosis against *T. absoluta*.

Tuta absoluta (Meyrick, Lepidoptera: Gelechiidae) is an oligophagous insect that feeds on solanaceous species, with a preference for the cultivated tomato *Solanum lycopersicum* (Subramani et al. 2021). It is one of the most important invasive tomato pests worldwide (Desneux et al. 2010; Mansour et al. 2018; Biondi et al. 2018), originating from Peruvian central highlands (Desneux et al. 2011). The wide geographic distribution and high diversity of solanaceous species, particularly domesticated ones, has facilitated the

rapid and continuous spread of *T. absoluta* into new regions (Biondi et al. 2018). While it has been demonstrated that females use VOC released by tomato to locate host plants (Bawin et al. 2015), some authors have shown that they prefer cultivated tomato as compared to wild relatives (Proffitt et al. 2011).

In this study, we combined plant volatile and phylogenetic analyses with behavioral assays to address the following questions: (i) what are the differences in volatile profiles at the intra- and interspecific levels within *Solanum* sect. *Lycopersicon*? (ii) does phylogeny explain these differences? (iii) what are the consequences on antixenosis? (iv) which specific VOCs promote repellency against *T. absoluta*? More generally, we attempted to bridge evolutionary and chemical ecology to better understand the evolution of mechanisms supporting the first barrier of anti-herbivore plant defenses.

2 Materials and methods

2.1 Plant materials and ecological diversity of tomato and wild relatives

Along with big-fruited cultivars of domesticated tomato (*S. lycopersicum* var. *lycopersicum*) and wild cherry tomatoes (*S. lycopersicum* var. *cerasiforme*), we explored the ecological diversity of VOC profiles and antixenosis of four wild species: *S. habrochaites*, *S. cheesmaniae*, *S. pennellii*, and *S. galapagense* (see Peralta et al. 2008 for complete taxonomy and Razifard et al. 2020 for history of domestication). Altogether, these species cover a large spectrum of the ecological diversity found across the 14 species or subspecies related to cultivated tomato. Geographically, *S. cheesmaniae* and *S. galapagense* are endemic from the Galapagos Islands, whereas *S. habrochaites* and *S. pennellii* have different distribution areas in the Andes, from Ecuador to Peru and Peru to Chile, respectively (Moyle 2008). In nature, *S. pennellii* is associated to arid habitats while *S. habrochaites*, *S. cheesmaniae* and *S. galapagense* are adapted to semi-arid habitats and *S. lycopersicum* var. *cerasiforme* is generally located in humid areas (Conesa et al. 2017). More generally, Ramírez-Ojeda et al. (2021) have shown that these species belong to very different ecological clusters including various ecogeographic areas, climatic descriptors and edaphic factors. At the same time, these authors have stressed different levels of intra-specific diversity across species. In our study, for each species, we integrated several accessions that can be considered as population reflecting intra-specific diversity. Accordingly, even if ecological diversity of *S. galapagense* and *S. lycopersicum* var. *lycopersicum* was restricted to one and two accessions respectively, we studied 3, 6, 7 and 10 different accessions of *S. pennellii*, *S. lycopersicum* var. *cerasiforme*, *S. habrochaites* and *S. cheesmaniae*, respectively (see Table S1 for geographic origins and habitat characteristics of each accessions). We adapted the number of accessions

tested per species according to their potential as genetic reservoirs of natural plant defenses for cultivated tomato.

2.2 Plant growth

For germination, seeds were sown in small pots (7 × 7 × 8 cm) containing potting soil substrate ('Einheitserde EUROHUM') and covered with aluminum foil for 72 hours. For *S. cheesmaniae* and *S. galapagense*, seeds were previously soaked in bleach (2%) for 30 to 45 min, respectively, to accelerate the degradation of the outer seed coat and, thereby, promote germination. After two weeks, seedlings were transplanted in bigger pots (12.8 × 12.8 × 20 cm) with same substrate. All the plants were grown in a climatic chamber under the following conditions: 24 ± 1 °C, 60–70% RH, 16:8h [light:dark] photoperiod. Depending on tomato species and accessions, we used 4–6-week-old plants to collect VOCs and test behavioral choice of *T. absoluta*. Thereby, we were able to account for growth heterogeneity linked to genetic diversity to study plants at a vegetative stage with analogous biomass.

2.3 Insect rearing

Tuta absoluta colony was initiated from larvae developing on naturally infested tomato plants from the INRAE Sophia Antipolis experimental station. These larvae were introduced into rearing cages (60 × 60 × 60 cm) containing renewed fresh cultivated tomato plants to allow their development. Cotton wools saturated with 50% honey in water, were used to feed adult moth in the cages (Salama et al. 2015). The cages were placed in a climatic chamber (24 ± 1 °C, 60–70% RH, 16:8h [light:dark] photoperiod). Gravid females were used for behavioral assays one day after mating as described in Ataide et al. (2017).

2.4 Headspace collection of volatiles released by domesticated tomato and wild relatives

VOCs emitted by uninfested plants at vegetative stage were sampled using a dynamic push-pull headspace trapping system. One whole plant was enclosed in a 12-L glass chamber in which incoming and outgoing airflows were controlled by two separate pairs of pump and flow meter. Incoming airflow was cleaned through a 1L-charcoal filter to limit contaminants from ambient air. Prior to VOC collections, glass chambers with plants were purged overnight at 2 L.min⁻¹ to remove burst emissions that could result from plant manipulation. Based on preliminary analyses, VOC collection was performed at 400ml.min⁻¹ for 30 min to have the best signal/noise ratio. The outgoing airflow passed through a cartridge filled with 200 mg of Tenax™ TA of 35/60 mesh to trap VOCs. Before VOC captures, cartridges were conditioned at 250 °C during 20 min under 50 ml min⁻¹ of nitrogen. Plant volatile emissions were sampled concomitantly on 5 plants in 5 identical independent trapping systems. In parallel, we sampled VOCs in glass chambers with no plant

material, pots or pots filled with substrates to identify compounds that were not released by plants during collection. The 29 accessions described above were collected randomly during 8 weeks based on different experimental batch of plants that were sown continuously every week. The 29 accessions were randomly distributed between experimental batch. The number of replicates for each accession ranges from n = 6 ('LA1447') to n = 11 ('RdB'). In total, we analyzed volatiles profiles released by 254 plants. Between two VOC collections, glass chambers were washed with disinfectant and ethanol and dried. All VOC collections were done between 8 AM and 10 AM in a unique place at constant temperature and lightened with white light (OSRAM, L13W/640 T5). Shoot biomass was then sampled and dried into oven at 65 °C for 72 h to standardize VOC emissions with plant dry mass.

2.5 VOCs analyses by gas chromatography combined mass spectrometry (GC-MS)

Volatile organic compounds were analyzed by gas chromatography-mass spectrometry (GC-MS) (Trace 1310 – TSQ 9000) combined with a thermodesorber (TD 100-xr). Tenax cartridges were desorbed for 5 min at 200 °C (10ml.min⁻¹) toward a cold trap maintained at –10 °C. The cold trap was flash heated at 250 °C for 5 min to transfer VOCs (transfer line at 250 °C) into a GC system equipped with a DB-5 MS column (30 m × 0.25 mm × 0.25 μm). The carrier helium was maintained at 1.2 ml.min⁻¹. The ionization source and transfer lines were set at 250 °C. Mass fragments were recorded between 35 and 350 m/z. Before injection, Tenax cartridges were peaked with 48.65 ng of tetraline (Sigma-Aldrich) as internal standard to account for variations in the sensitivity of the mass detector between different dates of injections. Several blanks were sampled during the experiments to subtract VOCs found in ambient air or released by our experimental system (e.g., soil, pot).

VOCs were detected using the R package 'xcms' (Smith et al. 2006) based on the 'CentWaveParam' algorithm (peak width between 3 and 20 s, mass resolution: 200 ppm, noise: 1.10⁶, signal-to-noise ratio: 10). VOCs were aligned with the ObiwrapParam method and grouped with the method 'PeakDensityParam' (minimum fraction: 1/3). Following this procedure, we obtained a matrix with 1257 detected ions. Using the CAMERA package, we grouped these ions into 307 VOCs with the 'groupFWHM' function. For each VOC, we kept the base peak (ion with the highest intensity) for further analyses. After subtracting artifacts and molecules presents in the capture system (potting soil, ambient air, connectors) or deriving from the analytical system, we considered that 77 VOCs were effectively released by tomato and wild relatives (Table S2). VOCs were semi-quantified after the standardization of peak areas with the area of internal standard (m/z = 104), shoot dry weight and time used for VOC capture. As a result, VOCs are expressed

in ng (tetraline equivalent).g (dry mass)⁻¹.h⁻¹. According to semi-quantification, we can compare concentrations of single compounds between several volatile profiles but not different compounds with various ionization rates.

We combined three different methods to identify the 77 VOCs (Table S2). First, we tentatively annotated VOCs based on comparisons of mass spectra retrieve from the NIST library (NIST08). Second, we compared the Kovats indices of the 77 VOCs with those that we computed experimentally based on the injections of (n)-alkane solutions (C7–C30, Sigma Aldrich). Third, we strictly identified 16 compounds covering the different chemical classes of VOC based on the injection of authentic standards (Sigma, Steinheim, Germany): (E)-2-hexenal, (E)-3-hexanol, 2-heptanone, α -pinene, β -myrcene, α -phellandrene, α -terpinene, limonene, γ -terpinene, terpinolene, 2-phenylethanol, methyl salicylate, carvone, ethyl-salicylate, 2-undecanone, β -caryophyllene. In addition, the injection of ginger essential oil (Sigma, Steinheim, Germany) was used to identify α -curcumene and α -zingiberene, i.e., two major components of ginger essential oil.

2.6 DNA extraction, genotyping and phylogenetic tree of domesticated tomato and wild relatives

DNA was extracted using DNeasy Plant Mini kit (Qiagen, 69104) from young leaves of 29 accessions and genotyped through Single Primer Enrichment Technology (SPET) using a custom 5K probe set described in Barchi et al. (2019). SNPs calling was obtained with GATK 4.0 and a VCF file was filtered to obtain only single biallelic SNPs (3655 SNPs). Maximum likelihood analysis was performed using RAxML version 8.0 to construct the phylogenetic tree. As RAxML only allows a single evolutionary model to be applied to partitioned analyses, all partitions were analyzed using the GTR +G model (Butterworth et al. 2020). The phylogenetic tree was built using all the 29 accessions of domesticated tomato and wild relatives (Table S1).

2.7 Behavioral response of *T. absoluta* to volatiles released by domesticated tomato and wild relatives

A total of 10 selected tomato accessions was used in the behavioral assays: 3 *S. cheesmaniae* accessions ('LA0421', 'LA0429', 'LA1412'), 3 *S. habrochaites* accessions ('LA1777', 'PI24', 'PI308'), 3 *S. pennellii* accessions ('LA0751', 'LA1297', 'LA1376') and one *S. lycopersicum* accession ('RdB') as positive control, i.e., attractive plant. This selection was based on two criteria. First, we expected that wild species may support higher defensive levels as compared to cultivated tomato. Second, these 10 accessions covered a large diversity of volatile profiles among the 29 accessions of tomato and wild relatives (Fig. S1). The responses of gravid females of *T. absoluta* to plant volatiles

were recorded with a Y-shaped olfactometer (length: stem 13 cm, arm 12 cm, diameter 2.1 cm) placed in a dark room with stable humidity and temperature (60% RH, 20 °C). The olfactometer was fixed in the middle of a black box with an inclination angle of 15°. Since females have a nocturnal behavior (Salama et al. 2015), behavioral choices were observed under a red light (Osram, L18W/60) fixed to the top of the black box. Similarly to Msisi et al. (2021), one arm connected to a plant was used as treatment, while the other arm connected to an empty glass chamber served as control. Purified and humidified air was forced into the two arms of the Y-tube olfactometer at a flow rate of 500 ml.min⁻¹. Male and female couples of *T. absoluta* were isolated from the rearing cage during mating before to identify and separate females. Because such manipulation may generate stress, gravid females were placed individually into containers and stored in dark conditions for 3 h prior behavioral tests. An individual gravid female was then introduced into the stem of the Y-shaped olfactometer and was let inside for 10 min to choose any of the two arms. During this period, if individuals did not choose any arms they were classified as not responsive and, consequently, not analyzed similarly to most of olfactometer studies. We considered that plants were attractive if females moved 2 cm forward the Y-intersections and remained in the arms connected to plants for 30 seconds (Calatayud et al. 2014). On the opposite, we considered that plants were repellent if females moved 2 cm forward the Y-intersections connected to the empty chamber and remained in this arm for 30 seconds. For each accession, we tested 10 gravid females on 3 different plants (n = 30). Between two tests, the Y-tube olfactometer was cleaned with water and ethanol (70%) and dried in the oven at 65 °C for 30 min to avoid odor contamination. Additionally, the two arms of the Y olfactometer were flipped to avoid environmental bias.

2.8 Choice assays under agronomic conditions

To confirm our Y-olfactometer results under more realistic conditions, we conducted a choice assay in the greenhouse using the most and least repellent accessions (*S. cheesmaniae* 'LA0421' and *S. habrochaites* 'PI24', respectively) compared to the highly attractive accession 'RdB' belonging to *S. lycopersicum*. We released between 200 and 220 adults of *T. absoluta* (male: female, 50:50) in large cages (3 × 3 × 2.6 m) separated by 1.5 m and made with insect-proof mesh. Each cage contained mixed crops with 12 plants belonging to 'LA0421' or 'PI24' and 12 plants belonging to 'RdB'. These choice assays were replicated four times (n = 4 cages) for each pair of accessions ('LA0421' Vs. 'RdB' and 'PI24' Vs. 'RdB'). Three weeks after the release of *T. absoluta* in the cages, we monitored the presence of *T. absoluta* larvae on all plants by recording the total number of mines (TNM) per plant, the leaf lesion type (LLT) on the whole plant as describe in Barbosa (1994) and Labory

(1996) and the total number of leaves attacked (TNLA) per plant.

2.9 Statistical analyses

All statistical analyses were performed in R version 4.3.2. Prior analyses, the dataset of volatile profiles was $\log(x + 1)$ transformed to meet the assumption of normality. The ecological diversity of VOC profiles released by the 29 accessions was analyzed with a redundancy analysis (RDA) based on the package ‘vegan’ (Oksanen et al. 2019). In brief, RDA is a supervised ordination method combining multivariate multiple linear regressions followed by a principal component analysis. These analyses are particularly relevant to handle datasets with a large number of variables across a limited number of samples, as it is often the case in metabolomics. The robustness of the RDA was estimated with proportions of variance explained by the ordination, permutations tests performed for each axe of the ordination (function ‘anova.cca’) and adjusted R^2 (function ‘RsquareAdj’). These three statistical parameters are displayed in Fig. 1.

The effects of phylogenetic drivers on VOC emissions were estimated on three features of plant volatile profiles: the number of VOCs released by plants (hereafter VOC richness), the total emission of sesquiterpenoids and of monoterpenoids. Based on the distribution of these features over the phylogenetic tree of tomato and wild relatives, we fitted three types of evolutionary models with the package ‘geiger’. As recommended by Broeckhoven et al. (2016), we compared the fits of white-noise, early-burst and Brownian-motion models. The white-noise model was used as a non-phylogenetic reference, i.e., traits evolve independently of the phylogeny. By contrast, the two other models assume phylogenetic drivers in VOC features. The early-burst model indicates that trait evolution decelerates exponentially with time (Harmon et al. 2010) while the Brownian-motion model suggests that trait evolution is constant. To compare these three models and identify the best fit, we used the sample-size corrected Akaike’s Information Criterion (AICc; the lowest value indicates the best model).

Responses of *T. absoluta* in the Y-olfactometer were analysed with one-sided exact binomial tests. We considered that plants were repellent when the proportion of females found in the control arm of the olfactometer was higher than proportions of females found in the plant-associated arm ($p.value \leq 0.05$). In opposition, plants were considered attractive if more females moved to the plants as compared to the control arm ($p.value \leq 0.05$). To study the relationships between VOC profiles and behavioural response of *T. absoluta*, we first compared the total emissions of the 4 repellent and the 2 attractive accessions based on a linear model and pairwise comparisons of estimated marginal means (package ‘emmeans’: Lenth 2023) with the ‘Benjamini-Hochberg’ p.value adjustment method. Second, we conducted untargeted comparisons of single VOC emis-

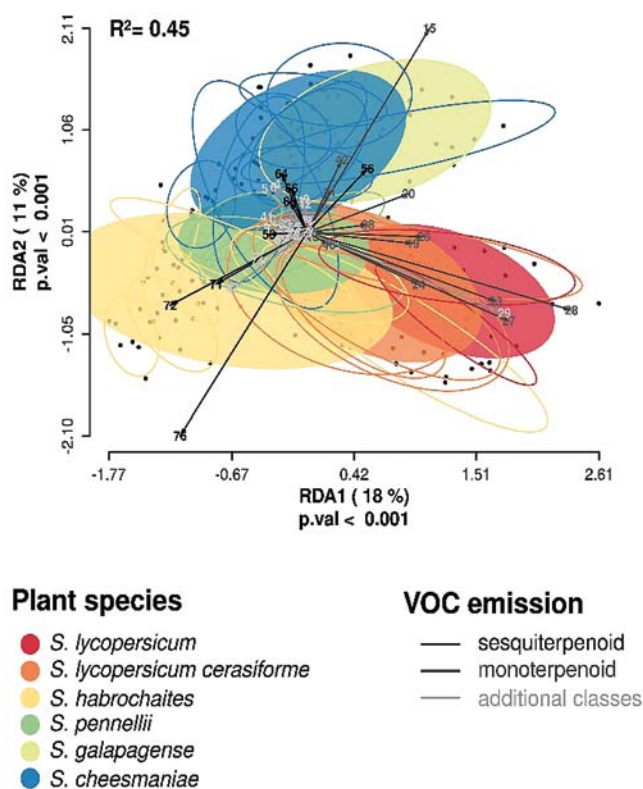


Fig. 1. Redundancy analysis of volatile profiles released by domesticated tomato and wild relatives. Colored ellipses and solid lines depict species and accessions, respectively. VOC numbers refer to Table S2.

sions between the 4 repellent and the 2 attractive accessions based on two-samples Wilcoxon tests ($p.value \leq 0.05$).

3 Results

3.1 Inter- and intra-specific diversity of VOC profiles in domesticated tomato and wild relatives

Overall, 77 VOCs were detected in the headspace collection of domesticated tomato and wild relatives (Table S2, Table S3). Volatile emissions clearly discriminated plants at the inter-specific levels (Fig. 1, Table S2). These differences of VOC profiles rely mainly on terpenoid emissions. At the inter-specific level, *S. lycopersicum* var. *lycopersicum* and *S. lycopersicum* var. *cerasiforme* clustered together based on high emissions of 6 monoterpenoids: α -phellandrene (VOC23), α -terpinene (VOC24), limonene (VOC26), γ -terpinene (VOC28) and two uncharacterized compounds, VOC19 and VOC27 (Fig. 1). In contrast, wild relatives were characterized by additional monoterpenoids, like α -pinene (VOC15) and more generally sesquiterpenoid emissions like

(3E,7E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT, VOC76). On the one hand, *S. habrochaites* and *S. pennellii* harbored high emissions of α -copaene (VOC58), α -curcumene (VOC71), α -zingiberene (VOC72) and TMTT (VOC76). On the other hand, *S. galapagense* and *S. cheesmaniae* released δ -elemene (VOC56), β -caryophyllene (VOC64), γ -elemene (VOC66) and α -humulene (VOC68). At the intra-specific level, despite partial overlaps in VOC profiles, the redundancy analysis pointed out some discrimination between accessions (Fig. 1, Table S3). This is particularly clear for the accessions of *S. cheesmaniae* since they are ordinated differentially in positive values of RDA2, i.e., without any inter-specific overlaps. In addition, among the 7 accessions of *S. habrochaites*, we recorded important variations in the emission of sesquiterpenoids like α -zingiberene (VOC72), ranging from 168 ± 41.80 and 216 ± 70.50 ng g⁻¹ h⁻¹ for ‘LA3863’ and ‘LA3864’ to 0.37 ± 0.09 , 0.66 ± 0.16 , 2.05 ± 0.52 , 5.19 ± 4.09 and 0.97 ± 0.22 ng g⁻¹ h⁻¹ for ‘LA1033’, ‘LA1777’, ‘PI24’, ‘PI308’ and ‘G1560’, respectively (Table S3).

3.2 Effects of phylogenetic drivers on plant volatile profiles released by domesticated tomato and wild relatives

Our phylogenetic tree points out the positions of green-fruited *S. habrochaites* and *S. pennellii* in the oldest branching taxa and, meanwhile, indicates polytomy (more than two lineages deriving from a common ancestral branch) in more recent red/yellow-fruited groups of tomato with a segregation between *S. cheesmaniae* and *S. galapagense* within one clade and *S. lycopersicum* var. *lycopersicum* and *S. lycopersicum* var. *cerasiforme* in another clade. Our findings reveal significant variations in the distribution of VOC richness and total emissions of sesquiterpenoids and monoterpenoids among clades (Fig. 2). Evolutionary models summarized in Table 1 suggest that these three features of VOC profiles were driven by phylogeny as compared to non-phylogenetic patterns (‘white-noise’ model). As shown in Fig. 2, the number of compounds released by plants was relatively high in ancestral species like *S. habrochaites* (36.10 ± 1.04), *S. cheesmaniae* (37.50 ± 0.83) or *S. galapagense* (37.90 ± 4.28) as compared

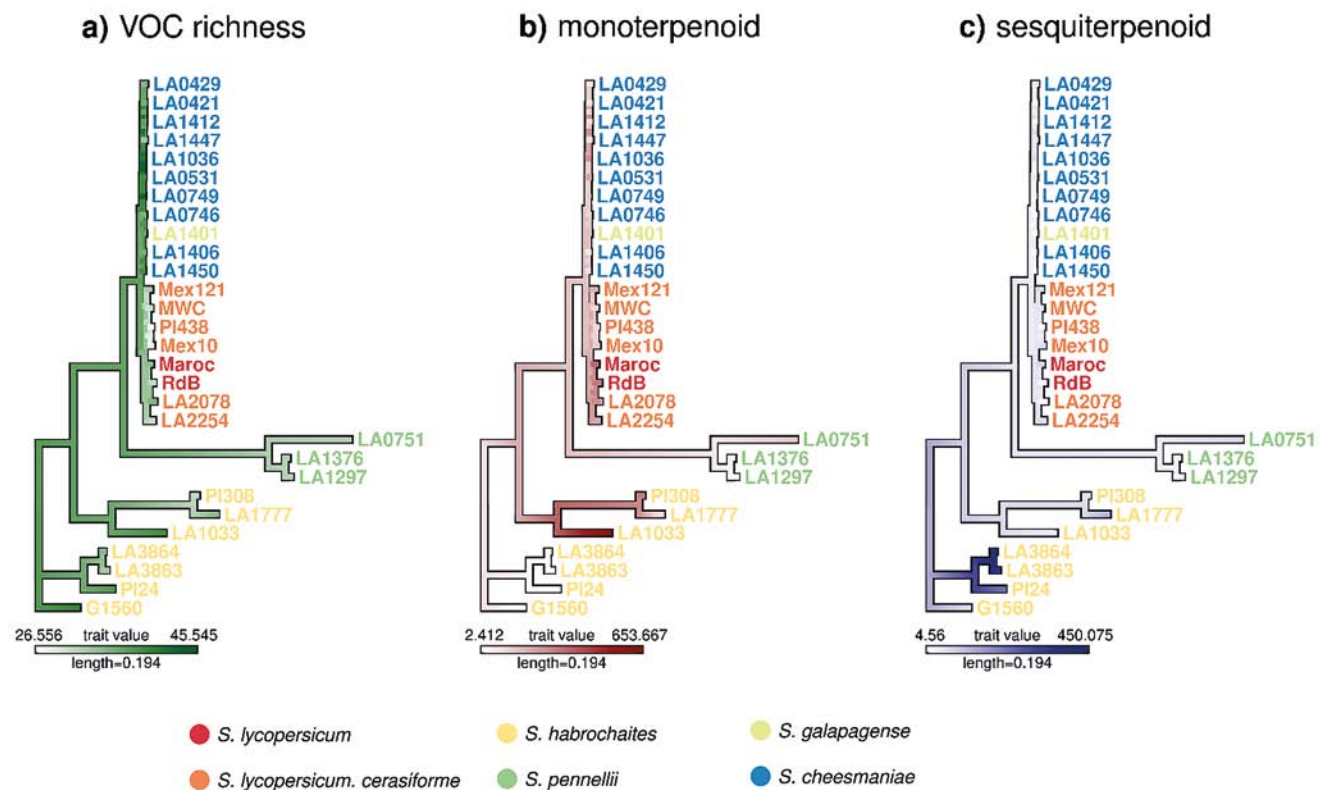


Fig. 2. Phylogenetic tree of 29 accessions belonging to domesticated tomato and wild relatives (genotyped by Single Primer Enrichment Technology using a custom 5K probe set) and evolution of volatile richness (a) total emissions of monoterpenoids (b) and total emissions of sesquiterpenoids (c). Volatile richness is the number of compounds released by plants. Total emissions of monoterpenoids and sesquiterpenoids are the sums of the 15 and 9 VOCs classified as monoterpenoids and sesquiterpenoids, respectively, in Table S2. For each plot, the legend indicates the range of feature values (number of compounds for Fig. 2a or ng. g⁻¹ h⁻¹ for Fig. 2b and 2c). Intense colors indicate high emissions of VOC features.

Table 1. Summary of the results of evolutionary models of VOC richness (number of compounds released by plants), total emissions of monoterpenoids and total emissions of sesquiterpenoids.

		White-noise	Brownian-motion	Early-burst
VOC richness	AICc	261.501	261.501	<i>206.449</i>
	lnL	-128.52	-128.52	<i>-99.745</i>
	Model parameter	$\sigma^2 = 0$	$\sigma^2 = 0$	$\alpha = -5.15093$
Monoterpenoid emission	AICc	360.631	<i>359.768</i>	362.26
	lnL	-178.085	<i>-177.653</i>	-177.65
	Model parameter	$\sigma^2 = 5345.285$	$\sigma^2 = 562769.6$	$\alpha = -0.664122$
Sesquiterpenoid emission	AICc	415.893	298.982	<i>297.494</i>
	lnL	-205.716	-147.26	<i>-145.267</i>
	Model parameter	$\sigma^2 = 0$	$\sigma^2 = 73906.808$	$\alpha = -11.063972$

Total emissions of monoterpenoids and sesquiterpenoids are the sums of the 15 and 9 VOCs classified as monoterpenoids and sesquiterpenoids, respectively, in Table S2. The best models (in italic) are supported by the highest maximum-likelihood estimate (lnL) and the lowest sample-size corrected Akaike's Information Criterion (AICc). White-noise models are non-phylogenetic references. Brownian-motion models assume constant evolution rate (Felsenstein 1973). Early-burst models indicate exponential decrease ($\alpha < 0$) or increase ($\alpha > 0$) of trait evolution (Harmon 2010).

to *S. lycopersicum* var. *cerasiforme* (30.7 ± 1.10) or *S. lycopersicum* var. *lycopersicum* (32.50 ± 1.39). Evolutionary models suggested that these differences arose from rapid changes in VOC richness followed by a decrease in trait variations during the radiation of tomato (i.e., 'early-burst' model, Table 1). This pattern was even more pronounced for sesquiterpenoid emissions (Table 1). Indeed, although sesquiterpenoid emission was extremely high in *S. habrochaites* (190.00 ± 25.46 ng g⁻¹ h⁻¹) it was sharply reduced for *S. lycopersicum* (48.41 ± 14.59 ng g⁻¹ h⁻¹), *S. pennellii* (46.93 ± 9.15 ng g⁻¹ h⁻¹), *S. cheesmaniae* (30.81 ± 4.11 ng g⁻¹ h⁻¹) and *S. galapagense* (20.81 ± 4.69 ng g⁻¹ h⁻¹) (Fig. 2). Finally, evolutionary models suggested that correlations between monoterpenoid emissions is proportional to the extent of shared ancestry (i.e., 'Brownian motion', Table 1). Fig. 2 indicated that the emission of monoterpenoid was relatively high for the three accessions of *S. habrochaites* originating from Peru ('LA1033', 'LA1777', and 'PI308') and *S. lycopersicum* ('Maroc', 'RdB').

3.3 Olfactory responses of *Tuta absoluta* to domesticated tomato and wild relatives

The 10 accessions selected for behavioral assays covered the large diversity of VOC reported above (Fig. S1). Over the 300 gravid females of *T. absoluta* we tested, about 70% responded to volatile stimuli. Based on exact binomial tests, we identified two attractive accessions: one belonging to *S. lycopersicum* ('RdB') and one belonging to *S. cheesmaniae* ('LA0429') (Fig. 3). In opposition, 4 accessions, including one *S. habrochaites* ('PI24'), two *S. pennellii* ('LA1376' and 'LA0751') and one *S. cheesmaniae* ('LA0421') were considered significantly repellent according to female preference towards control (Fig. 3). In the choice assay under agronomic conditions, 'PI24' and 'LA0421', the two accessions with lowest and highest antixenosis (Fig. 3), experi-

enced limited pest damages as compared to the attractive accession 'RdB' (Fig. S2).

3.4 Covariations between behavioral responses and volatile profiles of domesticated tomato and wild relatives

Overall, the total concentrations of VOCs released by plants triggering a behavioral choice varied significantly between accessions (Fig. S3). On the one hand, among the repellent accessions, antixenosis was higher for the accession with the highest total emissions rate, i.e. 'LA0421' (Fig. 3, Fig. S3). On the other hand, despite similar attractiveness (Fig. 3), 'RdB' released two times more volatiles as compared to 'LA0429' (Fig. S3). Out of the 77 VOCs detected, 14 were released in different concentrations between attractive and repellent plants (Fig. 4; two-samples Wilcoxon test). The two attractive accessions emit higher concentrations of two monoterpenoids (VOC19, 24.10 ± 19.37 ng g⁻¹ h⁻¹; VOC27, 31.00 ± 11.67 ng g⁻¹ h⁻¹), 2-phenylacetaldehyde (VOC29, 43.10 ± 15.29 ng g⁻¹ h⁻¹) and δ -elemene (VOC56, 2.50 ± 0.79 ng g⁻¹ h⁻¹). Conversely, 10 compounds were released in larger concentration by the four repellent accessions. They were identified as α -curcumene (VOC71, 0.17 ± 0.03 ng g⁻¹ h⁻¹), TMTT (VOC76, 86.90 ± 18.54 ng g⁻¹ h⁻¹), methyl salicylate (VOC47, 5.40 ± 1.65 ng g⁻¹ h⁻¹), β -myrcene (VOC21, 2.70 ± 0.44 ng g⁻¹ h⁻¹), 2,4-dimethyl heptene (VOC3, 0.65 ± 0.19 ng g⁻¹ h⁻¹), 1-hexanol (VOC9, 1.40 ± 0.50 ng g⁻¹ h⁻¹), 2-phenylethanol (VOC41, 2.50 ± 0.93 ng g⁻¹ h⁻¹), 1-dodecanol (VOC70, 0.28 ± 0.05 ng g⁻¹ h⁻¹), 2-tridecanol (VOC75, 0.16 ± 0.04 ng g⁻¹ h⁻¹) and VOC31 (1.40 ± 0.34 ng g⁻¹ h⁻¹). In addition, among *S. cheesmaniae*, since *T. absoluta* was attracted towards 'LA0429' and repelled by 'LA0421', we tested specific comparisons between both accessions (Fig. S3). Intra-specific variations in volatile emissions within *S. cheesmaniae* suggest that antixenosis may rely on

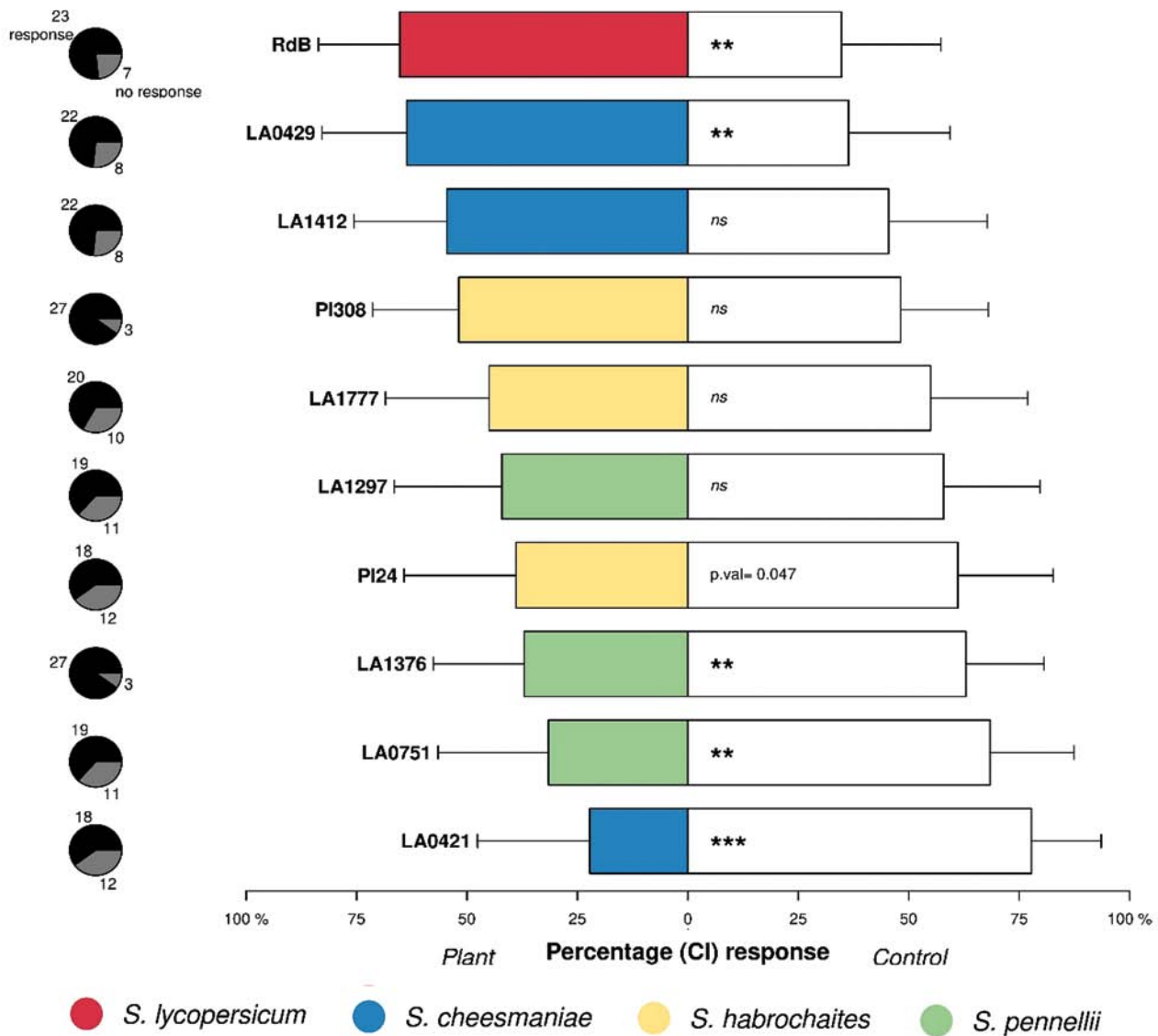


Fig. 3. Behavioral response of gravid females of *Tuta absoluta* to plant volatile profiles. Pie-charts indicate the number of responding (black) and non-responding (grey) females. CI: confident interval (95%); ** $p.value \leq 0.01$, *** $p.value \leq 0.001$ (exact binomial test; 'ns': non-significant).

7 additional VOC: α -pinene (VOC15), isolimonene (VOC20), α -phellandrene (VOC23), α -terpinene (VOC24), limonene (VOC26), γ -terpinene (VOC28) and alloocimene (VOC42).

4 Discussion

To our knowledge, this study is the first that highlights inter- and intra-specific diversity of volatile profiles released by domesticated tomato and wild relatives based on a clade-wide phylogenetic framework of *Solanum* sect. *Lycopersicon*. By doing so, we discuss evolutionary patterns explaining the diversity of VOC profiles according to domestication and natural history of plants adapted to a vast array of biogeographic areas. Further, we combine

chemical analyses with behavioral assays to estimate the consequences of VOC diversity on antixenosis against *Tuta absoluta*. Thereby, we screen genetic resources carrying plant resistance against a major pest of tomato and we identify compounds involved in the mechanisms underlying such resistance.

Recently, Vivaldo et al. (2017) have shown that VOCs are important components of plant phenotypes that can be used to classify species across distinct families. In our study, the five species of domesticated tomato and wild relatives released different VOC profiles dominated by monoterpenoids and sesquiterpenoids. Sesquiterpenoid emissions were higher in wild tomato species even if they differed according to their geographic origins. The two species distributed in central Andes (*S. pennellii* and *S. habrochaites*) were characterized

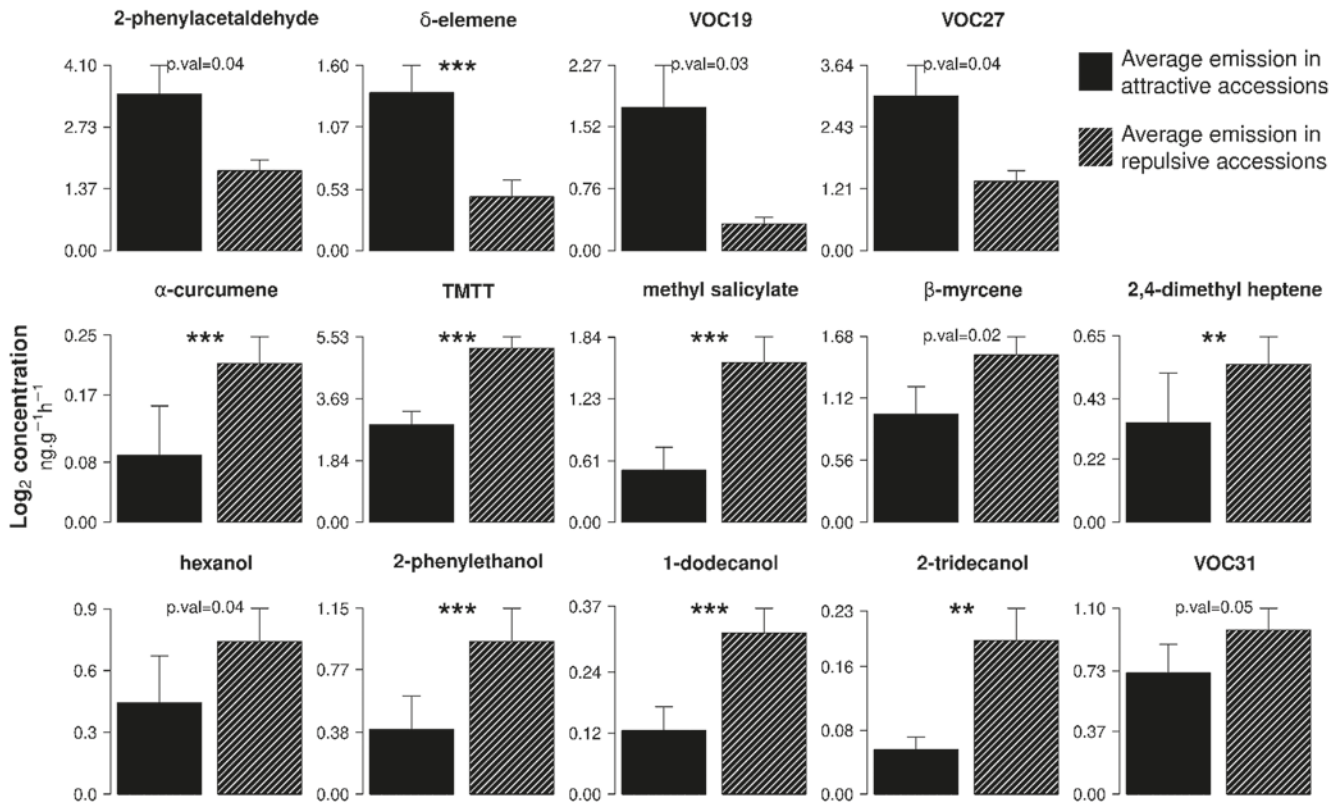


Fig. 4. The fourteen volatile compounds with different emission rates between repellent ('LA0421', 'LA1376', 'LA1297' and 'PI24') and attractive accessions ('LA0429', 'RdB'). TMTT: (3E,7E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. ** *p*.value ≤ 0.01 , *** *p*.value ≤ 0.001 (two-samples Wilcoxon test).

by emissions of α -copaene, α -curcumene, α -zingiberene and TMTT whereas the two endemic species from Galapagos Islands (*S. cheesmaniae* and *S. galapagense*) shared high emissions of δ -elemene, β -caryophyllene, γ -elemene and α -humulene. Thus, we can reasonably conclude that the radiation of tomato in different areas delimited by geographic barriers has prompted ecological divergences in volatile profiles. After the separation of Galapagos Islands from the Nazca plate 4–5 Million year ago (Mya), *S. cheesmaniae* and *S. galapagense* have likely evolved in isolation. Today, the 1000 km separating the archipelago from South America have resulted in strong differences between morphological features of mainland species and *S. cheesmaniae* or *S. galapagense* (Lucatti et al. 2013). Similarly, our results suggest that VOCs have diverged in response to the different environmental context. Moreover, this study shows that the sesquiterpenoids emission, and in less extent volatile richness, were drastically reduced in domesticated tomato (*S. lycopersicum* var. *lycopersicum*) and cherry tomato (*S. lycopersicum* var. *cerasiforme*). The combination of phylogenetic analyses and evolutionary modelling confirms that despite the high richness in volatile compounds and sesquiterpenoid emissions in ancestral branches of wild tomato clades, both features have sharply decreased with evolution following an 'early-burst' model. In general, these evolutionary models

are considered as signatures of adaptative radiation (i.e., the evolution of a phenotype towards various syndromes adapted to different ecological niches) of plant defenses (Agrawal et al. 2009). This suggests strong variations in volatile emissions during the emergence of *Lycopersicon* clades within *Solanaceae*, i.e. more than 7–8 million Mya, and progressive reduction of VOC richness and sesquiterpenoids as evolution ran its course. However, besides natural evolution, we cannot exclude that reduced richness of volatile profiles and low concentrations of sesquiterpenoid in modern cultivars may also derive from domestication process, at least in *S. lycopersicum* var. *lycopersicum*. While counter-selection of defensive traits is widespread in agronomic plants (Fernandez et al. 2021), domestication may have resulted in dramatic bottleneck effects in tomato.

In addition to inter-specific diversity, our results point out high intra-specific diversity of VOC profiles in domesticated tomato and wild relatives. Although this study includes a large number of accessions for some species, like *S. cheesmaniae*, *S. habrochaites* and *S. lycopersicum* var. *cerasiforme*, our results encourage to extend investigations of intra-specific diversity among other species for which we focused on a limited set of accessions. In the case of *S. habrochaites*, while three accessions originating from Ecuador ('LA3863', 'LA3864' and 'PI24') emitted high concentra-

tion of sesquiterpenoids, three other accessions growing in Peru ('LA1033', 'LA1777', 'PI308') released low concentration of these compounds but high concentration of monoterpenoids. In general, while *S. habrochaites* spans the greatest diversity of climates among wild relative clades of tomato, our results suppose that micro-evolution has resulted in different ecotypes based on local adaptations affecting VOC emissions. More particularly, this study corroborates molecular research indicating that populations of *S. habrochaites* found in Peru and Ecuador show different patterns of genetic variability (Sifres et al. 2011) and different families of genes encoding terpene synthase (Gonzales-Vigil et al. 2012). For *S. cheesmaniae*, similarly to Darwin's finches, Pailles et al. (2017) demonstrated how the colonization of the 13 islands of the Galapagos archipelago has driven morphological variations and intra-specific biodiversity. These phenotypic variations are correlated with resistance against invasive pests like *Bemisia tabaci* (Lucatti et al. 2013). Even for a single island, since populations of *S. cheesmaniae* can be found from sea level to high-elevation rocky areas (Peralta et al. 2008), we can expect that local adaptations may have prompted intra-specific diversity. In the present study focusing on 10 accessions distributed in 5 different islands of the archipelago, we showed that the emission of defensive VOCs like TMTT or methyl salicylate can exhibit 50- or 125-fold changes, respectively. Finally, in both *S. lycopersicum* var. *lycopersicum* and *S. lycopersicum* var. *cerasiforme*, intra-specific diversity of volatile profiles mainly relies on the emission of eight monoterpenoids. Recently, Dehimeche et al. (2021) have highlighted the importance of this class of compounds in the discrimination of volatile blends released by eight genotypes of *S. lycopersicum*.

Based on inter- and intra-specific variations of VOC emissions in domesticated and wild tomato, we expected strong differences in antixenosis against *T. absoluta*. In total, out of the 10 accessions tested in the olfactometer, two were found to be attractive and four were found to be repellent. Higher total emissions of VOC were associated with higher antixenosis in repellent plants. Hence, our results suggest that antixenosis relies, at least partially, on quantitative effects. However, for attractive plants, *T. absoluta* showed equal preference for a domesticated accession and a wild accession exhibiting 2-fold change in total amount of VOCs. Thereby, in addition to quantitative aspects, host-plant location by females likely involves qualitative differences in VOC emissions. In line with our study, a large body of literature have shown that domesticated tomato are attractive for females of *T. absoluta* (Anastasaki et al. 2018). However, much more remains to be done to investigate the attraction to *T. absoluta* on wild relatives of tomato to identify genetic resources carrying antixenosis. The general comparison between volatile profiles released by the two attractive and the four repellent accessions suggests that 10 compounds could support antixenosis. Among these, TMTT and methyl salicylate are involved in plant defenses in a large range of pathosystems

(Park et al. 2007). The monoterpene β -myrcene is abundant in different essential oils with repellent properties against *T. absoluta* (Ngongang et al. 2022) and is part of tomato herbivore-induced plant volatiles altering female performance of tomato leaf miner (Anastasaki et al. 2018). In tomato, while zingiberene and its derivative α -curcumene are good candidates to enhance plant resistance against whiteflies (Kortbeek et al. 2023), this group of compounds is also known for its defensive role against *T. absoluta* (Mahmoud et al. 2022). Further research is needed to investigate the potential of these compounds in repellent dispensers according to concentrations if they are used alone or respective ratio if they are mixed in blends.

However, it remains challenging to assert general rules in the identification of VOCs involved in antixenosis. In the present study, we showed that the behavioral response of *T. absoluta* is driven by the intra-specific diversity of volatile profiles, rather than general variations. Indeed, within *S. cheesmaniae*, our results indicate that the high-elevation accession 'LA0429' is attractive whereas the low-elevation accession 'LA0421' is repellent. These findings could result from local adaptations if we consider that plants growing at low elevation experience higher selective pressures related to insect herbivory than plants at higher elevation (Descombes et al. 2020). Interestingly, intra-specific comparison between 'LA0421' and 'LA0429' suggests that higher emission of VOC19, VOC27 and 2-phenylacetaldehyde may result in antixenosis for *S. cheesmaniae* although the inter-specific comparison indicates that these three compounds can be released in high concentrations by attractive accessions like the cultivated tomato 'RdB'. This finding supports the notion that *T. absoluta* responds to blends of compounds in varying ratios rather than individual VOCs. In general, besides the role of major compounds, it is difficult to integrate the influence of minor compounds, sometimes not even detectable, on insect response (Bruce et al. 2010). In the case of *T. absoluta*, it has been shown that small variations in VOC blends released by different tomato cultivars, as well as other host plants, result in different levels of attraction or repellency (Proffit et al. 2011; Anastasaki et al. 2018). In this context, there is still a long road ahead to develop dispensers with single or few repellent VOCs.

To sum-up, bringing together chemical and evolutionary ecology is valuable to explore clade-wide variations in VOC emissions and antixenosis. From a basic perspective, this line of research helps to understand an overlooked dimension of biodiversity based on biogeography and evolutionary processes. In addition, for agronomic models like tomato, this inter-disciplinary approach is of great interest for phylogenetically-driven screening of anti-herbivore plant defenses carried by genetic resources that have not been affected by domestication. Although the present work focused on antixenosis, further research is needed to explore variations of additional phytochemically-mediated mechanisms involved in plant defenses, like antibiosis (plant features reducing

pest performance after larvae start feeding) and plant-plant communication. We argue that the integration of several components of plant defenses will be required to develop agroecological cultivars adapted to low-pesticide cropping systems.

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Supplementary Table S1–S3, Figure S1–S4