Genetic diversity of the tomato russet mite supporting oligophagy and evidencing widespread of an invasive haplotype

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Abstract

Worldwide, the tomato russet mite (TRM), *Aculops lycopersici* (Eriophyidae), is a key pest on grown tomatoes besides infesting other cultivated and wild Solanaceae; however, information on TRM basics aspects supporting effective control strategies still lacking, mainly regarding its taxonomic unit and genetic diversity and structure. As *A. lycopersici* is reported on different species and genera of host plants maybe, populations associated with different host plants constitute specialized cryptic species, such as showed for other eriophyids previously considered generalists. The main aims of this study were to i) confirm the TRM taxonomic unity of populations from different host plants and localities as well as the species oligophagy; ii) to advance the understanding on TRM host relationship and invasion history. For this purpose it was evaluated the genetic variability and structure of populations from different host plants along crucial areas of occurrence, including that potentially of origin and the invaded ones, based on DNA sequences of mitochondrial (Cytochrome *c* oxidase subunit I) and nuclear (Internal Transcribed spacer, D2 28S) genomic regions. Specimens from South America (Brazil) and Europe (France, Italy, Poland, The Netherlands) were collected from tomato and other solanaceous species from the *Solanum* and *Physalis* genera. Final TRM datasets were composed by 101, 82 and 50 sequences from the *COI* (672 bp), ITS (553 bp) and D2 (605 bp) regions, respectively. Distributions and frequencies of haplotypes (*COI*) and sequence variants (D2 and ITS1) were inferred; pairwise genetic distances, and phylogenetic analysis were performed, including Bayesian Inference (BI) combined analysis. Genetic divergences for mitochondrial and nuclear genomic regions from TRM associated with different host plants were even lower than those observed in other eriophyid taxa confirming co-specific of TRM populations and oligophagy of this eriophyid mite. Four haplotypes (cH) were identified from the *COI* sequences being cH1 the most frequent, representing 90% of all sequences occurring in all host plants studied (Brazil, France, The Netherlands); the other haplotypes were present exclusively in Brazilian populations. Six variants (I) were identified from the ITS sequences: I-1 was the most frequent (76.5% of all sequences), spread in all countries and associated with all host plants, except for *S. nigrum*. Just one D2 sequence variant was found in all studied countries. The genetic homogeneity among populations highlights occurrence of a highly invasive and not host-specific haplotype. These results also do not corroborate the hypothesis that differential symptomatology/damage intensity by tomato varieties and solanaceous host plants could be due to the genetic diversity of the associated mite populations. Even this contribution was not primarily aimed to trace TRM invasion routes, genetic evidence, jointly with the main host plant history, corroborate the hypothesis of a TRM South American origin.

Introduction

The tomato russet mite (TRM), *Aculops lycopersici* (Tryon, 1917) (Eriophyidae), was described from tomato, *Solanum lycopersicum* L. (Solanaceae), from Queensland, Australia by Tryon in 1917; however, its origin has not yet been determined. Some authors redescribed this taxon setting up numerous synonyms (Massee 1937, Keifer 1940, 1966). Currently, this eriophyid mite is reported with cosmopolitan distribution, in almost all areas where solanaceous crops are grown (Jeppson et al. 1975; Duso et al. 2010; CABI 2020; Amrine and de Lillo personal communication). On tomatoes, heavy infestations cause yellowish-brown coloured stems or branches, dried leaves, and rusted fruits (Haque and Kawai 2002; Royalty and Perring 1988; Kumral et al. 2014); such damages can lead to 50% crop loss and even more than 65% in production (de Oliveira et al. 1982; Daiber 1985; Celar and Valič 2003). The troubles in controlling the TRM by chemicals (Yu 2008, Khalighi et al. 2016) make urgent the improvement of nonchemical and effective control strategies (de Lillo et al. 2018). However, TRM basic information to support the development of effective control strategies is still lacking, like taxonomy, genetic diversity and structure (*e.g.*, Guidolin et al. 2014).

The TRM has been considered an exception to the general statement that eriophyoid mites are highly specialized plant parasites; it is included in 5% minority of eriophyoids reported to infest different host plant genera (Lindquist and Oldfield 1996; Skoracka et al. 2010). In addition to tomato, the current TRM host range comprises at least ten *Solanum* species and six other genera of Solanaceae: *Browallia*, *Capsicum*, *Datura*, *Nicotiana*, *Petunia* and *Physalis* (Perring and Farrar 1986; Keifer et al. 1982; Duarte et al. 2020; Amrine and de Lillo personal communication); furthermore, it is reported on the genus *Convolvulus*, from family Polygonaceae (Rice and Strong 1962). It is possible that populations, reported as associated with different host plants constitute a few specialized cryptic species, as shown for other eriophyid species, previously considered generalists (Skoracka and Dabert 2010; Skoracka et al. 2012, 2014; Lewandowski et al. 2014; Navia et al. 2015). Further studies integrating molecular traits are still needed to confirm TRM taxonomic unit and its effective host range.

TRM infestation on different species/varieties of host plants show different symptomatology or damage severity. Tens of accessions from several species of *Solanum* (ex. *Lycopersicon*) were tested for susceptibility to TRM: among them, damage index was not correlated with mite density (Kitamura and Kawai 2006). Symptoms expressed in a host plant are closely related to herbivore-host plant interactions, which depends on reciprocal adaptations as each clade evolved in response to changes in the other (Douglas et al. 2009; Nallu et al. 2018). Therefore, the differentiated symptomatology/susceptibility presented by tomatoes and solanaceous host plants in response to TRM infestation can be due to **i**) genetic diversity of the mite populations/species; or **ii**) differences on host plant defense mechanisms. Studies are needed to test these hypotheses and, eventually, by which mechanism are corroborated.

It has been discussed that the original TRM host plant is not tomato but some other wild solanaceous plants (Oldfield 1996; Michalska et al. 2010; Navia et al. 2010). The severe damage caused by TRM to tomatoes, including the plant death (Keifer et al. 1982; Lindquist and Oldfield 1996), suggests a recent association instead of an old co-evolutionary history (Oldfield 1996; Michalska et al. 2010; Duarte et al. 2020). It is possible that TRM adopted tomato plants as an alternate host plant in areas of co-occurrence of the original wild host plant and the cultivated tomato. The currently cultivated tomato has origin in central South America (Blanca et al. 2012, 2015; Razifard et al. 2020), rendering the study of TRM genetic variability, in this area, particularly interesting. Furthermore, comparing populations of the supposed origin and invaded areas can reveal insights into the invasion process of this pest. Reconstruction of agricultural pests invasion routes can support the design of strategies to prevent new invasions and to the development of management strategies. Therefore, it allows an understanding of the environmental and evolutionary factors favouring the invasion potential (Liebhold and Tobin 2008; Estoup and Guillemaud 2010; Pautasso et al. 2010).

The specific goals of this TRM study were to: **i)** confirm the taxonomic unity of populations from different host plants and localities as well as the species oligophagy; **ii)** know the genetic variability and structure of populations along crucial areas of occurrence, including that potentially of origin and the invaded ones, in order to advance the understanding on host relationship and invasion history. For these purposes, phylogenetic and genetic diversity studies based on DNA sequences of mitochondrial and nuclear fragments from South American and European populations collected from tomato and other solanaceous species in the *Solanum* and *Physalis* genera were performed.

Material & Methods

Sampling

TRM specimens were collected from 26 populations from Brazil, France, Italy, Poland and the Netherlands, over seven solanaceous species belonging to two genera- *Solanum lycopersicum*, *S. muricatum* Ait., *S. aethiopicum* L., *S. nigrum* L., *S. sessiflorum* Dunal, *S. americanum* Mill., and *Physalis* sp.. Samples of leaves and branches were collected in natural areas and/or in crops. In Brazil, surveys were conducted in the Cerrado biome or in cultivated areas, including the Germplasm Bank of Solanaceae, at Embrapa Hortaliças, and experimental areas at “Fazenda Água Limpa (FAL)”, University of Brasilia, Federal District, Brazil. Collection data and sample codes of the *A. lycopersici* populations studied are shown in Table 1.

Table 1

Collection data of TRM populations obtained from wild and cultivated solanaceous plants from Brazil and Europa. Abreviations of countries where samples were collected: **BR**- Brazil; **FR**- France; **PL**- Poland; **IT**- Italy; **NL**- The Netherlands.

Sample code	Host plant táxon	Locality	Geographical coordinates	Date	Collected by
Al1	*Solanum lycopersicum*	BR: Distrito Federal. Brasília (Embrapa Recursos Geneticos e Biotecnologia)	15º43'51"S. 47º54'02"W	16/11/2017	M. E. Duarte
Al2	*Solanum lycopersicum*	BR: Distrito Federal. Paranoá	15º58'32"S. 47º29'32"W	30/11/2017	R.S. Mendonça
Al3	*Physalis* sp.	BR: Distrito Federal Gama (Embrapa Hortaliças	15º56'06"S. 48º08'24"W	13/12/2017	M. E. Duarte
Al4	*Solanum muricatum*	BR: Distrito Federal. Gama (Embrapa Hortaliças	15º56'05"S. 48º08'24"W	13/12/2017	M. E. Duarte
Al5	*Solanum aethiopicum*	BR: Distrito Federal. São Sebastião	15°54'04"S. 47°45'40"W	14/12/2017	M.L.S.C.M. Alves
Al6	*Solanum lycopersicum*	BR: São Paulo. Piracicaba	22°42'38"S. 47°38'04"W	31/03/2017	M. D. Santos
Al7	*Solanum lycopersicum*	FR: Montpellier	43°40'57"N. 3°52'31"E	2015	Navia. D.
Al8	*Solanum lycopersicum*	BR: Distrito Federal. Gama (Embrapa Hortaliças)	15º55'58"S. 48º08'25"W	14/08/2017	M. E. Duarte
Al9	*Solanum sessiliflorum*	BR: Distrito Federal. Gama (Embrapa Hortaliças)	15º55'56"S. 48º08'21"W	30/08/2017	R.S. Mendonça
Al10	*Solanum americanum*	BR: Distrito Federal. Gama (Embrapa Hortaliças)	15º55'58"S. 48º08'25"W	30/03/2017	R.S. Mendonça
Al11	*Solanum lycopersicum*	BR: Distrito Federal. Núcleo rural Samambaia	15º 48'08"S. 48º10'38"W	05/09/2017	M. E. Duarte & R.S. Mendonça
MLW1	*Solanum lycopersicum*	PL: Warsaw	52°09'43"N. 21°02'46"E	15/09/2016	M. Lewandowski
MLW2	*Solanum lycopersicum*	PL: Czersk	51°57'18"N. 21°15'25"E	15/09/2016	M. Lewandowski
MLW3	*Solanum lycopersicum*	PL: Konstancin	52°05'51"N. 21°09'38"E	15/09/2016	M. Lewandowski
MLW4	*Solanum lycopersicum*	IT: Scandicci (Firenze)	43°45'14"N. 11°11'34"E	26/09/2016	S. Simoni
MLW5	*Solanum lycopersicum*	IT: San Felice a Ema (Firenze)	43°44'19"N. 11°14'34"E	06/10/2016	S. Simoni
MLW6	*Solanum nigrum*	IT: Cascine del Riccio (Firenze)	43°43"54"N. 11°15'13"E	06/10/2016	S. Simoni
MLW7	*Solanum lycopersicum*	NL: De Lier	51°58'19"N. 4°15'11"E	21/11/2016	M. Lewandowski
MLW8	*Solanum lycopersicum*	PL: Wola Hankowska	50°52'45"N. 19°05'41"E	20/12/2016	M. Lewandowski
MLW9	*Solanum lycopersicum*	PL: Janów	52°03'31"N. 21°16'47"E	12/10/2017	M. Lewandowski
MLW10	*Solanum lycopersicum*	IT: San Severo	41°40'47"N. 15°22'17"E	17/09/2018	S. Simoni
MLW11	*Solanum lycopersicum*	IT: Battipaglia	40°35'26"N 15°00'54"E	17/09/2018	S. Simoni
MLW12	*Solanum nigrum*	IT: Battipaglia	40°35'01"N. 14°58'51"E	17/09/2018	S. Simoni
MLW13	*Solanum lycopersicum*	IT: Sarno	40°48'46"N. 14°36'43"E	17/09/2018	S. Simoni

Sample code	Host plant táxon	Locality	Geographical coordinates	Date	Collected by
MLW14	*Solanum nigrum*	IT: Cascine del Riccio (Firenze)	43°43'54"N. 11°15'13"E	19/09/2018	S. Simoni
MLW15	*Solanum lycopersicum*	PL: Gatka Nowa	51°40'57"N. 19°25'48"E	25/09/2018	M. Lewandowski

Samples were transported to the laboratory for further direct examination under dissecting stereomicroscope (40×). Eriophyid mites were collected and stored in Eppendorf tubes containing absolute or 70% ethyl alcohol, for molecular and morphological studies, respectively. For morphological identification, mite specimens were then mounted on microscope slides using modified Berlese medium (Amrine and Manson 1996) and observed under a phase-contrast microscope (100x, Eclipse 80i Nikon and Olympus BX51, Tokyo, Japan).

Molecular Studies

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from single specimens. For Brazilian samples, extractions were conducted using the DNeasy Blood Tissue Kit (Qiagen, Brazil). Intact mites were individually transferred from absolute ethyl alcohol to 1.5 mL microcentrifuge tubes containing 90 µL of ATL buffer (Qiagen); 10 µL of Proteinase K (Qiagen) was then added to each sample. The mixture was incubated at 56°C with shaking in a thermomixer for 18–22 h. Mites were not crushed. All other steps were following the standard Qiagen DNA extraction protocol 'Purification of Total DNA from Animal Tissue' by Mendonça et al. (2011). For European samples, genomic DNA was extracted using a Chelex® protocol. Individual specimens were transferred into a DNase-free 0.5 ml polyvinyl tubes containing 5 µ l of Proteinase K (20 mg/ml), crushed using a clean steel needle and 100 µl of 6% Chelex solution was added. After vortexing, the tubes were incubated initially for 30 min at 56°C and then for 8 min at 100°C. Then, the procedure adopted was according to the method described in Bouneb et al. (2014). The specimens submitted to DNA extraction, always that were found in the membrane of the extraction column, had their exoskeleton recovered and were mounted on microscope slides in modified Berlese medium. These slides were deposited as voucher specimens in the mite collection at Embrapa Genetic Resources and Biotechnology, Brasília, Brazil.

Three DNA fragments were PCR-amplified and sequenced per single mite: one mitochondrial gene - the Cytochrome *c* oxidase subunit I (*COI*) (DNA barcode region chosen by the Consortium for the Barcode of Life (http://barcoding.si.edu); two nuclear fragments: the subunit D2 region in 28S rDNA and the ITS nuclear region including ITS1 + 5.8S + ITS2.

Amplification and sequencing of the *COI* were performed using the degenerate primers LCO 1490 and HCO 2198 (for Brazilian samples) and bcdF01 and bcdR04 (for European samples) (Table 2). For Brazilian samples, PCR was conducted in 25 µL reaction volumes containing 2.5 µL of 10× reaction buffer supplied by the manufacturer (Qiagen), 2.5 µL $MgCl_2$ (25 mM), 0.25 µL dNTP mix (10 mM), 0.5 µL of each primer (10 µM), 0.12 µL U μL^{-1} (5 units) of *Taq* DNA polymerase for standard and specialized PCR applications (Qiagen), 14.53 µL of sterile water and 4 µL of DNA template; using a thermocycling profile of one cycle of 3 min at 95°C followed by 45 cycles of 45 s at 95°C, 30 s at 45°C, and 1.10 min at 72°C, and a final step of 10 min at 72°C. European samples were amplified in 12,5 µL reaction volumes containing 6.5 µL of Premix Ex Taq Hot Start (Takara), 0.25 µL of each primer (20 µM), 3.75 µL of sterile water and 2 µl of DNA template; using a thermocycling profile of 35 cycles of 20 s at 94°C, 30 s at 50°C, and 1.0 min at 72°C, according to the manufacturer's protocol.

Table 2
Amplified fragments and primers used in PCR reactions and DNA sequencing of TRM specimens.

Region	*Primer*	Sequence for the *primer* 5' – 3'	Lenght (bp)	Use	Reference
COI	bcd F01	CATTTTCHACTAAYCATAARGATATTGG	670 bp	PCR and sequencing	Skoracka & Dabert (2010)
	bcd R04	TATAAACYTCDGGATGNCCAAAAAA			Skoracka et al. (2012)
	LCO 1490	GGTCAACAAATCATAAAGATATTGG	~ 650bp	PCR and sequencing	Folmer et al. (1994)
	HCO 2198	TAAACTTCAGGGTGACCAAAAAATCA			
ITS	18S	AGAGGAAGTAAAAGTCGTAACAAG	~ 900 bp	PCR and sequencing	Ben Ali et al. (2000)
	28SC	ATATGCTTAAATTCAGCGGG			Navajas et al. (1998)
ITS1	MITS1	CCGTAGGTGAACCTGCGGAAGG	~ 514 bp	PCR and sequencing	Fenton et al. (1997)
	MITS4	CCACCGTTAATTGTGATTTATTTTGTC			
D2	fl230	TGAAACTTAAAGGAATTGACG	~ 2500 pb	PCR	Skoracka & Dabert (2010)
	D1D2 rev 04	GTTAGACTYCTTGGTCCGTG			
	fw2	ACAAGTACCDRTAGGGAAAGTTG	~ 516 pb	Sequencing	Skoracka et al. (2012)
	D1D2 rev 04	GTTAGACTYCTTGGTCCGTG			
	D1D2fw2	ACAAGTACCDRTAGGGAAAGTTG	~ 514bp	PCR and sequencing	Skoracka et al. (2013)
	28Sr0990	CCTTGGTCCGTGTTTCAAGAC			

For Brazilian samples, the ITS nuclear region (ITS1 + 5.8S + ITS2) was amplified and sequenced using the forward and reverse primers 18S and 28SC, respectively (Table 2). PCR was conducted in 25 µL reaction volumes with 2.5 µL of 10 × buffer (Qiagen), 1 µL MgCl2 (25 mM), 0.3 µL BSA (10 mg mL − 1, Biolabs), 1 µL dNTP mix (10 mM of each base), 0.5 µL of each primer (10 µM), 0.25-µL U μL^{-1} (5 units) of *Taq* polymerase (Qiagen), 16.95 µL water and 2 µL of DNA template; using a thermocycling profile of one cycle of 4 min at 94°C followed by 30 cycles of 30 s at 94°C, 30 s at 53°C, and 1 min at 72°C, and a final step of 10 min at 72°C. European samples were amplified and sequenced using the primers MITS1 and MITS4 (ITS1) (Table 2). PCR was conducted in 12,5 µL reaction volumes containing 6.5 µL of Premix Ex Taq Hot Start (Takara), 0.25 µL of each primer (20 µM), 2.75 µL of sterile water, and 3 µl of DNA template, using a thermocycling profile of 35 cycles of 20 s at 94°C, 30 s at 59°C, and 1.0 min at 72°C. After amplification, 4–5 µL of the PCR reaction was analyzed by electrophoresis on a 1% agarose gel and visualized by GelRed staining (Biotum, Fremont, CA, USA) to assess the product size and concentration. Both strand directions of the amplified fragments (*COI*, D2 and ITS) containing visible and single bands were sequenced. Samples from Brazil were directly sequenced in both directions using an ABI 3730 XLs automated DNA sequencer (Applied Biosystems, Korea). European samples were purified using Exonuclease I and Shrimp Alkaline Phosphathase enzyme mix (Thermo Scientific, USA) and then sequenced in both strand directions using the BigDye Terminator v3.1 chemistry on an ABI3730 Genetic Analyzer (Applied Biosystems, USA) in the DNA Sequencing and Oligonucleotide Synthesis Laboratory IBB PAS (Warsaw, Poland).

For Brazilian samples, amplification of the D2 region in 28S rDNA was performed using the primers f1230 and D1D2rev04 (Table 2). PCR was conducted in 25-µL volumes enclosing 2.5 µL of 10 × reaction buffer (Qiagen), 1 µL MgCl2 (25 mM), 1 µL dNTP mix (10 mM of each base), 0.625 µL of each primer (10 µM), 0.25-µL U µL − 1 (5 units) of *Taq* polymerase (Qiagen), 16 µL of sterile water and 3 µL of DNA template; using a thermocycling profile of one cycle of 3 min at 96°C followed by 35 cycles of 10 s at 95°C, 1 min at 50°C, and 2 min at 72°C, and a final step of 5 min at 72°C. For sequencing of the D2 region, the primers fw2 and D1D2 rev04 were used. European samples were amplified and sequenced using the primers D1D2fw2 and 28Sr0990 (Table 2). PCR was conducted in 12,5-µL reaction volumes containing 6.5 µL of Premix Ex Taq Hot Start (Takara), 0.25 µL of each primer (20 µM), 3.75 µL of sterile water, and 2 µl of DNA template, using a thermocycling profile of 35 cycles of 20 s at 94°C, 30 s at 52°C, and 1.0 min at 72°C.

Sequences, Genetic Diversity, And Phylogenetic Analyses

The software Staden Package v.1.6.0 (Staden et al. 2000) was used for checking, editing and assembling the raw data into sequence contigs. The *COI*, D2 and ITS sequences were aligned using the ClustalW multiple alignment procedure (Thompson et al. 1994) implemented in BIOEDIT v.7.0.4 (Hall 1999) with default gap-weighting parameters. No manual adjustments were made to the CLUSTAL alignment. The distributions and frequencies of haplotypes (*COI*) and sequence variants (D2 and ITS1) of the TRM populations were inferred using the option

'Haplotype Collapse' in the program ALTER (Alignment Transformation Environment) available at http://sing.ei.uvigo.es/ALTER/ (Glez-Peña et al. 2010).

Different primer combinations were used to generate sequences of the ITS region, producing dissimilarities in the size of the segment sequenced. One spanning the ITS1, 5.8S and ITS2 region with about 900 bp and the other the ITS1 fragment of about 514 bp. The latter region was present in all accessions and was selected for the subsequent analysis.

Analyses of the pairwise genetic distances between and within nucleotide sequences, as well the choice of the most appropriate evolutionary models for estimation of inter- and intra-lineage genetic variation were performed using MEGA v.7 (Tamura et al. 2013). The Hasegawa-Kishino-Yano (HKY) model (Tamura et al. 2013) was applied to the *COI* dataset; the Kimura 2-Parameters (K2P) model (Kimura 1980) was applied to the D2 datasets; and Tamura 3-parameter (T92) was applied to the ITS datasets. Standard error estimates were obtained by a bootstrap procedure (1000 replicates).

The phylogenetic analyses were conducted using the maximum likelihood (ML) optimality criterion. The best-fit models of nucleotide substitution for the three fragments were selected using the jModeltest v.2.1.1 program (Darriba et al. 2012) based on the likelihood scores for 88 different models. The Akaike information criterion corrected (AICc) and the Bayesian information criterion (BIC) were calculated. The ML models were tested in PhyML v.3.0 (Guindon and Gascuel 2003; Guindon et al. 2010), NJ in MEGA v.7 (Kumar et al. 2016), and Bayesian inference (BI) was tested in MrBayes v.3.2.6 (Ronquist et al. 2012). This software and these procedures were used to test NJ, ML and BI phylogenies in analyses of *COI*, ITS and D2 sequences.

The *COI A. lycopersici* sequence available in GenBank was included in the analyses (JX298841) (Bouneb et al. 2014), as well as one fragment extracted from the complete genome (WNKI00000000) (Greenhalgh et al. 2020). In addition, sequences of *Aculops strobilaceae* Xue and Hong, 2006 (KF782528) and *Aculops cajanusis* Xue and Hong, 2011 (KF782527) (Li et al. 2014) were included in the D2 analyses as internal group. Sequences of *Abacarus neosacchari* Duarte and Navia, 2019 (belonging to the Phyllocoptinae, Anthocoptini similarly to *Aculops*) were included as outgroup in *COI* (KX892640), D2 (KX855705) and ITS (KX855740 and KX855741) analyses. Sequences were also checked against *Aculops* sequences retrieved from GenBank (Bouneb et al. 2014; Li et al. 2014; Duarte et al. 2019, Greenhalgh et al. 2020) and used to edit a neighbor joining tree to validate their reliability. The alignment of *COI* sequences was confirmed by translating the aligned DNA into amino acids using MEGA v.6. To initially identify candidate protein-coding regions in DNA sequences searching start and stop codons, an open reading frame was determined using a graphical analysis tool (ORF FINDER) available at http://www.ncbi.nlm.nih.gov/projects/gorf/. GenBank deposit accession numbers for sequences obtained in this study are in Table 3. The complete dataset is available upon request.

Table 3
Characteristics of the samples used in this study. Haplotypes/genotypes found and sequence GenBank accession numbers.

Host plant táxon	Locality	Sample code	Haplotype/genotype			Accession No		
			COI	D2	ITS	COI	D2	ITS
Solanum lycopersicum	BR: Distrito Federal. Brasília (Embrapa Recursos Geneticos e Biotecnologia)	Al1_9	cH-1	-	-	MW173880	-	-
	BR: Distrito Federal. Paranoá	Al2_10	-	-	I-1	-	-	MT652098
	BR: Distrito Federal. Paranoá	**Al2_9***	**cH-1**	-	**I-1**	**MW173881***	-	**MT652099***
	BR: Distrito Federal. Paranoá	**Al2_16***	cH-1	**D2-1**	**I-2**	MW173882*	**MT652179***	**MT652100***
Physalis sp.	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al3_1*	cH-1	D2-1	I-1	MW173883*	MT652180*	MT652101*
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al3_2	cH-1	-	I-1	MW173884	-	MT652102
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al3_7	-	D2-1	I-1	-	MT652181	MT652103
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al3_15*	**cH-2**	D2-1	I-1	**MW173956***	MT652182*	MT652104*
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al3_18	cH-1	-	I-1	MW173885	-	MT652105
	BR: Distrito Federal Gama (Embrapa Hortaliças	Al3_21*	cH-1	D2-1	I-1	MW173886*	MT652183*	MT652106*
Solanum muricatum	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_4	-	-	I-1	-	-	MT652107
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_6*	cH-1	D2-1	I-1	MW173887*	MT652184*	MT652108*
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_8	-	-	I-1	-	-	MT652109
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_13	cH-1	-	I-1	MW173888	-	MT652110
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_16	cH-1	D2-1	I-1	MW173889	MT652185	MT652111
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_17	cH-1	-	I-1	MW148527	-	MT652112
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_19	-	D2-1	I-1	-	MT652186	MT652113
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_21*	cH-1	D2-1	I-1	MW173890*	MT652187*	MT652114*
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_22	cH-1	-	I-1	MW173891	-	MT652115
	BR: Distrito Federal. Gama (Embrapa Hortaliças	Al4_25	cH-1	D2-1	I-1	MW173892	MT652188	MT652116
Solanum aethiopicum	BR: Distrito Federal. São Sebastião	Al5_2*	cH-1	D2-1	I-1	MW173893*	MT652189*	MT652117*
	BR: Distrito Federal. São Sebastião	Al5_10*	cH-1	D2-1	I-1	MW173894*	MT652190*	MT652118*
	BR: Distrito Federal. São Sebastião	Al5_11	cH-1	D2-1	I-1	MW148528	MT652191	MT652119
	BR: Distrito Federal. São Sebastião	Al5_12	cH-1	-	-	MW173895	-	-
	BR: Distrito Federal. São Sebastião	Al5_13	cH-1	-	I-1	MW173896	-	MT652120
	BR: Distrito Federal. São Sebastião	Al5_16*	cH-1	D2-1	I-1	MW173897*	MT652192*	MT652121*
	BR: Distrito Federal. São Sebastião	Al5_18	cH-1	-	-	MW173898	-	-

Host plant táxon	Locality	Sample code	Haplotype/genotype			Accession No		
			COI	D2	ITS	COI	D2	ITS
	BR: Distrito Federal. São Sebastião	Al5_19	cH-1	D2-1	I-1	MW136001	MT652193	MT652122
	BR: Distrito Federal. São Sebastião	Al5_21	-	D2-1	I-1	-	MT652194	MT652123
Solanum lycopersicum	BR: São Paulo. Piracicaba	Al6_4*	cH-1	-	I-1	MW173899*	-	MT652124*
	BR: São Paulo. Piracicaba	Al6_5	cH-1	-	I-1	MW148529	-	MT652125
	BR: São Paulo. Piracicaba	Al6_6	cH-1	-	-	MW173900	-	-
	BR: São Paulo. Piracicaba	Al6_8	cH-1	-	-	MW173901	-	-
	BR: São Paulo. Piracicaba	Al6_12	cH-1	-	I-1	MW173902	-	MT652126
	BR: São Paulo. Piracicaba	Al6_13	cH-1	-	I-1	MW173903	-	MT652127
	BR: São Paulo. Piracicaba	Al6_15	cH-1	-	I-1	MW173904	-	MT652128
	BR: São Paulo. Piracicaba	Al6_17	cH-1	-	-	MW173905	-	-
	BR: São Paulo. Piracicaba	Al6_20	-	-	I-1	-	-	MT652129
	FR: Montpellier	Al7_11	-	-	I-1	-	-	MT652130
	FR: Montpellier	Al7_16	-	-	I-1	-	-	MT652131
	FR: Montpellier	Al7_26*	cH-1	-	I-1	MW173906*	-	MT652132*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_1	cH-1	D2-1	I-1	MW148530	MT652195	MT652133
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_2	cH-1	D2-1	I-1	MW173907	MT652196	MT652134
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_3	cH-1	-	I-1	MW173908	-	MT652135
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_4	cH-1	D2-1	I-1	MW148531	MT652197	MT652136
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_5*	cH-1	D2-1	I-1	MW173909*	MT652198*	MT652137*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_6*	cH-1	D2-1	**I-3**	MW173910*	MT652199*	**MT652138***
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_7	cH-1	D2-1	I-1	MW173911	MT652200	MT652139
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_8	cH-1	D2-1	I-1	MW136002	MT652201	MT652140
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_10	cH-1	-	-	MW173912	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_11	cH-1	-	I-1	MW173913	-	MT652141
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_12	cH-1	-	I-1	MW173914	-	MT652142
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_13	cH-1	-	-	MW173915	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_14*	**cH-4**	D2-1	I-1	**MW148536***	MT652202*	MT652143*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_15	cH-1	D2-1	I-1	MW173916	MT652203	MT652144
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_16	cH-1	D2-1	I-1	MW173917	MT652204	MT652145

Host plant táxon	Locality	Sample code	Haplotype/genotype			Accession No		
			COI	D2	ITS	COI	D2	ITS
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_17	-	-	I-1	-	-	MT652146
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_18*	cH-1	-	-	MW148526*	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_19	-	-	I-1	-	-	MT652147
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_20*	**cH-3**	-	I-1	**MW173963***	-	MT652148*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al8_21	cH-1	-	I-1	MW148532	-	MT652149
Solanum sessiliflorum	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_3*	cH-1	-	I-1	MW173918*	-	MT652150*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	**Al9_5***	cH-1	-	**I-4**	MW173919*	-	**MT652151***
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_6*	cH-1	-	-	MW173964*	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_10	cH-1	-	-	MW173920	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_11	cH-1	-	I-1	MW173921	-	MT652152
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_13	cH-1	-	-	MW173922	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_14	cH-1	-	I-1	MW173923	-	MT652153
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_16	cH-1	-	I-4	MW173924	-	MT652154
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al9_18	cH-1	-	I-4	MW173925	-	MT652155
Solanum americanum	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_4	cH-1	-	-	MW173926	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_6	cH-1	-	-	MW173927	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_7*	cH-1	-	I-1	MW173928*	-	MT652156*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_9*	cH-2	-	I-1	MW173957*	-	MT652157*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_10	cH-2	-	-	MW173958	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_13	cH-1	-	-	MW148533	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_14	cH-2	-	-	MW173959	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_15	cH-1	-	-	MW173929	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_16*	cH-2	-	I-1	MW173960*	-	MT652158*
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_18	cH-1	-	-	MW173930	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_19	cH-1	-	-	MW148534	-	-

Host plant táxon	Locality	Sample code	Haplotype/genotype			Accession No		
			COI	D2	ITS	COI	D2	ITS
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_21	cH-2	-	-	MW173961	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_22	cH-2	-	I-1	MW136003	-	MT652159
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_23	cH-1	-	-	MW148535	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_26	cH-2	-	-	MW173962	-	-
	BR: Distrito Federal. Gama (Embrapa Hortaliças)	Al10_27	cH-1	-	I-1	MW173931	-	MT652160
Solanum lycopersicum	BR: Distrito Federal. Núcleo rural Samambaia	Al11_1	-	-	I-1	-	-	MT652161
	BR: Distrito Federal. Núcleo rural Samambaia	Al11_2*	cH-1	-	I-1	MW173932*	-	MT652162*
	BR: Distrito Federal. Núcleo rural Samambaia	Al11_3	cH-1	-	-	MW173933	-	-
	BR: Distrito Federal. Núcleo rural Samambaia	Al11_4*	cH-1	-	I-1	MW173934*	-	MT652163*
	BR: Distrito Federal. Núcleo rural Samambaia	Al11_5	cH-1	-	-	MW173935	-	-
	BR: Distrito Federal. Núcleo rural Samambaia	Al11_6	-	-	I-1	-	-	MT652164
	BR: Distrito Federal. Núcleo rural Samambaia	Al11_10*	-	-	**I-5**	-	-	**MT652165***
	PL: Warsaw	MLW690	cH-1	D2-1	-	MW173936	MT652205	-
	PL: Warsaw	MLW691	-	-	I-6	-	-	MT652166
	PL: Czersk	MLW695*	cH-1	D2-1	**I-6**	MW173937*	MT652206*	**MT652167***
	PL: Konstancin	MLW696*	cH-1	D2-1	**-**	MW173938*	MT652207*	-
	PL: Konstancin	MLW697	-	-	I-6	-	-	MT652168
	IT: Scandicci (Firenze)	MLW699	cH-1	D2-1	I-6	MW173939	MT652208	MT652169
	IT: San Felice a Ema (Firenze)	MLW701	cH-1	D2-1	I-6	MW173940	MT652209	MT652170
	IT: Cascine del Riccio (Firenze)	MLW703	cH-1	D2-1	I-6	MW173941	MT652210	MT652171
Solanum sessiliflorum	IT: Cascine del Riccio (Firenze)	MLW705*	cH-1	D2-1	I-6	MW173942*	MT652211*	MT652172*
Solanum lycopersicum	NL: De Lier	MLW710*	cH-1	D2-1	-	MW173943*	MT652212*	-
	PL: Wola Hankowska	MLW713	cH-1	-	-	MW173944	-	-
	PL: Wola Hankowska	MLW714	-	D2-1	-	-	MT652213	-
	PL: Janów	MLW716	-	D2-1	-	-	MT652214	-
	IT: San Severo	MLW888	cH-1	D2-1	I-6	MW173945	MT652215	MT652173
	IT: Battipaglia	MLW889	cH-1	D2-1	I-6	MW173946	MT652216	MT652174
	IT: Battipaglia	MLW890	cH-1	-	-	MW173947	-	-
	IT: Battipaglia	MLW893	cH-1	D2-1	I-6	MW173948	MT652217	MT652175
	IT: Battipaglia	MLW894	cH-1	D2-1	-	MW173949	MT652218	-
	IT: Battipaglia	MLW896	cH-1	D2-1	I-6	MW173950	MT652219	MT652176

Host plant táxon	Locality	Sample code	Haplotype/genotype			Accession No		
			COI	D2	ITS	COI	D2	ITS
	IT: Battipaglia	MLW905*	cH-1	D2-1	I-6	MW173951*	MT652220*	MT652177*
	IT: Battipaglia	MLW906	cH-1	D2-1	I-6	MW173952	MT652221	MT652178
Solanum nigrum	IT: Battipaglia	MLW908	-	D2-1	-	-	MT652222	-
Solanum lycopersicum	IT: Sarno	MLW909	cH-1	-	-	MW173953	-	-
Solanum nigrum	IT: Cascine del Riccio (Firenze)	MLW910*	cH-1	D2-1	-	MW173954*	MT652223*	-
Solanum lycopersicum	PL: Gatka Nowa	MLW911	cH-1	D2-1	-	MW173955	MT652224	-

Table 4. DNA diversity indices. Intraspecific parameters based on *COI* barcoding region and the subunit D2 and ITS1 TRM sequences. S= total polymorphic positions; h= number of haplotypes; Hd = haplotype diversity; Hd StDev = Standard Deviation of Haplotype diversity; K = Average number of nucleotide differences.

Fragment	No. of sequences	Total no. of sites	S	Parsimony informative sites	h	Hd	Hd *StDev*	*Pi*	K
***COI* barcoding**	99	672	4	1	5	0,203	0,0027	0.00044	0.2087
ITS 1 region	81	553	9	5	8	0.429	0.00389	0.00166	0.8377
D2 subunit	46	605	0	0	1	0	0	0	0

Table 5
Estimates of average divergence (shown as percentages with standard error estimates in parentheses) for *COI* region sequence pairs within *Aculops lycopersici* haplotypes and between *A. lycopersici* haplotypes and *Abacarus neosacchari* outgroup species

	Haplotype 1		Haplotype 2		Haplotype 3		Haplotype 4		Outgroup
Haplotype 1 *Aculops lycopersici*	**0.00**	**(0.00)**							
Haplotype 2 *Aculops lycopersici*	0.21	(0.20)	**0.00**	**(0.00)**					
Haplotype 3 *Aculops lycopersici*	0.21	(0.21)	0.43	(0.29)	**n/c**	**(n/c)**			
Haplotype 4 *Aculops lycopersici*	0.21	(0.20)	0.43	(0.28)	0.43	(0.29)	**n/c**	**(n/c)**	
Outgroup *A. neosacchari*	26.12	(2.01)	26.34	(2.01)	26.12	(2.01)	26.34	(2.02)	**n/c**
Analyses were conducted using the P-distance parameter (P2) model									

Table 6
Estimates of average divergence (shown as percentages with standard error estimates in parentheses) for ITS region sequence pairs within and between *A. lycopersici* variants and the *Abacarus neosacchari* outgroup species.

	Var 1		**Var 2**		**Var 3**		**Var 4**		**Var 5**		**Var 6**		**Outgroup**	
A. lycopersici-var 1	**0.00**	**(0.00)**												
A. lycopersici-var 2	0.56	(0.35)	**n/c**	**(n/c)**										
A. lycopersici-var 3	0.28	(0.25)	0.85	(0.44)	**n/c**	**(n/c)**								
A. lycopersici-var 4	0.56	(0.33)	1.13	(0.47)	0.85	(0.42)	**0.00**	**(0.00)**						
A. lycopersici-var 5	0.28	(0.28)	0.28	(0.25)	0.56	(0.38)	0.85	(0.41)	**n/c**	**(n/c)**				
A. lycopersici-var 6	0.28	(0.26)	0.85	(0.44)	0.56	(0.32)	0.85	(0.44)	0.56	(0.40)	**0.00**	**(0.00)**		
Outgroup A*bacarus neosacchari*	32.9	(2.17)	32.96	(2.15)	33.24	(2.14)	33.52	(2.24)	32.68	(2.17)	32.68	(2.17)	**0.00**	**(0.00)**
Analyses were conducted using the P-distance parameter (P2) model														

Table 7
Estimates of average divergence (shown as percentages with standard error estimates in parentheses) for D2 region of 28S rDNA sequence pairs within and between *Aculops* and the *Abacarus neosacchari* outgroup species

	***A. lycopercsi* -Var 1**		***A. strobilaceae***		***A. cajanusis***		***A. neosacchari***	
Aculops lycopercsi -Var 1	**0.00**	**(0.00)**						
Aculops strobilaceae	30.53	(1.90)	**n/c**	**(n/c)**				
Aculops cajanusis	36.73	(2.44)	33.63	(2.18)	**n/c**	**(n/c)**		
Outgroup *Abacarus neosacchari*	34.51	(2.27)	25.22	(2.01)	28.98	(2.01)	**n/c**	**(n/c)**
Analyses were conducted using the P-distance parameter (P2) model								

To perform the Bayesian Inference (BI) combined analysis of *COI*, D2 and ITS fragments, the sequence files were individually organized using MEGA v.6. Alignments of the three fragments were performed separately by the CLUSTAL W multiple alignment method (Thompson et al. 1994) implemented in the BioEdit program. The files were then concatenated in a single matrix in Mesquite v.3.0.4 (a modular system for evolutionary analysis) (Maddison and Maddison 2016), and the BI combined analysis was performed in MrBayes v.3.2. The number of categories, used to approximate the gamma distribution, was set at four, and four Markov chains were run for 10,000,000 generations; the final average standard deviation of split frequencies was less than 0.01, and the stabilization of model parameters (burn-in = 0.25) occurred at approximately 250 generations. The edition of the phylogenetic tree was performed using TreeView v.0.5.0.

Results

Datasets and genetic diversity

COI

The final *COI* dataset consisted of 102 aligned sequences of 672 bps, 99 sequences representing twenty-five TRM populations associated with solanaceous plants obtained in this study (**Table 3**); two TRM sequences available in/extracted from the GenBank (as mentioned in M&M); ans one *Abacarus* mite sequence as an outgroup. No insertions or deletions were found. The translation of the *mt*DNA *COI* nucleotide sequences resulted in 230 amino acids in length. Alignment of these amino acid sequences revealed differences at four positions (variable sites), one was

parsimony informative. The G+C and A+T composition of the entire data set ranged from 36.79 to 38,57% and 61.47 to 63.21%, respectively. Polymorphism indices such as the number of variable sites (S), the haplotype number (h) and diversity (Hd), the average number of differences in nucleotides (K), and the diversity of nucleotides (*Pi*) for mitochondrial and nuclear sequences of *A. lycopersici* are presented in **Table 4**.

The average mean divergence over all the sequence pairs (including the out-group taxa) was 13.84% (SE = 1.17), ranging from 0.21 to 26.34%. The average mean divergence over TRM sequences was 0.36% (SE = 0.29) and ranged from 0.21 to 0.43% (**Table 5**).

ITS1

The final ITS1 dataset consisted of 84 sequences of 553 bps, including 81 sequences of TRM populations from Brazil and Europe, obtained in this study (**Table 3**); one TRM genome sequence and two sequences of *Ab. neosacchari* (as an outgroup) recovered from the GenBank. In the alignment, five sites were parsimoniously informative, and nine sites were variable (**Table 4**). The average mean divergence over all sequence pairs, including the outgroup taxa, was 13.81% (SE = 1.1%) and ranged from 0.28 to 33.52%. The average mean divergence over the *A. lycopersici* sequences was 0.65% (SE = 0.38%) and ranged from 0.28 to 1.13% (**Table 6**).

D2

The nuclear sequence data of the D2 region of the 28S rDNA comprised 49 aligned sequences of 605 bp (26 sequences from five TRM populations from Brazil and 20 sequences from Europe); one TRM genome sequence; and three outgroup sequences- two species of *Aculops* species and one of *Ab. neosacchari* (last four available in the GenBank). The D2 sequences obtained during this study are the first TRM sequences available in the GenBank for this fragment. No polymorphic sites and variable regions were detected within the TRM D2 sequences.

The average mean divergence over all sequence pairs (including the outgroup taxa) was 30.78% (SE = 2.10%) and ranged from 0.0 to 36.73%. The average mean divergence over the TRM sequences was 0.0% (SE = 0.0) (**Table 7**).

Haplotypes and sequence variants

Four haplotypes were identified from the TRM *COI* sequences (**Table 5**). Haplotype 1 (cH1) was the most frequent, representing 90% (91/101 sequences) of all sequences and spread in all countries and host plants considered (**Figure 1**). Haplotypes 2, 3 and 4 (cH2, cH3, cH4) were exclusively present among Brazilian populations: cH2 representing 7.9% (8/101 sequences) of all sequences and associated with *Physalis* sp. and *S. americanum*; cH3 and cH4, each represented in only one sequence, were both associated with *S. lycopersicum* (**Figure 1).**

Six sequence variants were identified from the TRM ITS sequences (**Table 6**). Sequence variant 1 (I-1) was the most frequent representing 76.5% (62/81 sequences) of all sequences occurring in Brazil, France and The Netherlands; it was associated with all host plants except for *S. nigrum*. Sequence variant 6 (I-6), representing 16% (13/81 sequences) of all sequences, was found exclusively in the European populations from Poland and Italy, associated with *S. lycopersicum* and *S. nigrum*. Sequence variant 4 (I-4), representing 3.7% (3/81 sequences), was found exclusively among Brazilian populations from *S. sessiliflorum*. Sequence variants 2, 3 and 5 (I-2. I-3. I-5), each represented by just one sequence, were found exclusively among Brazilian populations from *S. lycopersicum* (**Figure 1)**.

Only one D2 sequence variant (D2-1) (46 sequences) was found among TRM populations (**Table 7**); it was found in all studied countries (except France since no D2 sequences were obtained from this country) and associated with all host plants (except with *S. americanum* since no D2 sequences were obtained from this host) (**Figure 1)**.

Phylogenetic relationships

The general topologies of the *COI* phylogenetic trees inferred by the two selected models were similar by reaveling the same structure for TRM populations and the external group. Thus, only the ML model is shown (**Figure 2**). TRM sequences were clustered in two closely-related and low-supported clades: Clade I, which clusters sequences representing cH-1, cH-2 and cH-4 haplotypes, with sequences from all studied countries and host plants; Clade 2, which comprises the cH-3 sequence, obtained from a Brazilian tomato population. In Clade 1, cH-2 haplotype sequences obtained from Brazilian populations from *Physalis* and *S. americanum* comprise a sub-clade.

The topology of the ITS phylogenetic tree inferred by the selected model (**Figure 3**) also consisted in two low-supported clades: Clade 1 gathering sequences that represents I-1, I-3, I-4 and I-6 sequence variants, including sequences from all studied countries and host plants; Clade 2 comprising I-2 and I-5 sequence variants, all sequences obtained from tomato Brazilian populations. In Clade 1, I-6 haplotype sequences obtained from Italian and Polish populations from tomato and *S. nigrum* comprise a sub-clade.

The combined analyses (**Figure 4**) clustered all TRM sequences in one clade, being possible to distinguishing four closely-related sub-clades: Sub-clade 1 clustering specimens from one tomato Brazilian population; Sub-clade 2 clustering Brazilian specimens from tomato and

Physalis populations; Sub-clade 3 clustering specimens from Italy and Poland populations collected from tomato and *S. nigrum*; and Sub-clade 4 clustering specimens from Brazilian populations collected from *S. aethiopicum*. *S. americanum* and *S. sessiliflorum*.

Phylogenetic analysis suggests that TRM sequences constitute one genetic lineage; the sequence diversity observed inside the three fragments was low, predominantly invariant sites. The low observed bootstrap values might account for this lack of information, *i.e.* due to an insufficient number of informative sites, there is a low possibility to get a tree with strong bootstrap values.

Discussion

Recently, great advance in the knowledge of genetic aspects of TRM has been made with the availability of its complete genome, and that can now be explored to support the development of control strategies (Greenhalgh et al. 2020). Despite this, so far, there was not any information on the genetic variability or structure of this invasive pest along its occurrence areas. This can be crucial for pest management programs, since populations can develop different bioecological traits, such as host preference, susceptibility to biotic and abiotic stressors and cause different responses in the host plant (Porreta et al. 2007; Remais et al. 2011; Migeon et al. 2021). Furthermore, there were still doubts about the taxonomic status of the taxon as cryptic species could occur among populations associated with different host plants. For the first time, here, these crucial aspects were explored by accessing populations from different continents, and from cultivated and wild solanaceous host plants by novel approach to understanding evolutionary aspects and to support the development of TRM management practices.

TRM confirmed as an oligophagous eriophyid mite taxon

Both genetic diversity and phylogeny showed that TRM studied populations, associated with different solanaceous host plants, are co-specific. The divergence for the mithocondrial and nuclear studied genomic regions among studied populations/haplotypes was even lower than that observed for intraspecific variability in other eriophyid taxa. The highest *COI* divergence among haplotypes was 0.43% (i.e. < 0.5%) **(Table 5)**. Such distance corresponded with *COI* intraspecific genetic levels identified by Duarte et al. (2019) for seven *Abacarus* species (the same tribe that *Aculops*) in the same gene, e.g., 0.0 to 0.7%. and close that observed by Skoracka et al. (2012) for *Aceria tosichella* Keifer, 1969 species complex (0.4%). The usual limits of *COI* intraspecific divergence in more than 13 000 congeneric pairs including representatives from 11 phyla have usually been lower than 2% (Herbert et al. 2003) and most was less than 1% (Avise 2000). Concerning interspecific distances for Prostigmata mites (Eriophyidae sub-order) it has been higher than 4.3% for species in different families (Ros and Breeuwer 2007; Matsuda et al. 2012; Duarte et al. 2019; Pérez-Sayas et al. 2022). Similar results were obtained for the ITS: the average divergence between TRM sequence variants/populations was 0.02% (**Table 6**), absolutely corresponding to intraspecific distances when in comparison to divergences observed for other eriophyid mites. Duarte et al. (2019) observed ITS intraspecific diversity in *Abacarus* species ranging from 0.1 to 0.3%, and interespecific distances ranging from 4–17.9%. ITS divergence of 2% have been interpreted as discriminating lineages within *A. tosichella* populations (Skoracka et al. 2012). In this study, no variability in the nuclear D2 region was observed among the TRM populations, similar to that observed in *Abacarus* species, which reached 0.3% (Duarte et al. 2019).

Phylogenies, inferred from the three DNA fragments separately and from the Bayesian combined analysis, emphasize the close relationship among the TRM populations studied. The low support to nodes shows that populations cannot be consistently distinguished. Therefore, the hypothesis of the occurrence of cryptic species among TRM populations associated with different host plants was not corroborated for the studied populations.

Although populations from all plants reported as TRM hosts have not been evaluated in this study, the results obtained allow us to confirm that *A. lycopersici* is an oligophagous eriophyid mite that can infest at least two Solanaceae genera- *Solanum* (with at least six species) and *Physallis*.

High majority of eriophyid mites inhabits a single host plant species indicating close host-relationship. According to Skoracka et al. (2010), about 80% of eriophyoid species occupy one host plant species, about 95% infest plant species belonging to one genus, and about 99% to one host family. TRM can be ascribed in 5% of Eriophyoidea mites infesting host plants in two different genera. Further studies including populations from *Convolvulus* (family Polygonaceae), also reported as a host, should be performed to define if TRM is among the 1% of species that can infest plants in more than one family. The evolutionary and molecular aspects that allow eriophyoid mites to adapt to different host plants could be studied by comparing TRM genome with those of eriophyid mites presenting high host specificity though considering that the whole genome of eriophyoid mites is currently available only for TRM (Greenhalgh et al. 2020).

For many years, *Aceria tulipae* Keifer, 1938 had been treated as one exceptionally generalist eriophyid. Keifer (1969) and Shevtchenko et al. (1970), showed, that *Ac. tulipae* found on Liliaceae was, both morphologically and biologically, different from *Ac. tulipae* inhabiting wheat. As a consequence, a monocot-infesting species *Ac. tosichella* has been described as a separate taxon from *Ac. tulipae* inhabiting Liliaceae plants. Species in the *Ac. tosichella* complex have different host range or preferences (Carew et al. 2009; Skoracka et al. 2012, 2018; Navia et al. 2013), and abilities to transmit plant viruses (Schiffer and Lachmuth 2009; Skoracka et al. 2014; Wosula et al. 2016). Similar observations

were made on other supposed generalists inhabiting monocots: *Abacarus* species (Nalepa, 1896) infesting grasses (Skoracka and Dabert 2010); *Trisetacus* species infesting conifers (Lewandowski et al. 2014); *Retracrus* species infesting palm trees and heliconias (Navia et al. 2015). Therefore, many monocot-associated eriophyid mites, previously considered generalists, have showed to constitute complexes of cryptic species. However, the supposed low-specificity in eriophyid mites associated with dicotyledons plants has not been investigated. For instance, no studies investigated the occurrence of cryptic species on *Calacarus citrifolii* Keifer, 1955, the species with the wider host range of all superfamily reported on 21 plant families (de Lillo and Amrine - Computerized Database for Eriophyoidea, Filemaker Pro). Among species of economic importance, TRM does stand out to be an oligophagous species.

TRM genetic homogeneity in Europe revealing a highly invasive haplotype

Analysis of the diversity of sequences of the *COI* mitochondrial region showed that haplotype 1 (cH1) is dominant in Brazil, is associated with all host plants considered, and that it is the only one present in European populations (France, Italy, Poland and The Netherlands). The genetic homogeneity among TRM European populations highlights that cH1 is a highly invasive and not host-specific haplotype. This adaptation to infest a high number of plants, which enhances the range of pathways in mites' transport, certainly has favored TRM invasiveness and wide distribution.

A new introduced population can be composed of a sub-sample of genotypes, from one or several populations in the origin range. No intraspecific variation in the invaded range suggests i) single small initial invasive population, ii) multiple invasions of the same source, or iii) adaptative selection of the haplotype that has been established. The relationship between the success of invasive populations and their genetic diversity has been discussed for a long (Lee 2002; Estoup et al. 2016), by assessing genetic diversity as positive factor influencing survival and adaptation in invaded areas (Lee 2002; Petit et al. 2004; Puillandre et al. 2008). However, absence or low genetic diversity, caused by a population bottleneck, has been reported for many invasive species (Le Page et al. 2000; Sax and Brown 2000; Martel et al. 2004; Novak and Mack 2005; Puillandre et al. 2008), including mites (Navia et al. 2005; Soulignac et al. 2005; Boubou et al. 2012; Dowling et al. 2012) similarly to observed to TRM in this study. These studies suggested that even genetically homogeneous founder populations may retain the ability to respond to natural selection, adapt and expand in the invaded area. In such cases, the success of the invasion has been considered as the 'genetic paradox of invasions' (Sax and Brown 2000). For some invasive species, the paradox has showed to be spurious, as seen in introduced populations with low diversity in neutral markers that maintain high genetic variation in ecologically relevant traits. However, in other cases, it can be considered genuine (see Estoup et al. 2016): compensatory mechanisms maybe acting to counter the loss of genetic variation and unique aspects of the species' biology, as well as environmental interactions that could allow an invasive population to thrive, have been showed or proposed (Estoup et al. 2016; Schrieber and Lachmuth 2016; Eyer et al. 2018; Marin et al. 2019). Further studies need to be conducted to confirm genuine genetic paradox in TRM invasion and to better understanding evolutionary strategies that allowed its invasion success with no genetic variability.

The genetic homogeneity evidenced among TRM European populations do not primarily corroborate the hypothesis that a differentiated host response observed on different host plant species/varieties could be due to the genetic diversity of the associated mite pest. The results suggest that the differentiated symptomatology and damage intensity caused by TRM infestation is due to other biotic or associated abiotic factors related to host plant physiology- e.g. metabolic pathways and mechanisms in plant defense in different hosts (see Glas et al. 2014; Kant et al. 2015), or host response to drought stress, that in some cases can promotes the colonization success of eriophyid mites (Ximénez-Embún et al. 2017).

Towards TRM origin, host adaptation and invasion process

Most of the knowledge about the introduction routes of invasive species is derived from historical and observational data, which are often sparse, incomplete and, sometimes, misleading (Estoup and Guillemaud 2010). This difficulty is remarkable for the tiny eriophyoid mites, for which relevant historical records sometimes are scarce and often incomplete, since they can go unnoticed for a long time and be reported, out of time, when outbreaks occur and in taxonomical confused context (Navia et al. 2010). One such case is *A. lycopersici*, for which worldwide historical reports and taxonomic mistakes have not been allowed to timely and thoroughly understand its geographic expansion. The mite was described from Australia in 1917 (Tryon 1917); then it was erroneously described as new in 1937 in North Africa (Morocco) (Massee 1937); in 1940s it was for first reported in North America (USA) (Keifer 1940) and in Europe (Spain) (Planes 1941); in 1950s in the Middle East (Lebanon) (Talholk 1950) and in Asia (Georgia) (Tukalevskii and Rogachev 1959) and in the 1960s in South America (Brazil) (Costa and Carvalho 1962) and South Africa (Ryke and Meyer 1960). Another junior synonym of *A. lycopersici* was described in 2005 in China as *Tetra lycopersici* Xue and Hong, 2005 (Amrine and de Lillo, personal communication). In this context of historical untraceability patterns genetic data can be explored for tracing invasion routes (Estoup and Guillemaud 2010).

Although the objective of this work was not to trace invasion routes, since a better representation of populations worldwide would be necessary for this purpose, genetic diversity and a phylogeographical analysis based on both mitochondrial and nuclear markers analyzed jointly with the main host plant history corroborate the hypothesis of a South American origin for TRM. In general, the highest genetic diversity

for a species occurs in its area of origin. Our results showed a highest TRM genetic diversity in Central Brazil; four haplotypes and five sequence variants were present in the only studied area of Central Brazil while just one haplotype and two ITS sequence variants were present in populations of four European countries. Also, it is interesting to note that the haplotype cH2 was found exclusively associated with non-tomato solanaceous- *S. americanum* and *Physalis*- in Brazil.

Under the assumption that tomato does not constitute the original TRM host plant, but some other wild solanaceous plants (Oldfield 1996; Michalska et al. 2010; Navia et al. 2010) and that currently this mite presents a worldwide distribution (CABI 2022) the most likely is that TRM adopted tomato as an alternate host plant in areas of co-occurrence of the original wild host plant and the cultivated tomato ant that this host adaptation occurred before expansion of tomato as a cultivated crop in the 16^{th} century. The cultivated tomato has its origin in central South America (Blanca et al. 2012, 2015; Razifard et al. 2020), and then it presented a complex domestication history in South America and Mesoamerica (Razifard et al. 2020); by 500 BC, it was already being cultivated in southern Mexico (Smith 1994), and Aztecs raised several varieties of tomato (Townsend 2000). However, expansion of tomato cultivation to other colonies in the Caribbean and to the old continent (firstly Asia and Europe) only occurred at the beginning of the 16th century by Spanish colonizers (Smith 1994). The results of this first study support with genetic data the Neotropical origin of TRM however, it is not possible to know whether the mite was disseminated during the colonization period or afterwards, through the exchange of plant material. Phylogenomic analysis, including populations along wide tomato range in South and Central America from as many wild host plants as possible will enable to enlighten evolutionary history of this intriguing eriophyid mite that became a tomato and solanaceous pest. It is possible that the tomato domestication and breeding process may have unintentionally selected materials with higher susceptible to TRM. Determination of the original TRM host plant, supposedly better adapted to TRM herbivory, may be useful for revisiting breeding programs focusing in resistance.

Declarations

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Ethical Approval

not applicable

Competing interests

no

Authors' contributions

D.N, M.E.D, R.S.M conducted field collections in Brazil and M.L and S.S. in Europe; M.E.D conducted laboratory analysis in Brazil; and M.L. in Europe; R.S.M and M.E.D conducted data analysis. D.N, M.E.D, R.S.M and M.L, wrote the main manuscript text; M.E.D and R.S.M prepared figures 1-4. All authors reviewed the manuscript.

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Availability of data and materials

GenBank https://www.ncbi.nlm.nih.gov/genbank/

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Figures

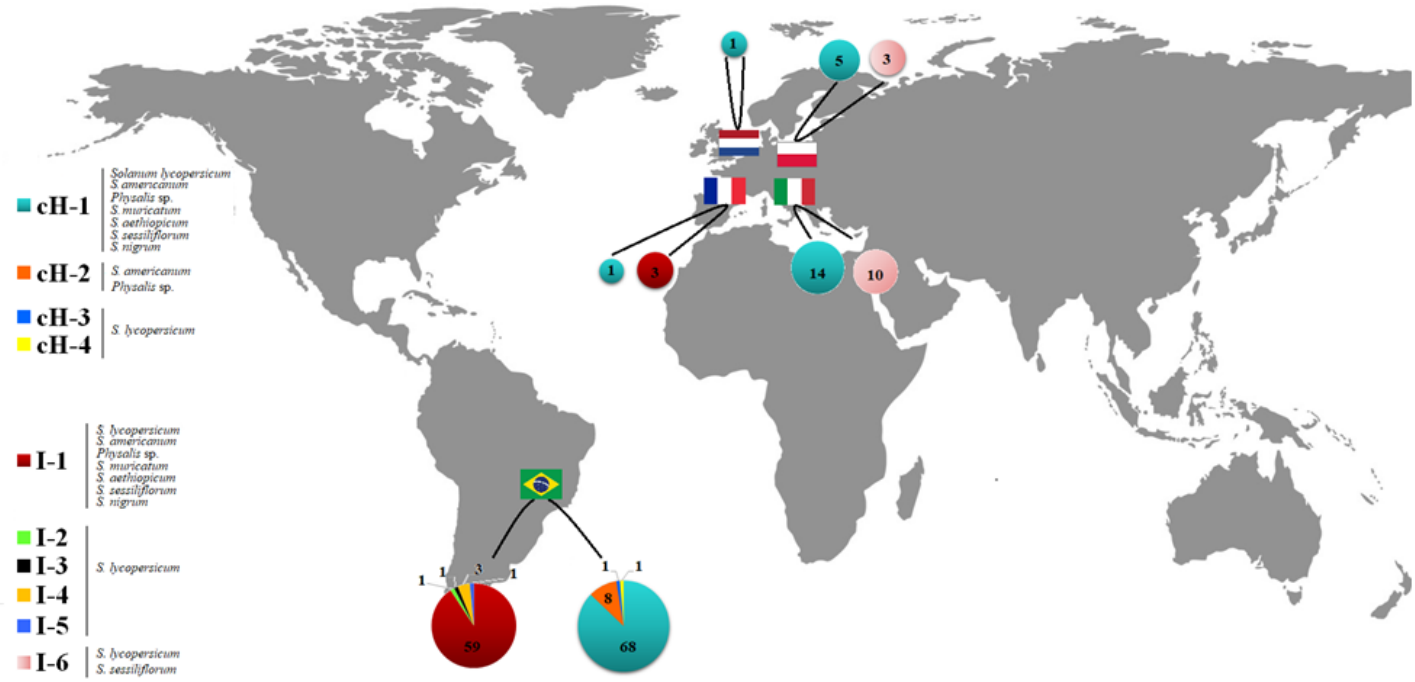

Figure 1

Geographical distribution of the TRM *COI* haplotypes (mitochondrial DNA) and ITS1 sequence variants (ribosomal DNA). The number of sequences (frequency) observed for each haplotype/sequence variant is inside or close to the pie chart. The host plant associated with each haplotype or sequence variant is reported. *COI* and ITS1 sequences retrieved from Genbank and those obtained in this study were included. The distribution of the D2 sequences was not shown in this graph since a single variant was observed in Brazil, Italy, Poland, and Netherland.

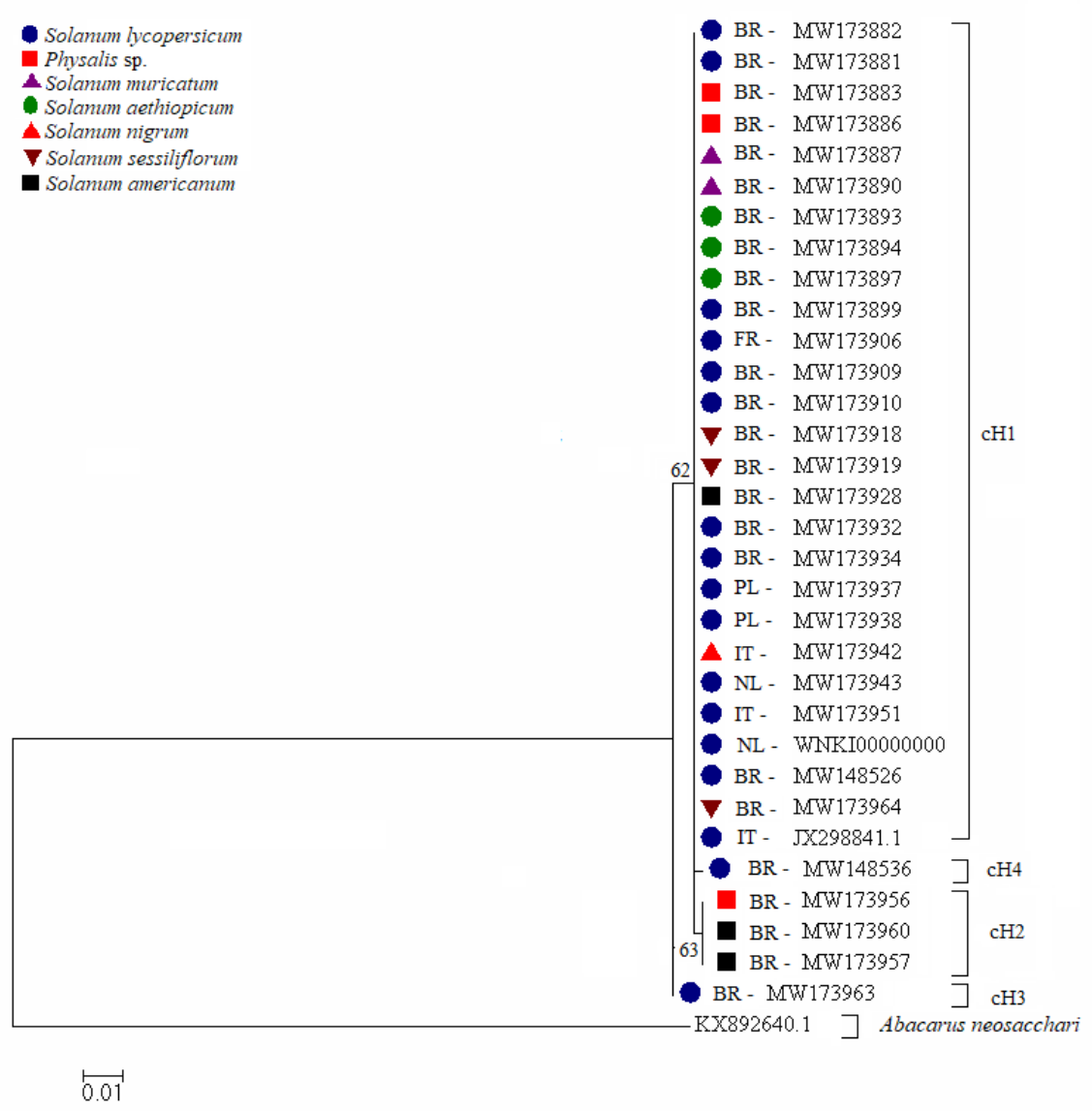

Figure 2

Maximum-likelihood (ML) tree performed using Hasegawa-Kishino-Yano (HKY) model on data from the *COI* sequences of TRM populations and the outgroup species.

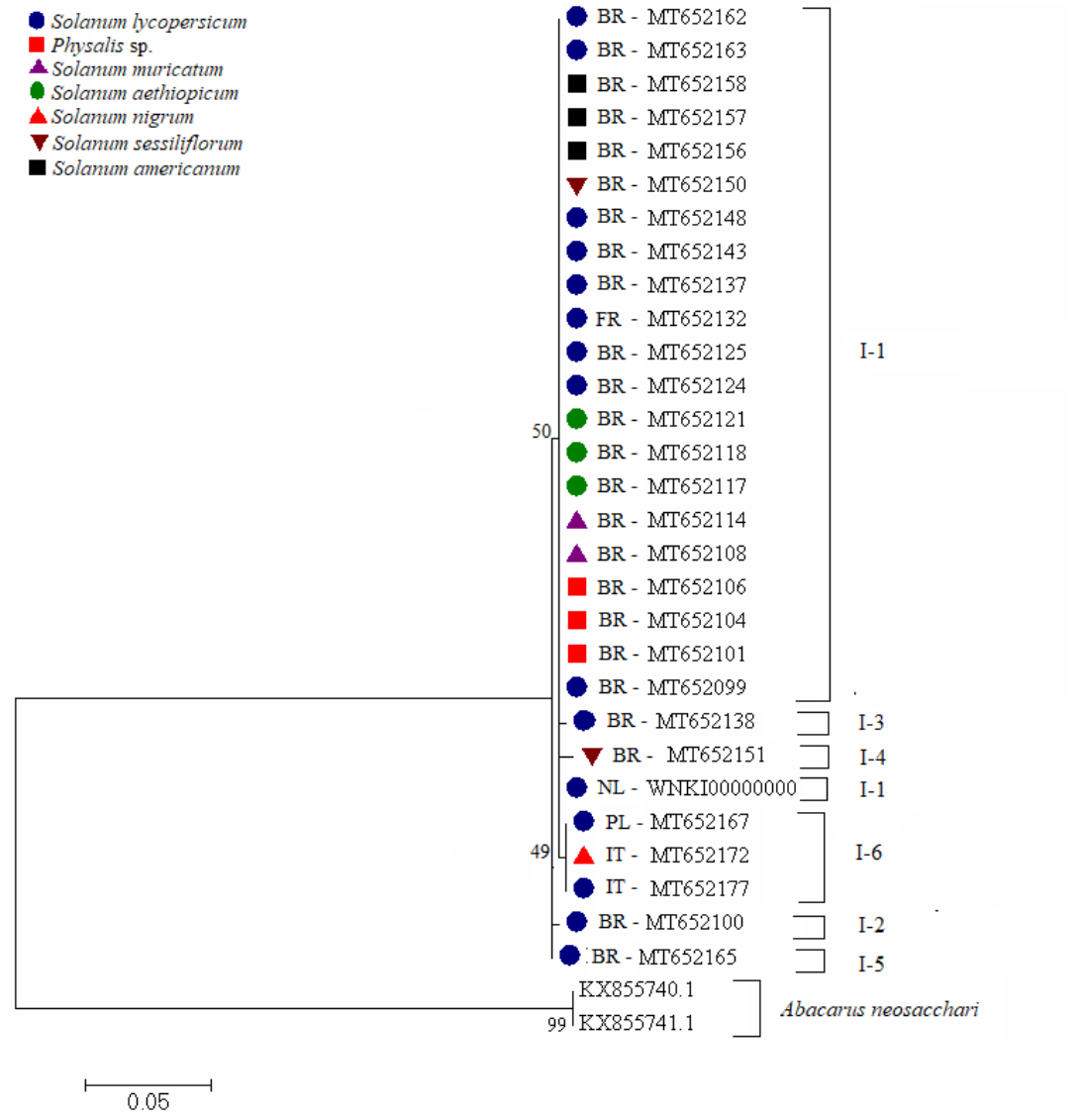

Figure 3

Maximum-likelihood (ML) tree performed using Kimura 2-parameter (K2P) model on data from the ribosomal region ITS of TRM populations and the outgroup species.

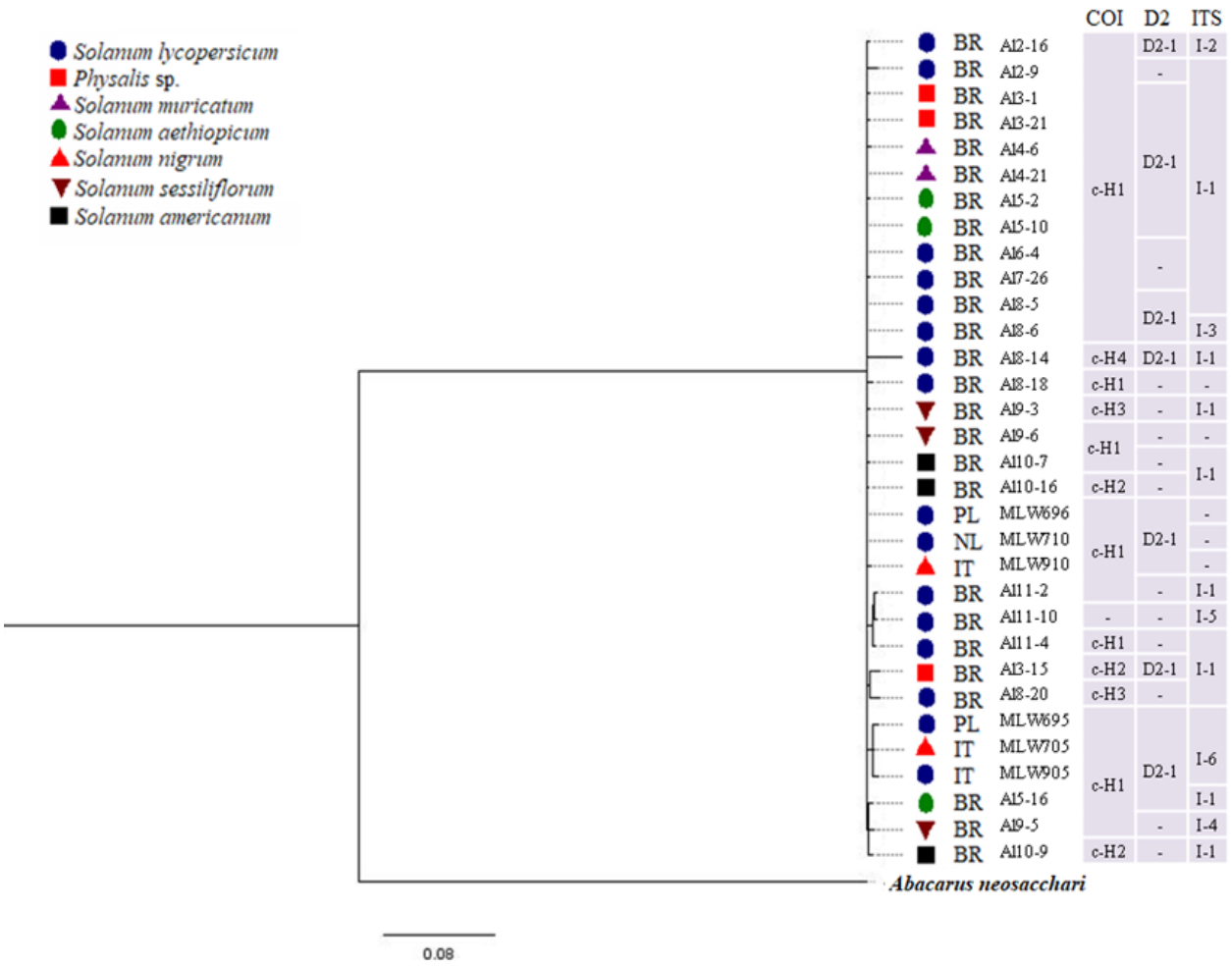

Figure 4

Combined Bayesian inference (BI) analysis tree for TRM populationscalculated from the concatenated cytochrome c oxidase subunit I sequences (COI). 28S r-RNA subunit D2 sequences and ribosomal region ITS.