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Tuta absoluta's population genetic structure across Africa: Two well-delineated but weakly differentiated groups suggesting few introductions and significant gene flow

Structure génétique des populations de *Tuta absoluta* à travers l'Afrique: deux groupes bien délimités mais faiblement différenciés suggérent peu d'introductions et un flux génétique important

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Abstract

1. Describing the genetic structure and diversity of invasive insect pest populations is essential to better understand a species' invasion history and success throughout its distribution range. *Tuta absoluta* (Meyrick) (Lepidoptera, Gelechiidae) is a destructive pest of tomato and many other solanaceous crops, with very high economic impacts. Its invasion threatens food security in a large part of the globe, in areas such as sub-Saharan Africa where the agricultural resilience has already been weakened by rapid human-induced changes due in particular to population growth, increased trade and global change.
2. This work aimed to investigate the diversity and genetic structure of 60 populations of *T. absoluta* using microsatellite markers, with a particular focus on sub-Saharan Africa.
3. Our results revealed distinct differentiation and diversity patterns between *T. absoluta* native versus invaded areas, and high genetic homogeneity among the African populations sampled. However, for the first time, two weakly differentiated but distinct genetic clusters in Africa were identified.
4. The results suggest few introduction events of the species in Africa or multiple introductions from genetically close areas, significant gene flow between outbreaks and seem to indicate the existence of two distinct clusters in Africa. This new data enable us to formulate hypotheses on the species' invasion patterns and the dynamics of its invasive populations.

5. These hypotheses must be verified with more extensive sampling over the whole range of *T. absoluta*, especially in its presumed native area.

KEYWORDS
genetic structure, insect pest populations, invasive alien species, microsatellite markers, South American tomato pinworm, sub-Saharan Africa

INTRODUCTION

Growing inter-continental trade has caused a dramatic rise in the frequency of alien species introductions, particularly insects, into new geographic regions (Seebens et al., 2017). The opening of new trade routes and local development of transport infrastructures increases exposure to invasions of previously relatively spared areas, especially in Africa (Seebens et al., 2018). Agro-ecosystems are particularly vulnerable to new pest introductions, with biological invasions generating a global cost of US$221.65 billion per year on a worldwide scale (Renault et al., 2022).

Sub-Saharan Africa's high population growth (Tabutin & Schoumaker, 2020) necessitates increased agricultural production, often reducing ecosystem resilience (Wang, 2020). Simultaneously, economic development and rising consumption, particularly in urban areas that are often distant from the source of production, lead to a rise in both intra- and inter-continental trade (Hulme, 2021). These factors together facilitate the introduction and spread of invasive species (Diagne et al., 2020; Kumschick et al., 2015; Parker et al., 1999). Agricultural production and food security are thus strongly threatened by these introductions of new species, especially in the African continent, as shown by several recent examples of spectacular insect invasions, both in terms of speed of expansion as well as economic impacts: *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) (Neuenschwander, 2001), *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) (Brévault et al., 2018) or *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Mansour et al., 2018).

The invasion history of a species can have a significant impact on its genetic structure and diversity, and in turn, affect its ability to establish and thrive in its new environment (Dlugosch & Parker, 2008; Garnas et al., 2016). However, various processes can counteract the potential deleterious effects resulting from bottlenecks at each invasion step (Estoup et al., 2016). Multiple introductions, for instance, have been observed for several invasive insect species (Ciosi et al., 2008; Javal et al., 2019; Lombaert et al., 2010). Another example is the bridgehead effect, where a population that has been successfully introduced serves as the origin of the colonizers that invade another region (Javal et al., 2019; Lesieur et al., 2019; Lombaert et al., 2010). These scenarios can maintain or even increase genetic diversity compared with the native population (Dlugosch & Parker, 2008; Estoup et al., 2016) or help the invasive population adapt to new environments (Lombaert et al., 2010; Whitney & Gabler, 2008).

It is critical to decipher the population structure of both native and invasive populations to identify an invasive alien species (IAS), manage established populations and prevent further introductions (Essl et al., 2015; Estoup & Guillemaud, 2010). Managing introduced populations requires a comprehensive understanding of the invasion dynamics, including evaluating factors such as the frequency of new introductions, the number of introduction events and the connections between various populations within native and invaded ranges (Roderick & Navajas, 2003). Molecular markers are particularly effective tools commonly used in this context (Estoup & Guillemaud, 2010). Among them, microsatellite markers allow the detection of fine and recent population dynamics processes.

The South American tomato pinworm, *T. absoluta*, is a major pest of tomato crops worldwide and has also been reported to cause significant damage to other solanaceous crops including potato, eggplant and sweet pepper (Bal et al., 2022; FERA, 2009). The species was first described from the Andes region in Peru in 1917, but it was reported as a pest in most South American countries only since the early 1980s (Campos et al., 2017). Outside its native area, it was first detected in Spain in 2006 (Urbaneja et al., 2007), where a single Chilean population seems to be at the origin of the invasion (Guillemaud et al., 2015). It then rapidly spread (Desneux et al., 2011) and was soon detected all around the Mediterranean basin, in the Middle East, Africa and in Asia, where it has become a serious threat to the production of many solanaceous crops both under greenhouse and open-field conditions (Desneux et al., 2011; Mansour & Biondi, 2021; Rwomushana et al., 2019; Shashank et al., 2016; Zhang et al., 2020). In 10 years, it had infested more than 60% of the tomato crops worldwide from Mediterranean Europe to South Africa and from West Africa to South Asia, which translates into an increase of its distribution area by 800 km per year (Campos et al., 2017). Considering the first report dates for the African continent, *T. absoluta* probably moved from Spain to the Maghreb area (2008), then to Eastern Africa (2010s) and spread throughout sub-Saharan Africa (2012–2013) to Southern African countries (2014–2017) (Biondi et al., 2018; Chidege et al., 2016; Mansour et al., 2018; Pfeiffer et al., 2013; Rwomushana et al., 2019; Santana et al., 2019; Tumuhaise et al., 2016). However, for Africa, this hypothesis remains to be proven.

The rapid expansion of this invasive species into new regions is primarily attributed to its high level of polyphagy, exceptional reproductive and adaptive capabilities (Campos et al., 2021) and strong resistance to insecticides (see the Arthropod Pesticide Resistance Database available at https://www.pesticideresistance.org; Guedes et al., 2019). It has also been related to the international trade of tomato fruits, the intensification and homogenization of agricultural environments and particularly in Africa to porous borders and unsuitable implementation of quarantine and phytosanitary measures when

they exist (Desneux et al., 2022; Marchioro & Krechemer, 2024; Tonnang et al., 2015). However, despite decades of invasions and significant damage over its whole range, little is ascertained about *T. absoluta*'s invasion pathway and history. Some population genetic studies have tried to address these questions, but the molecular markers used to resolve genetic diversity, population structure and invasive processes were in most cases inconclusive due to an overall low or unresolutive level of genetic variation within invaded areas (Bettaïbi et al., 2013; Cherif et al., 2017; Cifuentes et al., 2011; Guillemaud et al., 2015; Ndiaye et al., 2021; Shashank et al., 2018). Based on microsatellite markers and an extensive sampling performed in *T. absoluta*-invaded areas in countries reflecting different historical steps of its invasion worldwide, particularly in Africa, this study investigates the genetic diversity and structure of *T. absoluta* at various geographical scales.

MATERIALS AND METHODS

Sample collection and DNA extraction

A total of 736 *T. absoluta* specimens were collected in 60 localities mainly in Africa (54 localities) with a focus on Senegal and Niger, but also in Europe (three localities), South America (two localities) and Indian Ocean island (one locality) (Table 1; Figure 1). Sampling was conducted between 2009 and 2018, with some instances occurring shortly after the invasion while others took place a considerable time afterward (Table 1). Most localities were sampled once, but some were surveyed twice or three times in successive years, for example, in Tolkoboye, Niger, where the same field was sampled in 2016, 2017 and 2018 (populations 8, 9 and 10 in Table 1). Specimens were mainly collected in tomato fields. The majority of individuals collected were adults, with the exception of 6 larvae collected on sight at Algerian sites (two larvae per site, in populations 53, 54 and 55). Adults were caught using insect nets or pheromone traps placed in the middle of the field for 1 day, and larvae were collected by hand (Table 1). Genomic DNA was extracted from each specimen using the DNeasy Blood and Tissue Kit (Qiagen, France) according to the manufacturer's instructions.

Microsatellite genotyping

Twenty-seven primer pairs previously developed or used in population genetic studies (Bettaïbi et al., 2013; Guillemaud et al., 2012, 2015; Table S1) were tested by monolocus polymerase chain reaction (PCR) with DNA from 12 specimens of various geographical origins. PCR amplifications were performed in a final volume of 10 µL containing 5 µL of the Qiagen multiplex PCR Master Mix (1×) (including Taq, 200 µmol/L of each dNTP and 1.5 mmol/L $MgCl_2$), 2 µmol/L of primers, 1 µL of genomic DNA and 3 µL of RNase-free water. All PCRs comprised the following steps: (i) activation at 95°C for 15 min; (ii) 35 denaturation cycles at 94°C for 30 s, annealing at 62°C for 90 s and elongation at 72°C for 60 s and (iii) a final elongation step at 60°C for 30 min, as described in Streito et al. (2017). Nine of these loci finally provided successful and high-quality amplification with unambiguous allelic patterns (i.e., clear single band of expected size, no smear) and apparent polymorphism when scored by agarose gel electrophoresis. They were retained for multiplex PCRs with fluorescently labelled primers. Using the Multiplex Manager v1.2 software (Holleley & Geerts, 2009), they were arranged in two multiplex PCRs that minimized the formation of duplexes and maximized the range of amplification product sizes (Table S1).

The 736 DNA extracts were screened using these nine microsatellite loci. Standard 10 µL PCRs were performed as described by Streito et al. (2017). Diluted PCR products were run on an ABI Prism 3130XL automated sequencer (Applied Biosystems, Montpellier, France) using the GeneScan-500 LIZ™ size standard. Allele sizes were scored using GeneMapper™ 4.0 software (Applied Biosystems) and were confirmed manually. The genotypes that were either not successfully obtained or had unclear results were subjected to re-amplification and re-evaluation two times. If the results remained ambiguous, they were omitted from subsequent analyses. All samples with genotypes missing at more than two loci were removed. Consequently, 689 samples were considered for the analyses (653 specimens from Africa, 15 specimens from Europe, 21 specimens from South America and 19 specimens from the Indian Ocean; Table 1).

Statistical analysis

Marker characteristics

To determine whether all nine loci retained were suitable for our *T. absoluta* population genetics study, GenePop 4.7.5 on the Web (Raymond & Rousset, 1995, http://genepop.curtin.edu.au/) was used to compute the observed number of alleles (A_N) and the allele size range. The same platform was also used to test linkage disequilibrium (LD) between each pair of microsatellite loci, deviation from Hardy–Weinberg equilibrium (HWE) and the inbreeding coefficient (F_{IS}) of each locus over the whole sampling. As multiple tests were conducted, sequential Bonferroni correction of the *p*-values was performed. As a potential deviation factor from HWE, null allele frequency ($f_{NULL\text{-}ALLELE}$) was estimated (FreeNA package, Chapuis & Estoup, 2007). Loci with a mean estimate of null-allele frequency greater than 0.15, significant heterozygote deficiencies after Bonferroni correction ($p < 2.64 \times 10^{-5}$), and a highly substantial inbreeding coefficient (F_{IS} >0.25) were not retained in the study, resulting in the exclusion of two out of the nine microsatellite loci (i.e., Ta222 and Ta252) (Table S1).

Levels of genetic diversity and differentiation

For each population sampled containing more than eight individuals, standard genetic variability indexes were estimated using GenAlEx

TABLE 1 Origin of the *Tuta absoluta* specimens analysed and main genetic diversity parameters of the single populations.

	N pop	Country	Locality	Lat	Long	Sampling date	Sample size	Mean number of alleles (A_N)	Allelic richness	Mean number of private allele	Private alleles richness	F_{IS}	H_O (mean ± SD)	H_E (mean ± SD)	Date of first report of *T. absoluta*	Reference
Indian Ocean	1	Mayotte	Mamoudzou	−12.8275	45.1662	2017	19	4.571	1.59	0.036	0.036	0.3229	**0.402 ± 0.092**	0.571 ± 0.079	2015	EPPO (2016)
Africa	2	Kenya 1	Mwea	−0.8233	37.6173	2018	19	5.143	1.69	0.031	0.031	0.1625	**0.577 ± 0.082**	0.666 ± 0.047	2014	Mansour et al. (2018)
	3	Kenya 2	Nairobi	−1.2920	36.8219	2018	19	5.429	1.68	0.037	0.037	0.0205	0.669 ± 0.089	0.665 ± 0.066		
	4	Niger 1	Niamey	13.5115	2.1253	2013	17	6	1.73	0.048	0.048	0.1490	**0.624 ± 0.073**	0.703 ± 0.053	2013	Haougui et al. (2017)
	5	Niger 2	Saga	13.4814	2.1321	2017	21	4.857	1.62	0.004	0.004	0.0967	**0.558 ± 0.097**	0.601 ± 0.091		
	6	Niger 3	Saga	13.4814	2.1321	2017	18	5.286	1.64	0.031	0.031	−0.0749	0.683 ± 0.084	0.619 ± 0.062		
	7	Niger 4	Mansari	13.3880	1.9933	2015	6	-	-	-	-	-	-	-		
	8	Niger 5	Tolkoboye	14.2147	2.1208	2016	23	5.286	1.6	0.029	0.029	0.0404	0.577 ± 0.100	0.587 ± 0.086		
	9	Niger 6	Tolkoboye	14.2148	2.1209	2017	24	5.143	1.63	0.019	0.019	0.0052	0.628 ± 0.082	0.617 ± 0.066		
	10	Niger 7	Tolkoboye	14.2149	2.1210	2018	18	5.429	1.67	0.023	0.023	0.0242	0.651 ± 0.092	0.648 ± 0.070		
	11	Niger 8	Doutchi	13.6452	4.05361	2016	14▲	4.429	1.55	0.010	0.010	0.0774	0.510 ± 0.100	0.532 ± 0.083		
	12	Niger 9	Nagoual	13.2708	1.9127	2016	17	5	1.66	0.023	0.023	0.0272	0.647 ± 0.065	0.645 ± 0.051		
	13	Niger 10	Karey Gorou	13.4202	1.9397	2016	9	4.571	1.71	0.030	0.030	−0.0802	0.762 ± 0.092	0.665 ± 0.055		
	14	Niger 11	Bourboukabé	13.6497	2.1497	2016	2◆	-	-	-	-	-	-	-		
	15	Niger 12	Bourboukabé	13.6497	2.1497	2018	17	5.571	1.61	0.036	0.036	−0.0447	0.642 ± 0.114	0.596 ± 0.103		
	16	Niger 13	Kahé	13.3411	2.1633	2016	4	-	-	-	-	-	-	-		
	17	Senegal 1	Diebang	12.8239	−14.9204	2014	9	5.143	1.72	0.032	0.032	0.2836	**0.524 ± 0.118**	0.679 ± 0.065	2012	Pfeiffer et al. (2013)
	18	Senegal 4	Ziguinchor	12.5641	−16.2639	2014	3	-	-	-	-	-	-	-		
	19	Senegal 5	Ziguinchor	12.5641	−16.2639	2017	5	-	-	-	-	-	-	-		
	20	Senegal 6	Bel Air	14.7030	−17.4262	2014	20	5.286	1.67	0.019	0.019	0.0267	0.657 ± 0.077	0.658 ± 0.078		
	21	Senegal 7	Bel Air	14.7030	−17.4262	2017	3	-	-	-	-	-	-	-		
	22	Senegal 8	UCAD	14.6912	−17.4592	2014	2	-	-	-	-	-	-	-		
	23	Senegal 9	Dakar	14.7030	−17.4262	2016	1	-	-	-	-	-	-	-		
	24	Senegal 10	Mballing	14.3791	−16.9478	2014	18	5.286	1.68	0.020	0.020	0.1551	**0.580 ± 0.079**	0.665 ± 0.074		
	25	Senegal 11	Mbour	14.4228	−16.9653	2017	14	5.571	1.68	0.067	0.067	0.2396	**0.508 ± 0.074**	0.650 ± 0.051		
	26	Senegal 12	Sanar UGB	16.0626	−16.4258	2017	19	5.714	1.69	0.027	0.027	−0.1207	0.774 ± 0.089	0.675 ± 0.067		
	27	Senegal 13	Sanar UGB	16.0626	−16.4258	2016	1	-	-	-	-	-	-	-		
	28	Senegal 14	Diogo	15.3002	−16.8196	2015	1	-	-	-	-	-	-	-		
	29	Senegal 15	Diogo	15.3002	−16.8196	2017	8	3.857	1.61	0.109	0.109	0.2127	**0.490 ± 0.097**	0.566 ± 0.069		
	30	Senegal 16	Tieudem	14.9109	−17.0950	2014	20	5.286	1.64	0.026	0.026	0.0845	**0.587 ± 0.070**	0.624 ± 0.077		

TABLE 1 (Continued)

	N pop	Country	Locality	Lat	Long	Sampling date	Sample size	Mean number of alleles (A_N)	Allelic richness	Mean number of private allele	Private alleles richness	F_{IS}	H_O (mean ± SD)	H_E (mean ± SD)	Date of first report of *T. absoluta*	Reference
	31	Senegal 17	Ndieguene	14.9510	−17.0721	2017	19	5.714	1.67	0.028	0.028	0.0568	0.632 ± 0.102	0.651 ± 0.074		
	32	Senegal 18	Thilène	16.2660	−16.1734	2014	3	-	-	-	-	-	-	-		
	33	Senegal 19	Bokhol	16.5330	−15.4125	2014	2	-	-	-	-	-	-	-		
	34	Senegal 20	Richard-Toll	16.4625	−15.6531	2014	2	-	-	-	-	-	-	-		
	35	Senegal 21	Fanay Diery	16.5500	−15.2333	2014	1	-	-	-	-	-	-	-		
	36	Senegal 22	Niangue Diery	16.6600	−14.9593	2014	1	-	-	-	-	-	-	-		
	37	Senegal 23	Darou Gueye	16.2088	−16.2827	2014	2	-	-	-	-	-	-	-		
	38	Senegal 24	Dagana	16.5312	−15.4923	2014	2	-	-	-	-	-	-	-		
	39	Senegal 25	Dagana	16.5312	−15.4923	2017	15	5.286	1.65	0.058	0.058	0.3840	**0.406 ± 0.091**	0.631 ± 0.096		
	40	Senegal 26	Jamby	15.6341.	−13.3410	2017	4	-	-	-	-	-	-	-		
	41	Senegal 27	Agnam thiodaye	15.6450	−13.2756	2017	2	-	-	-	-	-	-	-		
	42	Senegal 28	Pakane	13.7000	−15.6500	2014	8	4.714	1.71	0.037	0.037	0.1658	**0.615 ± 0.105**	0.659 ± 0.073		
	43	Senegal 29	Dalacolon	13.7615	−15.6146	2014	3	-	-	-	-	-	-	-		
	44	Senegal 30	Kaolack	14.16520	−16.0757	2017	8	3.571	1.59	0.052	0.052	0.3557	**0.390 ± 0.110**	0.550 ± 0.071		
	45	Tanzania 1	Duluti	−3.3734	36.8063	2017	15	4.714	1.69	0.010	0.010	0.3264	**0.469 ± 0.088**	0.662 ± 0.055	2014	Chidege et al. (2016)
	46	Tanzania 2	Illula	−7.6766	36.0366	2017	19	5	1.66	0.109	0.109	0.2588	**0.498 ± 0.084**	0.643 ± 0.068		
	47	Burkina Faso 1	Ouagadougou	12.3714	−1.5196	2017	18	5	1.61	0.065	0.065	0.2795	**0.438 ± 0.091**	0.592 0.105	2016	Son et al. (2017)
	48	Burkina Faso 2	Bobo dioulasso	11.1833	−4.2833	2017	22	5	1.62	0.014	0.014	0.0198	**0.604 ± 0.085**	0.602 ± 0.071		
	49	Togo	Lomé	6.1724	1.2313	2017	15	4.857	1.6	0.031	0.031	0.1164	**0.539 ± 0.101**	0.580 ± 0.094	Before 2014	El-Lissy (2014)
	50	Tunisia 1	Chott meriem	35.9380	10.555	2017	24	5.286	1.64	0.041	0.041	0.0207	0.625 ± 0.088	0.625 ± 0.081	2008	EPPO (2009a,), Abbes et al. (2012)
	51	Tunisia 2	Foussana	35.3494	8.6277	2017	23	6.143	1.69	0.036	0.036	0.0734	0.638 ± 0.083	0.671 ± 0.073		
	52	Tunisia 3	Chebika	35.6186	9.9261	2017	1	-	-	-	-	-	-	-		
	53	Algeria 1	Sidi maouf	35.6878	0.5516	2018	24	6.571	1.65	0.033	0.033	−0.0359	0.673 ± 0.109	0.636 ± 0.097	2008	EPPO (2008)
	54	Algeria 2	Sidi khettab	35.9089	0.5419	2018	25	6.571	1.67	0.066	0.066	0.0458	0.643 ± 0.080	0.661 ± 0.075		
	55	Algeria 3	Djendel	36.7792	7.1956	2018	24	5.714	1.69	0.027	0.027	0.0989	**0.619 ± 0.063**	0.671 ± 0.068		
South America	56	Argentina	Barrancas	−36.821309	−69.916845	2010	13•	4.286	1.63	0.194	0.194	0.0469	0.604 ± 0.062	0.609 ± 0.059	1964	Bahamondes and Mallea (1969)
	57	Colombia	Boavita Boyaca	6.330753	−72.585693	2011	8•	3.143	1.48	0.058	0.058	0.1436	0.411 ± 0.053	0.445 ± 0.061	1960s	Mansour et al. (2018)

(Continues)

TABLE 1 (Continued)

	N pop	Country	Locality	Lat	Long	Sampling date	Sample size	Mean number of alleles (A_N)	Allelic richness	Mean number of private allele	Private alleles richness	F_{IS}	H_O (mean ± SD)	H_E (mean ± SD)	Date of first report of *T. absoluta*	Reference
Europe	58	France	Prunelli-di-Fiumorbo	42.003145	9.374888	2010	4●	-	-	-	-	-	-	-	2008	EPPO (2009b), Tonnang et al. (2015)
	59	Greece	Al Pelagia	35.405607	25.016649	2009	5●	-	-	-	-	-	-	-	2008	Tonnang et al. (2015)
	60	Italy	Rotondella	40.171952	16.524564	2009	6●	-	-	-	-	-	-	-	2009	Roditakis et al. (2010), Tonnang et al. (2015)

Note: Most specimens were sampled in tomato crop fields except for those indicated with ◆, collected on pepper and ▲ on field border plant. Specimens marked with • were previously analysed in the study from Guillemaud et al. (2015).

Abbreviations: A_N, mean number of alleles per locus; A_R, mean allelic richness over loci; F_{IS}, fixation index; H_O, observed heterozygosity (bold values are for populations that showed a significant departures from Hardy–Weinberg equilibrium with a test for heterozygote deficiency); H_E, expected heterozygosity.

v6.51 (i.e., the mean number of alleles (A_N), allelic richness (A_R), mean observed (H_O) and unbiased heterozygosities (H_E); Peakall & Smouse, 2012) or FreeNA (null-allele frequency; Chapuis & Estoup, 2007). Private allelic richness (P-A_R) was obtained by rarefaction using HP-RARE to correct sampling bias caused by unequal sample sizes (Kalinowski, 2005). Deviation from HWE and F_{IS} value of each population were computed with GenePop 4.7.5 on the Web (Raymond & Rousset, 1995). All genetic analyses were performed on a total of 36 populations (with $n \geq 8$) out of 60.

Levels of pairwise genetic differentiation (F_{ST} values) among the 36 remaining populations were assessed from each microsatellite dataset harbouring no null alleles (1) using the excluding null alleles (ENA) method ($F_{ST\text{-}ENA}$) as implemented in FreeNA (Chapuis & Estoup, 2007) and (2) without using the ENA method (F_{ST}). The ENA method accounts for the positive bias caused by null alleles in F_{ST} estimation and provides precise estimates of F_{ST} even in the presence of null alleles. The overall significance of genotypic differentiation per population pair was estimated using Fisher's exact tests implemented in GenePop 4.7.5 (Raymond & Rousset, 1995) at 5% significance levels.

Inferring population genetic structure

The genetic structure of the *T. absoluta* populations under study was analysed using a Bayesian model-based clustering analysis implemented by a Markov Chain Monte Carlo (MCMC) method using Structure 2.3.4 software (Pritchard et al., 2000). The number of clusters (K) was assessed based on the individual genotypes at multiple loci. Given the low levels of divergence between the populations and the limited number of specimens in some sampling areas, we used the sample group information (LOCPRIOR tool) to conduct our analysis, as suggested by Hubisz et al. (2009). Each run included a burn-in period of 200,000 iterations, followed by 1,000,000 MCMC iterations. Twenty independent runs were conducted for each K value, ranging from 1 to 10. The most likely values of K, which represents the most probable number of genetic clusters, and quantification Q (individual assignment) of how likely each individual is to belong to each cluster were also estimated using the admixture model with correlated allele frequencies. The value of K that best captured the structure was determined by computing ΔK (Evanno et al., 2005) using Structure Harvester (Earl & von Holdt, 2012). A decision between the several possible K values was made by analysing changes in the individual assignments (Q) as K values were incremented (Pritchard et al., 2000) and taking into account the highest average and slight standard deviation of the posterior probability for K across the various runs as implemented by Structure software, as suggested by Janes et al. (2017). Clumpak program (available at http://clumpak.tau.ac.il, Kopelman et al., 2015) was used to check for multimodality of the results of the 20 runs from the Structure software and provided a summation and graphical representation of the results. The spatial distribution of the delineated genetic clusters in populations of each continent was mapped with the free and

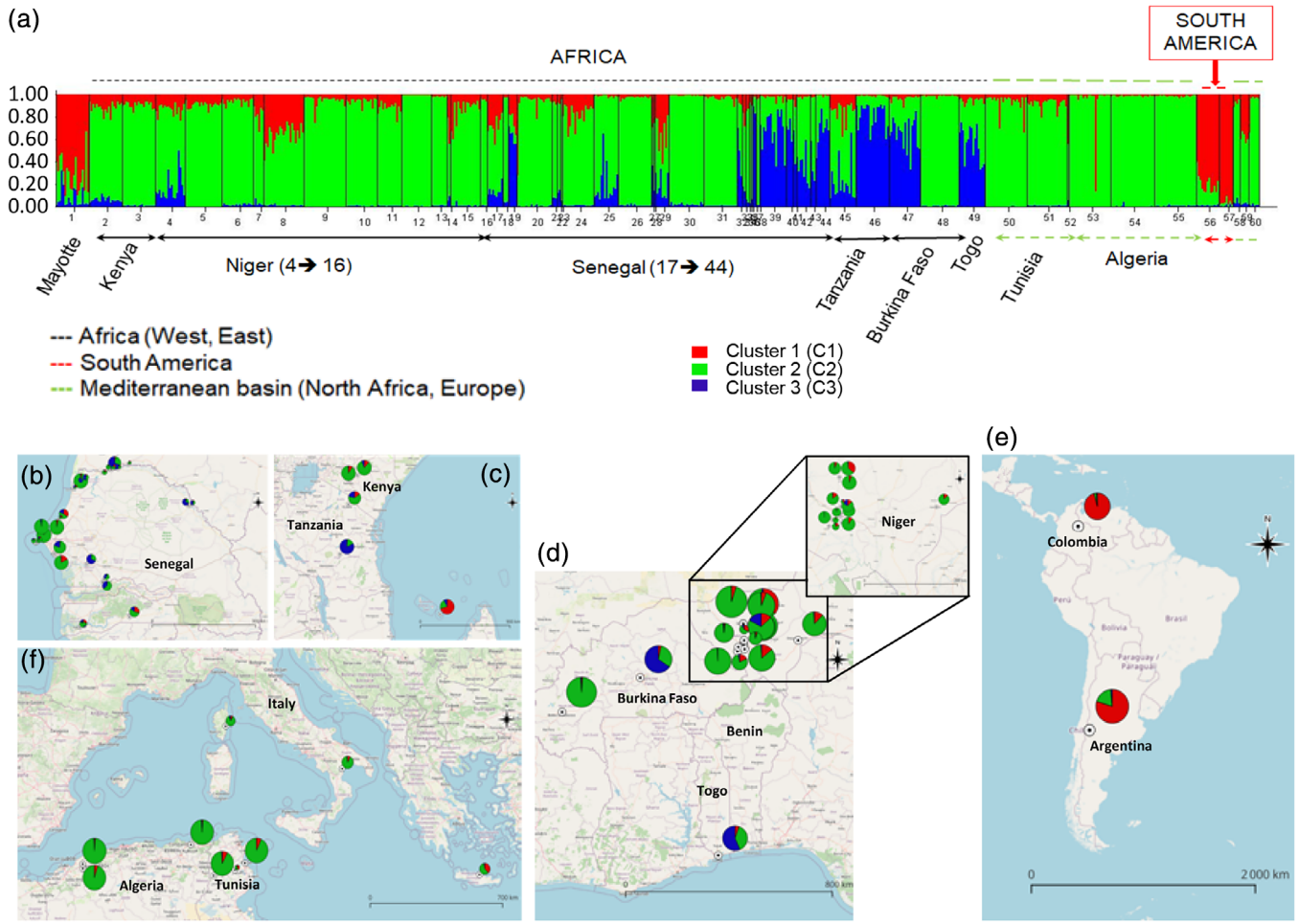

FIGURE 1 (a) Inference of population genetic structure in *Tuta absoluta* based on 7 polymorphic microsatellite loci. Results of successive Bayesian multi-loci clustering analysis on the 60 populations from the species' putative area (i.e., South America) and invaded ones (i.e., Africa, Europe and Mayotte) with the delineation of three main genetic clusters (C1, C2 and C3). Each vertical bar represents one of the 689 specimens genotyped. The proportion of each colour for a specimen is proportional to the inferred ancestry values (Q) in each genetic cluster. The population codes are as listed in Table 1. Distribution of *T. absoluta* populations and their genetic clusters inferred following analyses with the software Structure in each sampled area: In Senegal (b), East Africa (c), West Africa (d), South America (e) and the Mediterranean basin (f).

open-source QGIS software 3.28.5 (QGIS.org, 2023) on an OpenStreetMap base map (Haklay & Weber, 2008).

Finally, since demographic bottlenecks can affect allele richness and heterozygosity, tests were conducted to identify their signatures in the microsatellite data for each of the 36 populations with $n \geq 8$. These analyses were performed using Bottleneck v.1.20.2 (Piry et al., 1999). The underlying assumption is that recent bottlenecks result in a shift from an L-shaped distribution of allelic frequencies toward a distribution with fewer alleles in the less frequent categories. The descriptor ('mode-shift' indicator) of the allele frequency distribution and the non-parametric Wilcoxon sign-rank test (Cornuet & Luikart, 1997) under a two-phase mutation model (TPM) (variance 30.00, probability 70%, 1000 simulations) were used as recommended for studies with fewer than 20 microsatellite loci (Di-Rienzo et al., 1994). Probability values were determined using a one-tailed Wilcoxon test for heterozygote excess ($p < 0.05$) and a shifted-mode of allele frequency distribution was considered as indicative of bottlenecks.

RESULTS

Marker characteristics

No significant LD was detected for any locin pairs across all populations, the mean frequency of null alleles for each locus retained was low ($f_{NULL\text{-}ALLELE}$ <0.14, mean value = 0.07), and four out of seven conformed to HWE, with two others displaying *p*-values close to non-significance. As a result, these seven microsatellite loci were assumed to segregate independently in the analyses and to be conformed to be used for the population genetics study. The number of alleles per locus ranged from 7 to 16 (Table S1) (overall, mean $A_N = 10.89$), and the mean number of alleles per population ranged from

3.14 (population 57) to 6.6 (populations 53 and 54). Expected and observed heterozygosities revealed a narrow range of high values ($0.445 < H_E < 0.703$ and $0.390 < H_O < 0.774$) (Table 1).

Patterns of genetic diversity and differentiation at various geographical scales

All populations exhibited private alleles, albeit with low richness ranging from 0.004 (population 5, Saga in Niger) to 0.194 (population 56 in Argentina) after rarefaction. Detailed summary statistics for each population (with $n \geq 8$) are listed in Table 1. All populations with high inbreeding depression (F_{IS} values >0.20) also deviate from Hardy Weinberg, but the reverse is not necessarily true (e.g., population 5 (Saga, Niger) deviates from HWE: $F_{IS} = 0.097$) (Table 1). In 18 out of 36 populations (with $n > 8$), departure from HWE was also often characterized by heterozygosity deficits (76% of the statistically significant differences between H_E and H_O, $p < 0.05$). Based on Wilcoxon tests ($p < 0.05$) and the 'mode-shift' indicator implemented in the Bottleneck software, no population in our sampling have experimented recent demographic bottlenecks.

Populations from invaded African areas exhibited expected heterozygosity (H_E) values ranging from 0.532 to 0.703, with these extreme values observed in Nigerian populations 11 and 4, respectively. Likewise, observed mean heterozygosity (H_O) values ranged from 0.390 to 0.774, with the great majority of African populations displaying significantly higher H_O values than the insular population (population 1, Mayotte; H_O: 0.402) and those two from South America, particularly from Colombia (population 57; H_O: 0.411). In Niger, specifically, almost all the highest genetic diversity indexes were displayed in population 4 (Niamey, sampled in 2013) against all others from the Tillaberi region (populations 5–10 and 12–16), while the lowest ones were found in the population 11 (Doutchi) from the Dosso region. Genetic diversity indexes (Allelic richness, H_E and H_O) locally increased with time for the same tomato field in Tolkoboye sampled in 2016, 2017 and 2018 (Table 1). Populations from Senegal gathered both the highest (0.774) and the lowest (0.390) levels of observed heterozygosity in populations 26 and 44, respectively (Table 1).

Pairwise F_{ST} values estimated with (Table 2) or without (Table S2) correcting for the presence of null alleles (ENA method) showed similar patterns, which is consistent with the low-frequency rate of null alleles in the dataset. The following description of F_{ST} results is based on using the ENA method. Pairwise $F_{ST\text{-}ENA}$ values ranged from 0 to 0.313, with the majority below 0.15, indicating low differentiation levels within the sampling area. All pairwise $F_{ST\text{-}ENA}$ values higher than 0.15, which indicates moderate to high levels of differentiation, involved the Colombian population (population 57) against all the other populations, whatever their geographic origin, and to a lesser extent, the Argentinian population (population 56) against the population one from Mayotte and some from Africa (populations 8 from Niger, 44 in the Groundnut Basin in Senegal, 46 in Tanzania and 50 in Tunisia). The upper pairwise $F_{ST\text{-}ENA\ T}$ value was observed between the two South American populations (Table 2, Table S2). Even if the overall $F_{ST\text{-}ENA}$ values were very close to each other, especially at the African area level, the level of genetic differentiation was shown to be statistically significant in 74% of cases (465 out of 630 of the pairwise comparisons) (non-significant results are given in Table S3).

Population structure and characteristics of the genetic clusters

The Bayesian approach to assess population structure showed that the most likely value of genetic cluster (K), based on Janes et al. (2017), was 3, followed by $K = 6$ (Figure S1). Replicate Structure runs led to one major solution for all K values and to minor solutions for values from $K = 4$, except for $K = 7$ (i.e., genuine multimodality; Jakobsson & Rosenberg, 2007; Figure S2). Most specimens (84.4%) were mainly ($Q > 0.70$) assigned to one of the three clusters inferred by the Structure analysis (C1, C2 and C3). More precisely, 6%, 84% and 10% of all *T. absoluta* specimens strongly assigned ($Q > 0.70$) to a genetic cluster were gathered into the clusters C1, C2 and C3, respectively. Other non-assigned specimens (15.6% with $Q < 0.70$) were shown to exhibit a mixed genetic background, with one of the three clusters still being dominant over the two others most of the time ($0.35 > Q > 0.69$) (Figures 1 and 2; Table S4).

At a population level, most African populations are very genetically homogeneous, with a single dominant cluster (C2, green in Figure 1). Several populations exhibit a genetic profile characterized by the presence of a prominent second cluster (C3, blue in Figure 1). Specifically, this cluster is prevalent in seven Senegalese populations (19, 29, 37, 39–41, 44) as well as in populations from Burkina Faso (population 47) and Togo (population 49) in West Africa and Tanzania (population 46) in East Africa for both $K = 3$ and $K = 6$ (Figure S1). A notable observation in Senegal is the presence of C2 and C3 dominant populations in the northern region confined to relatively small areas. Populations with a major C2 genetic background were observed in the coastal areas, the region of Dakar and the Niayes. Those with a major C3 genetic background were found in the Saint Louis and Matam valleys and the Groundnut basin, with one site in the Southern region of Senegal (population 19) (Figure 1). The pattern was different in Niger, where all assigned *T. absoluta* (populations 6 to 16) were exclusively assigned to the cluster C2 ($Q > 0.70$) with also many specimens characterized by a mixed genetic background including a minor C1 genetic background ($0.21 < Q \leq 0.58$) (identified by the colour red in Figure 1) particularly in the population Tolkoboye 1 (population 8). This C1 cluster was also dominant in the Mahorese population (population 1, in the Indian Ocean), which exhibits a distinct population structure compared with other African populations. Specifically, this C1 genetic background is relatively uncommon in other African populations studied, but it is nevertheless found in some populations of the Mediterranean basin (population 52 in Tunisia and 59 in Greece), represented, however, by very few specimens (only 1 for population 52 and 5 for population 59). This cluster is mainly found in the native area of *T. absoluta* in South America (population 56 in Argentina and population 57 in Colombia). All *T. absoluta* specimens from South

TABLE 2 Pairwise F_{ST} values between the populations (only populations with eight or more sampled specimens were considered) with the ENA (excluding null alleles) correction.

Mayotte	Kenya1	Kenya2	Niger1	Niger2	Niger3	Niger5	Niger6	Niger7	Niger8	Niger9	Niger10
Kenya1	0.072706										
Kenya2	0.062418	0.020271									
Niger1	0.030014	0.010997	0.019425								
Niger2	0.054753	0.032015	0.013014	0.012255							
Niger3	0.082428	0.044355	0.030849	0.018436	0.005421						
Niger5	0.023144	0.065368	0.052104	0.029083	0.041863	0.060334					
Niger6	0.082303	0.068648	0.039307	0.023697	0.029446	0.023175	0.060316				
Niger7	0.074742	0.04739	0.01648	0.020098	0.013984	0.003972	0.062574	0.004356			
Niger8	0.059962	0.068902	0.058773	0.041103	0.007927	0.029011	0.046356	0.04169	0.053928		
Niger9	0.101185	0.038493	0.026297	0.023193	0.022372	0.043959	0.081819	0.02048	0.019835	0.060476	
Niger10	0.046326	0.013058	0.006493	−0.005012	−0.001779	0.021351	0.030332	0.018657	0.015295	0.034185	−0.005528
Niger12	0.061078	0.05717	0.029971	0.026336	−0.005955	0.018613	0.05386	0.037459	0.030098	−0.001439	0.038983
Senegal1	0.038384	0.013154	0.006552	−0.014014	0.012322	0.035321	0.04745	0.043127	0.034755	0.043036	0.028735
Senegal6	0.069376	0.034845	0.020619	0.009496	0.002683	0.024474	0.054817	0.035412	0.021879	0.048811	0.024613
Senegal10	0.047291	0.037623	0.034237	−0.003877	0.021654	0.035043	0.052239	0.041888	0.04343	0.043507	0.042132
Senegal11	0.072995	0.008956	0.014021	0.004693	0.007104	0.006302	0.078092	0.044256	0.032448	0.036728	0.044256
Senegal12	0.094763	0.017223	0.046068	0.016307	0.041455	0.052105	0.076204	0.06569	0.044095	0.091948	0.053601
Senegal15	0.05364	0.035525	0.046436	0.021744	0.02684	0.032844	0.077083	0.075748	0.038795	0.048322	0.044531
Senegal16	0.093094	0.043492	0.035727	0.015745	0.003126	0.023919	0.072607	0.036964	0.033788	0.028995	0.021961
Senegal17	0.085934	0.009068	0.020236	0.009734	0.005163	0.009795	0.064009	0.029313	0.015828	0.030254	0.015741
Senegal25	0.081873	0.060006	0.065259	0.022703	0.069207	0.068232	0.055269	0.07732	0.081723	0.089368	0.106041
Senegal28	0.092808	0.010276	0.014988	−0.00216	0.010819	0.011783	0.072349	0.031679	0.017077	0.043467	0.025651
Senegal30	0.098537	0.095032	0.10789	0.044655	0.097571	0.075737	0.1028	0.097475	0.08815	0.108072	0.105372
Tanzania1	0.043109	0.019956	0.027875	0.009884	0.041789	0.042515	0.043592	0.069279	0.036581	0.07443	0.059885
Tanzania2	0.110589	0.058929	0.074049	0.053333	0.088824	0.093274	0.085277	0.109914	0.101118	0.128336	0.105557
BurkinaFaso1	0.103457	0.033987	0.069292	0.046707	0.04097	0.0685	0.098575	0.106005	0.090976	0.057719	0.079703
BurkinaFaso2	0.081987	0.025967	0.027595	0.023529	0.006532	0.01565	0.062267	0.040562	0.025143	0.029216	0.013551
Togo	0.096491	0.052407	0.085703	0.034222	0.03699	0.054212	0.082574	0.097097	0.085196	0.045967	0.085383
Tunisia1	0.069587	0.032086	0.039435	0.032622	0.041899	0.047223	0.048971	0.051077	0.040387	0.075058	0.051868
Tunisia2	0.067321	0.015982	0.014151	0.011736	0.003532	0.015412	0.055437	0.027936	0.00211	0.042118	0.006067
Algeria1	0.074589	0.023683	0.023137	0.018374	0.018318	0.027717	0.054923	0.027734	0.023991	0.043825	0.021523
Algeria2	0.084837	0.019316	0.010045	0.023167	0.010262	0.021756	0.062457	0.029805	0.011002	0.046035	0.008995
Algeria3	0.06851	0.007358	0.006353	0.001598	0.00644	0.017054	0.044933	0.028092	0.020102	0.039182	0.012805

(Continues)

TABLE 2 (Continued)

Mayotte	Kenya1	Kenya2	Niger1	Niger2	Niger3	Niger5	Niger6	Niger7	Niger8	Niger9	Niger10
Argentina	0.157688	0.092167	0.136079	0.083621	0.106516	0.119414	0.170452	0.131427	0.131895	0.123737	0.131175
Colombia	0.23107	0.21423	0.202869	0.189964	0.247722	0.227505	0.241079	0.255458	0.220781	0.296788	0.265771

Niger12	Senegal1	Senegal6	Senegal10	Senegal11	Senegal12	Senegal15	Senegal16	Senegal17	Senegal25	Senegal28	Senegal30
0.019808											
0.005933	0.026606										
0.016811	0.02175	0.013142									
0.00943	0.024111	−0.001126	0.021255								
0.012344	0.019965	0.007204	0.019847	0.011739							
0.035998	0.062755	0.030158	0.015692	0.038405	0.033312						
0.01215	0.026622	0.032379	0.062287	0.029774	0.032659	0.080949					
0.008468	0.002866	0.017737	0.009296	0.005358	0.01392	0.034344	0.036108				
0.006032	0.008919	0.010138	0.013557	0.020355	0.003184	0.01078	0.030464	−0.000864			
0.070642	0.073017	0.034754	0.050491	0.046513	0.029194	0.056524	0.105417	0.063877	0.052259		
0.02005	0.018904	−0.017271	0.007775	−0.000996	−0.010999	0.011697	0.041574	−0.009085	−0.018683	−0.000172	
0.086481	0.104676	0.056977	0.108608	0.073923	0.072838	0.117066	0.063847	0.099057	0.087401	0.05436	0.039353
0.008812	0.057238	0.007415	0.040969	0.036111	0.035563	0.044167	0.032669	0.060761	0.040734	0.06179	0.028751
0.06666	0.107822	0.034665	0.079502	0.081026	0.068829	0.086212	0.108661	0.089508	0.076704	0.052211	0.031326
0.057871	0.038278	0.039277	0.056552	0.056284	0.03077	0.06867	0.051833	0.039732	0.019197	0.061615	0.010279
−0.011191	0.014028	0.035792	0.028694	0.031423	0.024076	0.045452	0.015628	0.007058	0.001	0.088943	0.01254
0.069533	0.02807	0.040126	0.055948	0.060133	0.038516	0.068361	0.046611	0.038673	0.024779	0.054575	0.013822
0.019181	0.050834	0.055909	0.042211	0.055719	0.048594	0.03946	0.044972	0.056354	0.026501	0.069773	0.048636
−0.009143	0.012485	0.011361	0.017345	0.020022	0.018789	0.022758	0.009063	0.007483	−0.005092	0.069613	−0.003312

TABLE 2 (Continued)

Niger12	Senegal1	Senegal6	Senegal10	Senegal11	Senegal12	Senegal15	Senegal16	Senegal17	Senegal25	Senegal28	Senegal30
0.004992	0.020438	0.026496	0.018458	0.018983	0.023467	0.017865	0.045855	0.014525	−0.002861	0.061341	0.008948
0.004673	0.014315	0.025211	0.017678	0.036415	0.018497	0.029298	0.030855	0.015585	−0.004651	0.065739	0.001539
−0.008751	0.018275	0.013866	0.004352	0.006962	0.004875	0.018115	0.031235	0.001008	−0.003735	0.044407	−0.011079
0.132324	0.118966	0.090412	0.103932	0.1256	0.084823	0.108509	0.138847	0.115372	0.091575	0.142472	0.101046
0.235683	0.256825	0.172647	0.216209	0.19953	0.232909	0.226772	0.233108	0.259182	0.237962	0.246577	0.202957

Tanzania1	Tanzania2	BurkinaFaso1	BurkinaFaso2	Togo	Tunisia1	Tunisia2	Algeria1	Algeria2	Algeria3	Argentina	Colombia
0.085699											
0.111925	0.025283										
0.113356	0.078277	0.083271									

(Continues)

TABLE 2 (Continued)

Tanzania1	Tanzania2	BurkinaFaso1	BurkinaFaso2	Togo	Tunisia1	Tunisia2	Algeria1	Algeria2	Algeria3	Argentina	Colombia
0.101072	0.042025	0.09655	0.041934								
0.08096	0.092262	0.103273	−0.00252	0.049615							
0.115125	0.046922	0.101246	0.07722	0.038236	0.081918						
0.080219	0.017932	0.066334	0.044096	0.000722	0.052013	0.02019					
0.10307	0.048812	0.098371	0.048599	0.008718	0.055569	0.012938	0.006119				
0.100177	0.037935	0.084345	0.04935	0.004913	0.061566	0.016144	−0.007861	0.001493			
0.085651	0.022482	0.058564	0.036951	−0.001165	0.051547	0.024451	0.000001	0.001593	0.000326		
0.172189	0.145825	0.168224	0.109768	0.139595	0.083724	0.166669	0.123461	0.136851	0.130569	0.120223	
0.275367	0.16052	0.212686	0.295295	0.265748	0.298493	0.235531	0.201543	0.252022	0.228243	0.222152	0.313146

Note: FST values between 0 and 0.15 are marked in green, and values between 0.15 and 0.5 are marked in yellow.

America, except one from Argentina, were strongly assigned (mean $Q > 0.89$) to this C1 cluster.

The three identified clusters displayed very similar allelic richness and expected heterozygosity but significantly differed for all other genetic estimators (Table S4). The clusters 1 and 3 exhibited lower mean number of alleles and observed heterozygosity than the widely represented African cluster 2 which was the only genetic cluster not to show high inbreeding depression and heterozygote deficiency (Table S4). The level of genetic differentiation between all three clusters was low, with and without ENA correction, with the upper F_{ST} value being between C1 and C3 and the lower one between both African clusters, C2 and C3 (Table S5). This is consistent with the F_{ST} values estimated between all African and Mediterranean populations included in these clusters (Table 2).

DISCUSSION

Tuta absoluta larvae cause significant crop damage worldwide and reduced yields of multiple crops, mainly tomatoes (Biondi et al., 2018). This impact is particularly severe in Africa (Brévault et al., 2014; Rwomushana et al., 2019), where the first report occurred 15 years ago in North Africa. Since then, the species has rapidly spread to nearly the entire continent (Mansour et al., 2018). Despite extensive documentation on damage and management methods, there is still a lack of precise information on the initial and current populations in Africa. The present study aims to provide new insights into the genetic diversity and structure of *T. absoluta* populations in Africa, exploring their potential invasion history at various spatial scales.

Putative native area *versus* invaded areas: Distinct differentiation and diversity patterns

In our study, the South American populations were grouped into a single genetic cluster. However, a significant genetic differentiation was revealed between Colombia and Argentina, even higher than against all other localities surveyed worldwide. Even though the sampling size both in terms of number of localities and number of specimens per locality was low, this result is supported by previous studies within the native area of *T. absoluta*, based on more sampled populations and using both microsatellite markers and genome assembly methods. They specifically revealed structuration between the North and the South of the South American continent (Guillemaud et al., 2015) but also with a third cluster in the Andes region (South America, Lewald et al., 2023), previously undetectable with less resolutive markers (Cifuentes et al., 2011). In Guillemaud et al. (2015) (Supporting Information), the same Colombian population exhibited very high pairwise F_{ST} values with all *T. absoluta* populations from the Mediterranean basin and South America, even those belonging to the same genetic cluster. The locality sampled, Boavita, in the Northern Province of Boyacá (Colombia), has an altitude of more than 2110 m. a.s.l.,

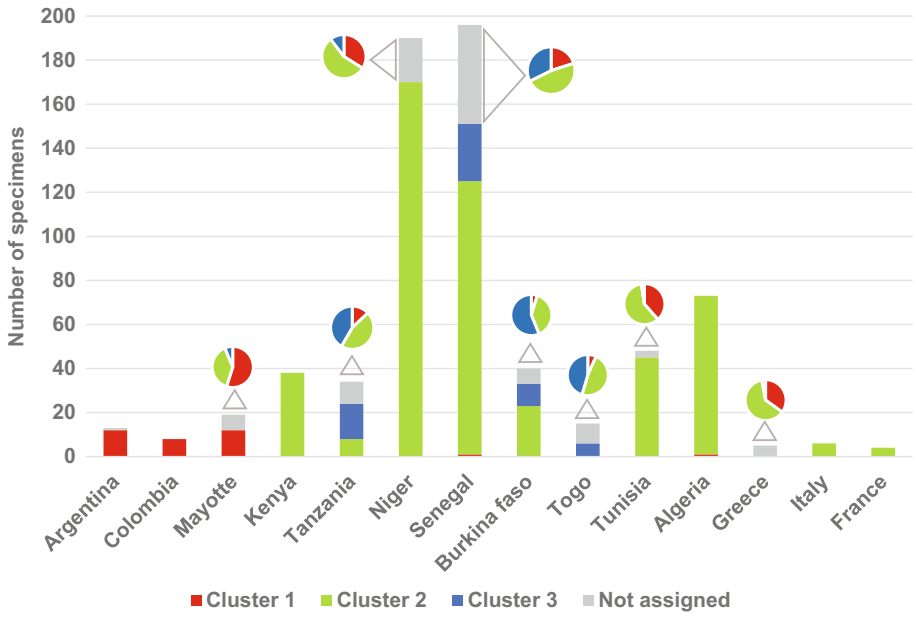

FIGURE 2 In the histogram graph, number of specimens assigned to genetic clusters C1, C2 or C3 ($Q > 0.70$) or to the category 'not-assigned' ($Q < 0.70$) per country. In the pie charts, the average individual assignment (average Q) to each genetic background of not-assigned specimens collected in the country.

which can indeed represent a natural physical obstacle to the *T. absoluta* dispersion and gene flow even over short distances. The inbreeding factor was also very high in this locality. In their native habitats, it is generally assumed that gene flow between populations is influenced by various factors that limit dispersal, such as biogeography and physical obstacles, and populations are expected to be genetically structured (Goldberg & Lande, 2007; Hewitt, 2000). This is not necessarily the case in areas of introduction, where the history of the invasion mainly influences the genetic structure of the populations.

The two South American populations also paradoxically displayed a lower level of genetic diversity (mean number of alleles, heterozygosities) than most of the other populations collected in the Mediterranean basin (Guillemaud et al., 2015) and in Africa (this study). Thus, despite expected recent demographic bottlenecks and inbreeding depression usually associated with all invasion steps, *T. absoluta* populations from invaded areas, even from those which have been recently invaded, seem to have quickly counteracted reductions in genetic diversity and inbreeding depression. No signature of demographic bottleneck was even observed. Evidence for levels of genetic diversity similar or even higher in introduced *versus* native range populations of invasive species has already been reported in other invasive species (e.g., Dlugosch & Parker, 2008; Estoup et al., 2016; Roman & Darling, 2007; Uller & Leimu, 2011). Mechanisms associated with invasion history characteristics (i.e., hybridization, mass introductions, repeated or multiple introductions and gene flow among invasion routes), species reproductive and biological traits and genetic traits have indeed been shown to counteract global genetic depletion during invasion (Estoup et al., 2016; Schrieber & Lachmuth, 2017). In our study, the low levels of differentiation observed, the presence of mixed genetic background in most sampled specimens and the low severity of the bottlenecks undergone in Africa suggest gene flow and intraspecific hybridization of individuals across the non-native area. In *T. absoluta*, as in many other invasive insects, long- and short-distance dispersal may be favoured by human activities, natural elements (e.g., wind) and the species' flight capacity (Jones et al., 2019). Indeed, *T. absoluta* adults were demonstrated to fly 0.4 km overnight (Salama et al., 2015), but this was probably underestimated since the method used (i.e., Capture–Release–Recapture) does not consider insects moving outside the largest recapture radius and only considers a linear flight distance which does not take into account insect wanderings (Ranius, 2006). Particularly in Africa, the high gene flow of a large number of individuals can also be related to international and regional trade of *T. absoluta* host plants, mainly tomato fruits, and to porous borders and inappropriate implementation of quarantine and phytosanitary measures (Desneux et al., 2011; Marchioro & Krechemer, 2024; Tonnang et al., 2015). Moreover, *T. absoluta* is characterized by a high reproductive potential as the species can yield up to 10–12 generations per year under the prevalent climatic and resource conditions found (Cherif et al., 2019; Tonnang et al., 2015) in many African countries. Under such conditions and suitable environment, also characterized by reduced biotic pressure due to a limited number of natural enemies (the 'enemy release hypothesis' Keane & Crawley, 2002), newly introduced populations can thus rapidly locally and widely re-expand, grow and gain genetic diversity greater than in the more stressful native-area.

Weakly differentiated clusters but with different genetic background in invaded areas

Outside its native area, nearly all the previously studied *T. absoluta* populations have shown remarkable genetic homogeneity and a lack

of population structure, regardless of the markers used or the geographic area under study. For instance, Shashank et al. (2018) found important genetic homogeneity in India and Nepal, invaded since 2014 and 2016, respectively, using the mitochondrial marker COI. The same pattern was observed in Turkey, where the pest was first detected in 2009 (İnak et al., 2021), and in Tunisia, invaded in 2008 (Cherif et al., 2017). Guillemaud et al. (2015) revealed a notable lack of genetic differentiation within the invaded regions around the Mediterranean basin, which they attributed to the invasion history of the species in the area rather than the sensitivity of the markers used. Similarly, using mtDNA, Ndiaye et al. (2021) found very high homogeneity across Africa, attributed to a particular invasion scenario that combined extensive gene flow, bottlenecks, the specific reproductive system of the species and human activities. Based on a comprehensive sampling conducted across eight African countries, our results are broadly consistent with most previous observations from other invaded regions. They reveal a global genetic homogeneity and a weak diversity among populations. No clear geographical pattern could be identified in our Structure analysis, and the F_{IS} values were globally low (but F_{IS} >0), indicating a low level of inbreeding in the invasive populations. All these results suggest a specific invasion scenario in Africa, characterized by significant gene flow between populations, few introduction events of numerous individuals or at least introductions from genetically very poorly differentiated geographical areas, as shown in other insect invasions worldwide (Kerdelhué et al., 2014; Lombaert et al., 2011; Lye et al., 2011). This scenario would resemble the one hypothesized by Guillemaud et al. (2015) for *T. absoluta* in the Mediterranean region. They suggested that the invasion of *T. absoluta* in the Mediterranean area most probably resulted from a single introduction followed by a large expansion without a demographic bottleneck.

However, despite this apparent genetic homogeneity over *T. absoluta* African range, our study revealed two main African genetic clusters: one predominantly encompassing specimens from all countries even in North Africa and another little represented but geographically well-delineated cluster, identified both in West Africa and in East Africa. It is interesting to note that this genetic cluster was virtually absent in *T. absoluta* from the Mediterranean basin, South America and Mayotte, as well as from certain African localities or countries such as Kenya and Niger. This little-represented genetic cluster might be more recently introduced in Africa than the other one, less successful in expanding or less frequently found in the zone of origin. Contrary to what was observed for the predominant African cluster, this small cluster was also characterized by a high inbreeding coefficient and heterozygote deficiency, similar to the South American and Mahorese clusters, suggesting that *T. absoluta* from these clusters might face constraints (e.g., physical, genetic, size effect) limiting random reproduction. Along these lines, some studies documented the existence of deuterotokous parthenogenesis in some *T. absoluta* populations (Abbes & Chermiti, 2014; Caparros Megido et al., 2012) and under certain environmental pressure (Grant et al., 2021). As reproductive mode may indeed affect gene flow, differentiation and diversity patterns, the hypothesis of two *T. absoluta* African lineages with different reproductive strategies should also be examined.

Unexpectedly, *T. absoluta* from the island of Mayotte, an overseas territory in the Indian Ocean off the coast of South-Eastern Africa and more than 10,000 km away from America, were grouped into the 'South American' genetic cluster. As far as we know, trade in vegetables that could serve as vector for *T. absoluta* was very limited between South America and Mayotte, which, in 2014–2015, that is during the period of the first report of *T. absoluta* in the island, produced 44% of the tomatoes consumed locally and imported almost all the rest from Madagascar (DAAF Mayotte, 2016). Thus, its genetic clustering with Colombia and Argentina might result from an accidental introduction event of an invasive South American population on the island. Precise information regarding the extent of trade between Mayotte and its closest African neighbours is lacking, but its insularity may have contributed to its level of genetic differentiation against many populations.

Conclusion: New insights but still many gaps on African *T. absoluta* population structure

Our markers were shown to delineate two main weakly differentiated African clusters characterized by different diversity and inbreeding levels. At country and local scales, specimens of both genetic clusters may occur separately or sympatrically and may hybridize. Even though no clear geographical structure was identified, our markers revealed various patterns in Africa. Tanzania and Burkina Faso, for example, were characterized by genetically distinct populations, whereas specimens sampled in Niger were genetically close and homogeneous. Populations in Senegal were characterized by the coexistence of both main clusters, and higher levels of genetic diversity were found in the Niayes and the Dakar region, where *T. absoluta* was first reported in this country (Pfeiffer et al., 2013).

Altogether, our results indicate either a limited number of introduction events or multiple introductions from a single genetically homogeneous source and probably no or very limited demographic bottleneck. High gene flow also probably contributes to the quick recovery of genetic diversity and counteract inbreeding depression even in the recently invaded areas (i.e., date of first report). Together with the high polyphagy and tolerance to environmental stresses (Campos et al., 2021), this must have facilitated establishment out of the native range. For most of the study area, our results suggest that the source populations of the African lineages do not have a genetic background similar to that of our Colombian and Argentinian populations, that is, in the presumed native area of the species. Therefore, specimens from native populations at the source of the two African genetic lineages have likely been unsampled (Slatkin, 2005). A much more extensive sampling over the whole range of *T. absoluta*, especially in its native area, would be necessary to formally analyse the invasion source and pathways of this species in Africa.

AUTHOR CONTRIBUTIONS

Marion Javal: Data curation; formal analysis; methodology; visualization; writing – original draft. **Arame Ndiaye:** Data curation; formal analysis; investigation; methodology; writing – review and editing.

Anne Loiseau: Investigation; methodology; writing – review and editing. **Bal Amadou Bocar:** Investigation; resources; writing – review and editing. **Madougou Garba:** Funding acquisition; investigation; resources; writing – review and editing. **Thierry Brévault:** Investigation; resources; writing – review and editing. **Nathalie Gauthier:** Conceptualization; formal analysis; funding acquisition; methodology; resources; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All DNA extracts and genotypes are preserved at the *Centre de Biologie pour la Gestion des Populations* (CBGP), Montferrier sur Lez (France) under the authority of N. Gauthier. The data and related documentations that support the findings of this study are openly available in DataSuds repository (IRD, France) at 10.23708/RE36VC. Data reuse is granted under CC-BY-SA licence.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Difference in log-likelihood among *K* values and the maximal mean likelihood and small standard deviation of the posterior probability of *K*. The values corresponding to the cluster number considered for inferring population genetic structure are marked with green.

Table S1. Characteristics of the nine polymorphic microsatellite loci retained from Guillemaud et al. (2012) study in our *Tuta absoluta* genetic population study.

Table S2. Pairwise F_{ST} values between the populations (only populations with eight or more sampled specimens were considered) without the ENA (excluding null alleles) correction. FST values between 0 and 0.15 are marked in green, and values between 0.15 and 0.5 are marked in yellow.

Table S3. *p*-values for each population pair differentiation across all loci. Only non-significant results are shown.

Table S4. Description and genetic diversity of the three clusters (with $Q > 0.70$) delineated, with the additional not strongly assigned specimens ($Q < 0.70$), using Structure software and Evanno's method.

Table S5. Pairwise F_{ST} values between the three genetic clusters (only populations with 10 or more sampled specimens were considered) with and without the ENA (excluding null alleles) correction.

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