THIAGO LEANDRO COSTA

CLIMATIC NICHE, GEOGRAPHIC DISTRIBUTION AND MANAGEMENT OF *Tuta absoluta*

Thesis submitted to the Plant Sciences Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae*.

Adviser: Marcelo Coutinho Picanço

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ABSTRACT

COSTA, Thiago Leandro, D.Sc. Universidade Federal de Viçosa, February 2023.
Climatic niche, geographic distribution and management of *Tuta absoluta*.
Adviser: Marcelo Coutinho Picanço.

The Neotropical tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is a destructive tomato pest species with continual successful invasions and establishment worldwide. To develop realistic management strategies for different regions, it is essential to understand its geographic distribution and invasion stage, besides of novel and eco-friendly pest management tools. Therefore, this thesis was comprised of three chapters. The first chapter sought to disentangle the climatic niche of *T*. *absoluta*. The results suggest that *T*. *absoluta* has occupied almost all suitable climatic habitats in the invaded range that resemble its native range. Evidence of niche shift was found and mostly attributed to niche expansion. In the second chapter, reciprocal projections were used to model the potential distribution of *T*. *absoluta* and estimate its invasion stage. The potential distribution of *T. absoluta* varies depending on the source of occurrence records. Also, models revealed that this pest had not yet colonized all the appropriate climate regions in Europe, Africa, and Asia. Most populations are in quasi-equilibrium; however, a significant number are apparently sink populations. The third chapter examined the insecticidal activity of an emulsion based on *Pogostemon cablin* essential oil. The emulsion exhibited similar effects on mortality and sublethal exposure on oviposition rate and adult avoidance. Thus, this thesis contributed to the climatic niche study, geographic distribution, and management of *T. absoluta*.

Keywords: Biological invasion. Invasive species. Niche change. Plant-based pesticide

RESUMO

COSTA, Thiago Leandro, D.Sc. Universidade Federal de Viçosa, fevereiro de 2023. **Nicho climático, distribuição geográfica e manejo de *Tuta absoluta*.** Orientador: Marcelo Coutinho Picanço.

Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae) é uma praga destrutiva do tomateiro com contínuas invasões e estabelecimento bem-sucedidos em todo o mundo. Para desenvolver estratégias de manejo realistas para diferentes regiões, é essencial compreender sua distribuição geográfica, estágio de invasão, além de ferramentas inovadoras e ecologicamente corretas para seu manejo. Assim, esta tese foi composta por três capítulos. O primeiro capítulo buscou destrinchar o nicho climático de *T. absoluta*. Os resultados sugerem que *T. absoluta* ocupa quase todos os habitats climáticos adequados na região invadida que se assemelham à sua região nativa. Evidências de mudança de nicho foram encontradas e atribuídas principalmente à expansão de nicho. No segundo capítulo, projeções recíprocas foram usadas para modelar a distribuição potencial de *T. absoluta* e estimar seu estágio de invasão. A distribuição potencial de *T. absoluta* varia conforme a fonte de pontos de ocorrência. Além disso, os modelos revelaram que esta praga ainda não havia colonizado todas as regiões climáticas apropriadas na Europa, África e Ásia. A maioria das populações está em quase-equilíbrio, no entanto, um número significativo são aparentemente “drenos”. No terceiro capítulo, foi examinada a atividade inseticida de uma emulsão à base de óleo essencial de *Pogostemon cablin*. A emulsão apresentou efeitos similares na mortalidade e a exposições subletais na taxa de oviposição e repelência de adultos. Assim, esta tese contribui para o estudo do nicho climático, distribuição geográfica e manejo de *T. absoluta*.

Palavras-chave: Invasão biológica. Espécie invasora. Mudança de nicho. Pesticida vegetal.

SUMMARY

1. GENERAL INTRODUCTION

Considered one of the leading fresh vegetable consumed worldwide, tomato (*Solanum lycopersicum* L.), has its probable center of origin in the Andean region, comprising Ecuador (including the Galapagos Islands), Peru, Colombia, Bolivia and northern Chile (Rick 1982, Hachmann et al. 2014). Brazil ranks 10th among the main producing countries on the global scene, with a production of approximately 3.75 million tons in 2020, behind China, India, Turkey, United States, Egypt, Italy, Iran, Spain and Mexico (FAOSTAT 2022).

On the national scene, tomatoes have a relevant economic role, especially in the states of Góias, São Paulo, Minas Gerais and Bahia, which are the leading producers of this vegetable, representing 70% of national production (IBGE - Instituto Brasileiro de Geografia e estatística 2022). Tomato also has great socioeconomic appeal as it is responsible for the direct and indirect generation of several jobs along its production chain, mainly due to the high use of labor (Fontes and Silva 2002). It is estimated that tomato cultivation can generate between five and six direct jobs per cultivated hectare and the same number of indirect jobs (Treichel 2016).

To become a more relevant player on the global scene, several challenges need to be overcome by Brazilian tomato growers. Among them, stand out the high costs of production inputs, price fluctuations, pests and diseases. In this context, the tomato leaf miner *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), recently proposed to be reinstated as *Phthorimaea absoluta* Meyrick 1917 (Chang and Metz 2021), is a critical invasive pest of tomato crops worldwide and considered a severe threat to the tomato industry (Guedes and Picanço 2012, Campos et al. 2017, Biondi et al. 2018). The larvae cause drastic tomato yield losses (up to 100%) owing to their feeding activity on leaves, stems, flowers and fruits (Silva et al. 2011, Campos et al. 2017). *Tuta absoluta* is considered a specialist pest, and despite having tomato as its primary host, it feeds on other Solanaceous plants (cultivated and uncultivated) such as potato, eggplant, pepper, tobacco (Campos et al. 2017, Mansour et al. 2018, Cherif and Verheggen 2019), and black nightshade (Cherif and Verheggen 2019, Campos et al. 2021).

In Brazil, *T. absoluta* was first reported in 1979, and two years later, it was already present in the country's central tomato-producing regions, causing severe yield losses (Muszinski et al. 1982, Guedes and Picanço 2012, Gontijo et al. 2013, Galdino et al. 2015). *Tuta absoluta* is native to South America, and its invasion and spread in Europe in 2006 changed its importance to a significant threat to global tomato production (Desneux et al. 2011, Guedes and Picanço 2012). Currently, *T. absoluta* is found in approximately 80 countries across five continents (EPPO 2007). Additionally, changing environmental conditions may affect species distribution or favor their establishment in previously inadequate habitats (Early and Sax 2014), promoting a severe effect on global agricultural production (Lesk et al. 2016).

An essential strategy for preventing the movement of *T. absoluta* to unexplored areas and thereby the raising ecological and economic impacts is to predict which regions are suitable or unsuitable for its establishment. A variety of modeling approaches have been implemented to assess species´ ecological niches and project their potential distribution (Broennimann and Guisan 2008, Broennimann et al. 2012, Guisan et al. 2014, Kumar et al. 2014, Santana et al. 2019, Eckert et al. 2020, Pili et al. 2020). They can be divided into mechanistic, correlative/statistical and process-based simulations models (Peterson et al. 2015). Mechanistic models rely on the first principles of biophysics and physiology, and thus require collecting and validating a large amount of physiological data (Peterson et al. 2015). Correlative/statistical models are based on associations of species occurrence and preexisting environmental data (Peterson et al. 2015, Eckert et al. 2020). Process-based simulations (or ´hybrid´) rely on assumptions on niche dimensions and dispersal capabilities to estimate occupied distributional areas and related habitats (Peterson et al. 2015).

Two correlative techniques have been extensively implemented to compare ecological niches in the last few years: ordination and ecological niche modeling (ENM; also known as species distribution modeling (SDM)) (Guisan et al. 2014, Eckert et al. 2020, Lei and Liu 2021). The former is solely based on direct observations (i.e., do not rely on any model), and examines the variations in environmental characteristics between the native and invaded ranges of the species in environmental space, generally using univariate or multivariate tests (Guisan et al. 2014, Eckert et al. 2020) The latter is based on predictions of ENMs, more specifically, comparing the overlap of reciprocal ENMs predictions (i.e., models fitted to native and invaded range). The basic idea underlying correlative ENMs is to predict species' realized niche based on species occurrence and environmental variables. ENMs have been successfully used to predict species' potential occurrence and dispersion in response to environmental changes (Kumar et al. 2014, Tonnang et al. 2017, Lantschner et al. 2018). This knowledge enables planning strategies and tactics for pest management, as well as practices for preserving beneficial organisms (Guisan et al. 2013).

Both approaches, ordination and ENM, assume that climatic variables are crucial to determining pest species' occurrence and distribution in agricultural ecosystems (Jung et al. 2016), which is particularly important in a scenario of climate change and agricultural expansion. They can be considered complimentary because while ordination offers perceptions of changes in a climatic niche, ENM indicates the areas at risk (Eckert et al. 2020). These techniques are based on the niche concept, and two assumptions are usually made when modeling species: (i) the species fill all potentially suitable environments and are in (quasi-) equilibrium with their environment; (ii) the ecological niche is stable in space and time (i.e., transferability) (Gallien et al. 2012, Guisan et al. 2014, Zhu et al. 2017). However, in the case of alien species, both assumptions are generally violated (Guisan et al. 2013, Eckert et al. 2020, Pili et al. 2020, Liu et al. 2022). Therefore, pooling data from a species' native and invaded ranges helps mitigate the impact of these assumptions (Escobar et al. 2014, Zhu et al. 2017, Eckert et al. 2020).

The management of the tomato leafminer is carried out mainly through chemical control, particularly due to its efficiency, ease of use and excellent cost-benefit. However, using pesticides without the proper technical criteria and without obeying the premises of resistance management can lead to side effects on humans and the environment, besides of potentially the own pest management through undesriagble effects on natural enemies and evolution of insecticide resistance. Given this, the market has sought new perspectives, especially molecules considered safer from an environmental and human health point of view. Much of this effort falls on plant-derived insecticides such as essential oils (Regnault-Roger et al. 2012, Turchen et al. 2020, Collares et al. 2023). Essential oils are substances of the secondary metabolism of plants that have biological activity usually exhibiting low environmental persistence and selectivity in favor of non-target organisms (Santos et al. 2018, Isman 2020, Giunti et al. 2022).

To bring new insights to the invasion and spread of *T. absoluta* worldwide, and a new alternative to its management, this thesis was made in three chapters. In the first chapter, the objective was to disentangle and compare the ecological niche of *T.*

absoluta along its invasive range. In the second chapter, by intentionally violating the equilibrium assumptions, new insights were created regarding the potential sites of invasion of *T. absoluta* . Finally, in the last chapter, a new and ecofriendly alternative based on an emulsion of Patchouli essential oil was assessed and proposed for the management of *T*. *absoluta* in tomato crops.

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~~3.~~ CHAPTER 1: NICHE EXPANSION IS THE LEADING CAUSE OF NICHE SHIFT IN THE INVADED RANGE OF *Tuta absoluta*

ABSTRACT

Realized niche shifts can occur during the invasion process and reflect ecological and microevolutionary processes, resulting in niche expansion (or unfilling) of alien species. The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is a devastating tomato pest species with ongoing successful invasions and establishment events worldwide. This study examined realized climatic niche differences between native and invaded ranges of *T. absoluta* using an ordination approach. Uncorrelated bioclimatic variables were selected, and then a principal component analysis was performed to define the environmental space of native and invaded ranges. Native and invaded realized niches were compared using metrics of niche changes. The two principal components captured 70.19% of the environmental variance. Invaded niche centroid moved toward lower precipitation of driest and wettest months and higher mean diurnal range. Depending on the percentage of marginal climates excluded from the models, native and invaded niches differed significantly, keeping a similar pattern. Niche overlap varied from 31.69% to 38.55%, with most of the native niche circumscribed in the invaded one. Only 4.87% of the native niche is still unfilled. Niche expansion (31.26%) and stability (68.74%) were significant. The results suggest that *T*. *absoluta* has occupied almost all suitable climatic habitats in the invaded range that resemble its native range. Additionally, we provide evidence that *T*. *absoluta* surpassed bioclimatic barriers and broadened the climatic range during the invasion process. Thus, niche expansion is the leading cause of niche shift in the invaded range by this pest.

Keywords: biological invasion, ecological niche, niche dynamics, niche shift, climatic niche

1. INTRODUCTION

One distinctive aspect of the Anthropocene is the widespread redistribution of alien species (Lewis and Maslin 2015). The invasion process can be separated into three distinct and interconnected stages: introduction, naturalization, and spread (Richardson et al. 2000). Introduction means that humans have transported the species across a major geographical barrier. Then, the naturalization process itself occurs when abiotic and biotic barriers to survival and to reproduction are overcome. Finally, invasion requires that introduced species spread and produce reproductive offspring into areas away from the founding population (Richardson et al. 2000, Gallagher et al. 2010,Guisan et al. 2014, Di Cola et al. 2017). Among the several barriers that need to be overcome during the progression of invasion, the climate suitability in the introduced range is claimed to be the primary abiotic barrier (Hayes and Barry 2008).

Although only a few introduced species successfully adapt to become invasive in new habitats, those species that become invasive pose significant losses and management challenges to the global scenario (Gallagher et al. 2010, Hill et al. 2012, Paini et al. 2016, Zhu et al. 2017, Srivastava et al. 2020). Understanding the driving factors responsible for species establishment is an overarching and challenging goal of invasion studies (Guisan et al. 2014, Di Cola et al. 2017). In this sense, the niche concept is a fundamental (and controversial) notion for understanding and predicting the possible outcomes of biological invasions. The Hutchinsonian notion of niche establishes that the ecological niche is an “n-dimensional hypervolume” shaped by the environmental conditions and resources under which a species can ‘exist indefinitely’ (Colwell and Rangel 2009). Therefore, it becomes clear from this understanding that climatic similarity between a species' native range and its invading region is essential to invasion success (Gallagher et al. 2010).

The fundamental climatic niche (i.e., direct physiological requirements of a species) was determined only for quite a few species. Most of the effort was focused on empirical estimation of the realized niche (i.e., the proportion of the species fundamental niche occupied) because of the constraints imposed by biotic exclusions, population dynamics, and dispersal limitations (Wiens et al. 2009, Guisan et al. 2014). Therefore, when a species is introduced into a new area, environmental conditions pose limitations to the species' persistence under scrutiny (Hayes and Barry 2008, Hill et al. 2012, Guisan et al. 2014). Invasive species exhibit niche conservatism when maintaining the niche space established by the fundamental niche. However, if there is any change in the boundaries or centroid of the niche envelope, a niche shift is considered (Guisan et al. 2014). This change may be the result of adaptive evolution, changes in biotic interactions, dispersal limitations, or preadaptation to conditions outside the initial range (Pearman et al. 2008, Alexander and Edwards 2010, Hahn et al. 2012).

Two approaches have been extensively used to compare niches between ranges: ordination and reciprocal ENMs (Guisan et al. 2014, Zhu et al. 2017, Pili et al. 2020). The former is a straightforward approach based on direct species observations (i.e., do not rely on any model/prediction) and comparison using either univariate or multivariate tests (e.g., PCA) (Guisan et al. 2014, Di Cola et al. 2017), while the latter is based on predictions of ENMs. Typically, comparing the overlap of reciprocal ENMs predictions, that is, predicting distribution based on models fitted in native and invasive ranges (Fitzpatrick et al. 2007, Hill et al. 2012, Zhu et al. 2017). Although both approaches are helpful, the ordination method is recommended to assess niche shifts (Guisan et al. 2014).

Different niche shift metrics can be calculated to quantify and compare realized climatic niches, but the COUE framework is the formalized and most used so far (Guisan et al. 2014, Pili et al. 2020). This framework relies on commonly used metrics to quantify and decompose niche shift into three categories: (O) 'overlap/stability' (i.e., niche space occurring in both exotic and native range), (U) 'unfilling' (i.e., the proportion of the native niche non-overlapping with the exotic niche), and (E) 'expansion' (i.e., the proportion of the exotic niche non-overlapping with the native niche). Additionally, centroid shift (C) measures the change in mean niche position (Guisan et al. 2014).

Many agricultural pest species were introduced to areas outside their native range worldwide, causing significant losses to crop and forest production (Paini et al. 2016). The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is one of the most frequently mentioned invasive species causing severe losses to tomato crops and adversely affecting food security worldwide (Guedes and Picanço 2012, Campos et al. 2017, Biondi et al. 2018). *Tuta absoluta* is native to South America, but since its first detection in Spain in 2006, it has rapidly invaded and spread in Europe, changing its importance to a significant threat to global tomato production (Desneux et al. 2011, Guedes and Picanço 2012). Currently, *T. absoluta* is found in approximately 80 countries spanning five continents (Asia, Africa, North America, South America and Europe) and continues to spread to new areas (Santana et al. 2019, GBIF 2022).

To grasp the factors that result in *T. absoluta* successfully colonizing areas outside its native range is crucial to prevent the invasion of novel areas and improve management practices in already invaded ones. Thus, this study strives to disentangle the main bioclimatic variables associated with *Tuta absoluta* distribution in its native and invaded range by assessing its respective climatic niche spaces.

2. MATERIALS AND METHODS

Species records

The database for *T. absoluta* records previously reported in Santana et al. (2019) was updated. This database included records until October 2017. Literature on *T. absoluta* records from this period was searched on the Web of Science using the terms: “*Tuta absoluta*”, “*Phthorimaea absoluta*”, “First record”, and “First report.” Additionally, the Global Biodiversity Information Facility – GBIF (GBIF 2022) was also used to obtain updated records. In total, we ended up with 411 occurrence records spanning 80 countries and five continents (Asia, Africa, North America, South America, and Europe). Main data updates included records in Africa, Asia, and Europe, particularly from Benim, Botswana, Burundi, China, Côte d'Ivoire, Myanmar (formerly Burma), Pakistan, Romania, Tajikistan, Tanzania, and Togo.

As the sampling efforts are not evenly distributed along the occurrence locations, the records were filtered using the *thin* function of the *´spThin´* R package (Aiello-Lammens et al. 2019). Using this procedure, only one record was maintained per 10 km, reducing sampling bias and spatial autocorrelation. As a result of thinning, 198 occurrence records were held, of which 32 were within the native range and 166 within the invasive range.

Climate data

Bioclimatic variables were obtained from WorldClim v.2.1 (Fick and Hijmans 2017), representing averages of monthly minimum, mean, and maximum temperature and precipitation for 1970-2000 with a spatial resolution of ~10 km (5 arc-minutes) (Fick and Hijmans 2017). Bioclimatic variables representing a combination of means, extremes, and seasonality that are ecologically relevant to *T. absoluta* and were not highly inter-correlated were selected. Bio8, Bio9, Bio18 and Bio19 were excluded from the analysis since they present discontinuities in their interpolated surfaces (Booth 2022). Multicollinearity among variables was accessed using the *vifstep* function from the *usdm* R package, and only variables with Variable Inflation Factor (VIF) < 5 were selected (Naimi 2017). After excluding the collinear variables, the linear correlation coefficients ranged between 0.04112367 (min correlation, bio14 ~ bio3) and -0.6261628 (max correlation, bio15 ~ bio14). The VIFs of the remained variables are shown in Table 1.

Niche Shift

The occurrence records and bioclimatic variables were used to assess whether the realized niche of *T. absoluta* has shifted in the native range (South America) and the invasive range (Africa, Asia, and Europe). Each bioclimatic variable was measured across the available backgrounds in native and invasive ranges and projected onto the first two axes of a principal components analysis (PCA). PCA distinguishes between climatic niches of the chosen presence and background data and can effectively identify niche overlaps, differences and shifts (Broennimann et al. 2012).

Niche change was decomposed into unfilling, stability, and expansion following the COUE framework (Guisan et al. 2014). Using the COUE framework, native and invasive niches of *T. absoluta* were quantified by weighted PC biplots and decomposed following a set of proposed metrics. The environmental space based on the selected bioclimatic variables was combined and projected on the first two axes of a principal components analysis (PCA). Ecologically relevant environmental backgrounds were determined according to Guisan et al. (2014). The environmental space described by the two PCA axes was then divided on a grid of 100 x 100 cells, having minimum and maximum values defined by those present in the available environmental background. Then, scores of species records from each geographic range were projected and grouped onto a gridded environmental space. A Gaussian kernel density function with a standard bandwidth was used to calculate densities of occurrences and available environments in each grid cell of the gridded environmental space (Silverman 2018). This approach enabled the comparison of occurrence density between native and invasive niches as records were similarly gridded (Broennimann et al. 2012). The background environment included all grid cells in countries where *T. absoluta* was present under natural conditions.

Niche overlap between species native and invaded ranges was quantified using Schoener’s index *D* of niche overlap. This index estimates similarity in occurrence densities between niches over environmental spaces, resulting in values ranging from 0 (no overlap) to 1 (complete overlap). Schoener’s *D was* used to test for niche equivalency and similarity (Warren et al. 2008) in the environmental space (Broennimann et al. 2012). The niche equivalency test determines whether two realized niches are equivalent (i.e. whether the niche overlap is effectively identical) by randomly combining pooled occurrences from both ranges. The niche similarity test determines whether two species' niches are more or less similar than would be expected by chance by randomly shifting the niches within the conditions present in the research area (Di Cola et al. 2017). Here, to determine whether native and invaded niches were equivalent, occurrence records were randomly allocated to the native and invaded niches 1000 times. The observed and simulated Schoener's D were compared. Niche similarity was tested by shifting the centroid of observed occurrence densities in the invaded range to random locations within the environmental space 1000 times, and comparing observed and simulated estimates of Schoener’s D.

Niche unfilling was determined by calculating the proportion of the native niche non-overlapping with the exotic. Niche stability was determined by calculating the ratio of the exotic niche overlapping with the native, and the niche expansion was calculated as the proportion of occupied invaded niche that did not overlap with the occupied native niche. Niche shift metrics were computed using 100 and 90% of the available in each range to remove marginal climates (Petitpierre et al. 2012). All analyses were performed using the function in the R package *´ecospat´* version 3.3 (Warton et al. 2022).

3. RESULTS

The two principal components captured 70.19% of the environmental variance, with the first axis explaining 39.64% and the second axis 30.55%. Bio2 and Bio15 were the bioclimatic variables that most contributed to the first axis, and Bio3 and Bio13 were the ones that most contributed to the second axis (Figure 2).

The invaded niche centroid of *T. absoluta* moved toward lower precipitation in the driest (Bio13) and wettest months (Bio14) and higher mean diurnal range (Bio2). The native and invaded niches overlap to a large extent. Niche overlap index Schoener's D between native and invaded niches was 0.,3271 (32.71%) when considering all available environment and 0.2884 (28.84%) when considering 90% of the available environment (i.e., excluding 10% of marginal climate). Comparing observed niche overlap values to null distributions revealed that native and invaded niches were more similar than expected by chance (p = 0.0099). Examining the niche unfilling, stability and expansion of *T. absoluta* in the invaded range demonstrates a substantial expansion (36.77–37.84%) of realized niche into new climates. Only 6.70–6.73% of the species' native niche remains unfilled. Niche stability was also observed (62.16–63.23%). Thus, niche shifts between the native and invaded ranges of *T. absoluta* can be mainly attributed to niche expansion in the invaded area (Figure 3).

Individually analyzing the dynamics of the bioclimatic variables across a gradient reveal that Bio2, Bio3, Bio5, Bio13 and Bio15 were the bioclimatic variables that most contributed to this niche expansion in the invaded region. Bio2, Bio5, Bio13 and Bio15 had a more comprehensive range of values in the invaded range compared to the native range, thus broadening the environmental space where *T. absoluta* may occur. In the invaded range, *T. absoluta* may occupy niche climates with mean diurnal temperature (Bio2) both lower and higher than those in the native range. The highest densities of occurrence for Bio3 and Bio13 are marked at distinct and lower values, indicating the invaded niche moved towards lower Isothermality and Precipitation of the wettest month. The highest densities of occurrence for Bio5 and Bio15 in the invaded range occurred at slightly higher values, indicating the invaded niche moved towards a higher maximum temperature in warmest month and precipitation seasonality. Bio14 is the only bioclimatic variable that conferred a more comprehensive range of occurrence in the native range, indicating this is one of the main variables responsible for the observed niche unfilling (Figure 4).

4. DISCUSSION

This study revealed a niche shift between native and invaded ranges of *T. absoluta* mostly attributed to expansion in the invaded range. Overall, high niche stability, low niche unfilling and moderate niche expansion was observed between these two ranges. The native and invaded realized climate spaces of *T. absoluta* present a partial overlap, with most native space being a subset of the invaded space.

The PCA correlation plot suggests that compared to the native niche, the invaded niche centroid has mainly moved toward lower precipitation in wettest (Bio13) and driest months (Bio14) and higher mean diurnal range (Bio2). Indeed, a recent study has shown that European populations of *T. absoluta* present improved upper thermal thresholds than previously reported for South American populations (Campos et al. 2021). Improved thermal tolerance was also observed in a recent invasion of *T. absoluta* in semi-arid Botswana (Machekano et al. 2018). Interestingly, *T. absoluta* also has shown intriguing thermal plasticity, with larvae being more plastic than adults, which can be advantageous in new environments and facilitate invasion (Tarusikirwa et al. 2020).

The partial overlap between the two niches, with a massive part of the native niche circumscribed within the native range, suggests that *T. absoluta* has almost completely colonized the extent of its native realized niche in its invaded range, and a few suitable climate spaces are remaining unoccupied. This pattern may be associated with improved thermal thresholds (i.e., expanded thermal tolerance toward warmer and colder conditions) and genetic differentiation (Guillemaud et al. 2015). This result suggests that *T. absoluta* fill its native fundamental niche, but the environmental tolerance has changed post-introduction. Therefore, invasive populations can occupy not only the same niche space as native populations, but also more marginal climates.

Invasive species may respond to new environments in various ways, including niche conservatism, niche expansion along multiple or specific environmental variables, or shifting into a completely different niche (Guisan et al. 2014). Changes between native and invaded climatic niches of *T. absoluta* can mainly be attributed to the expansion of the invaded niche, which led to a shift of the niche centroid and displacement of niche envelope, irrespective of the percentage of marginal climate excluded from the analysis. Niche expansion (Lei and Liu 2021) is less common than niche unfilling in invasive species (Strubbe et al. 2013, 2015). This suggests that *T. absoluta* has overcome some abiotic barriers and/or that some individuals have adapted to more extreme or newer climatic conditions, thereby colonizing novel environments in the invaded range. The absence of genetic structure in the population from southern Spain to Israel and from Israel to Morocco is a shred of strong evidence that a single introduction in Spain or Africa led to an expansion and genetic differentiation (Guillemaud et al. 2015).

A phylogenetic study suggests that the origin of the European population around the Mediterranean was a single introductory event from Central Chile, which permitted the introduced population to surpass founder effects associated with the initial introduction (Guillemaud et al. 2015). Moreover, native populations of *T. absoluta* in South America are genetically heterogenous, especially when comparing populations from north and south locations of the continent. This fact may also imply that the source of the introduced population might be adapted to a subset of a species' fundamental niche. Therefore, it is not surprising that the climatic niche spaces of native and invasive populations are distinct.

In this study, there is evidence that, in the invaded range, *T. absoluta* occupies niche spaces that present lower precipitation but higher precipitation seasonality. Indeed, *T. absoluta* is highly affected by precipitation, a vital mortality factor, especially during the rainy season (Bacci et al. 2019). Additionally, areas with low seasonality (i.e., well-distributed rainfall) are considered less suitable for *T. absoluta*, compared with regions with marked dry seasons (Santana et al. 2019). Moreover, the invaded range is characterized by lower isothermality but a more comprehensive range of mean diurnal temperature and maximum temperature. Several recent studies provide evidence that *T. absoluta* may occupy temperature ranges greater than previously reported (Machekano et al. 2018, Tarusikirwa et al. 2020, Campos et al. 2021). These results align with these studies and highlight the need for further studies to characterize the thermal requirements of other populations across the invaded range.

5. ACKNOWLEDGMENTS

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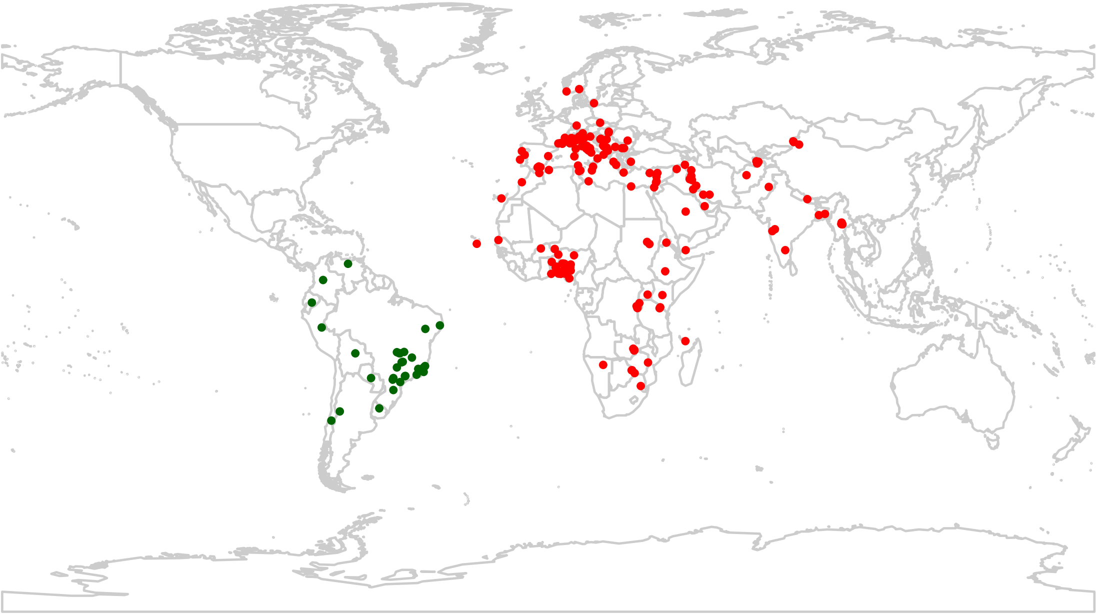

Figure 1. Occurrence records of *Tuta absoluta*. Green dots denote the native population and red dots the invasive population

Table 1. Bioclimatic variables obtained from the Worldclim database and computed variance inflation factor (VIF) for uncorrelated variables. Uncorrelated variables used in the study are shown in bold.

Variable	Description	Unit	VIF
BIO1	Annual mean temperature	°C	-
BIO2	**Mean diurnal range (mean of monthly (max temp – min temp))**	**°C**	**1.6158**
BIO3	**Isothermality (bio2/bio7) (×100)**	**°C**	**1.8570**
BIO4	Temperature seasonality (standard deviation ×100)	°C	-
BIO5	**Maximum temperature of warmest month**	**°C**	**1.7368**
BIO6	Minimum temperature of coldest month	°C	-
BIO7	Temperature annual range (bio5-bio6)	°C	-
BIO8	Mean temperature of wettest quarter	°C	-
BIO9	Mean temperature of driest quarter	°C	-
BIO10	Mean temperature of warmest quarter	°C	-
BIO11	Mean temperature of coldest quarter	°C	-
BIO12	Annual precipitation	mm	-
BIO13	**Precipitation of wettest month**	**mm**	**1.9152**
BIO14	**Precipitation of driest month**	**mm**	**2.0224**
BIO15	**Precipitation seasonality (coefficient of variation)**	**mm**	**3.05751**
BIO16	Precipitation of wettest quarter	mm	-
BIO17	Precipitation of driest quarter	mm	-
BIO18	Precipitation of warmest quarter	mm	-
BIO19	Precipitation of coldest quarter	mm	-

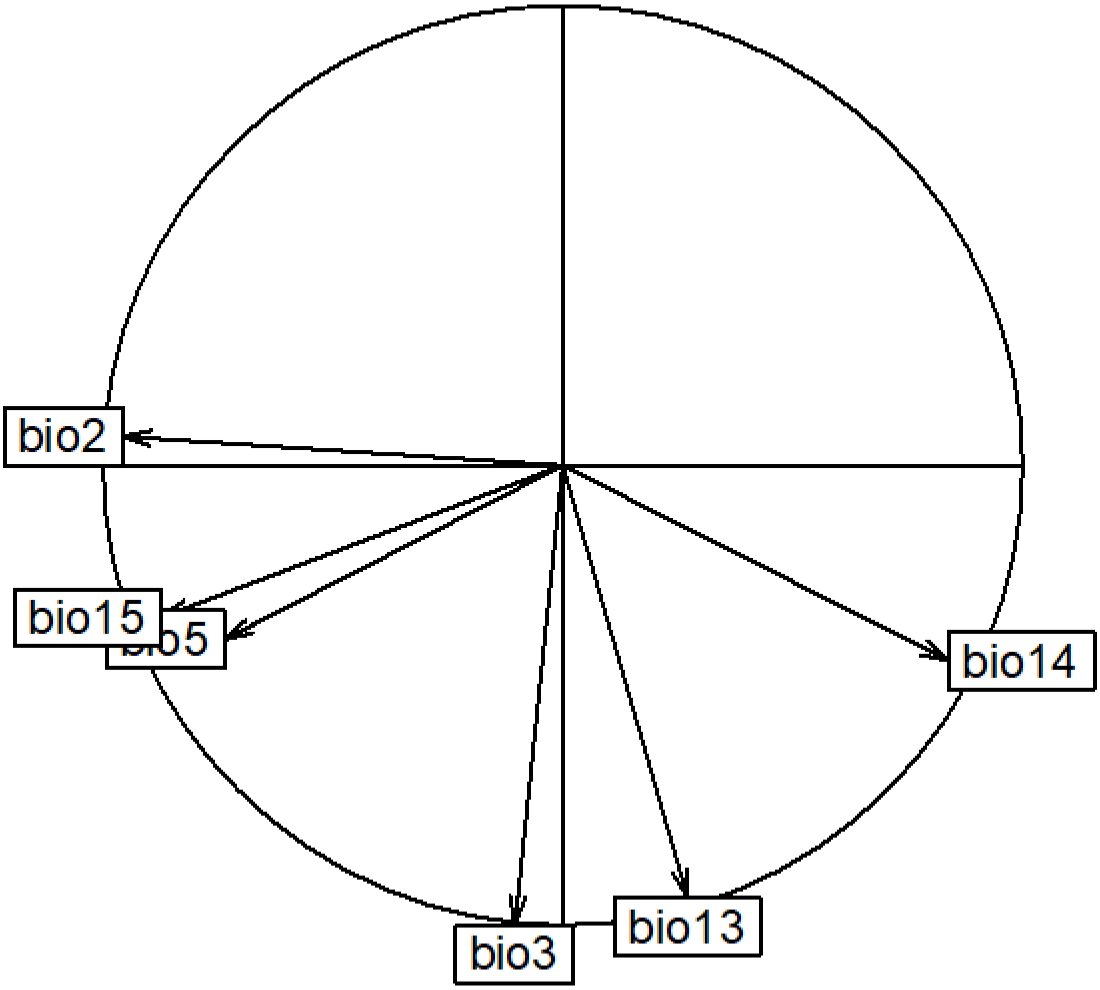

Figure 2. The principal component analysis correlation circle plots for *Tuta abs*oluta show the contribution of predictors in the niche space to the first and second PCA axes. bio2 = temperature seasonality; bio3 = isothermality; bio5 = maximum temperature of warmest month; bio13 = precipitation of wettest month; bio14 = precipitation of driest month; bio15 = precipitation seasonality. Axis 1 = 39.64%; Axis 2 = 30.55%.

Table 2. Summary results of niche change metrics (stability, unfilling, and expansion), overlap index (Schoener's D), and niche equivalency and similarity tests (*p* values). I90 and I100 represent respectively the intersection of 90% and 100% of available environments in the native and invaded ranges.

Niche change metric	***I100***	***I90***
Stability (%)	62.12	63.23
Unfilling (%)	6.73	6.70
Expansion (%)	37.84	36.77
Overlap (Schoener's D)	32.71	28.84
Equivalency test (p value)	0.0099	0.0091
Similarity test (p value)	0.0040	0.0060

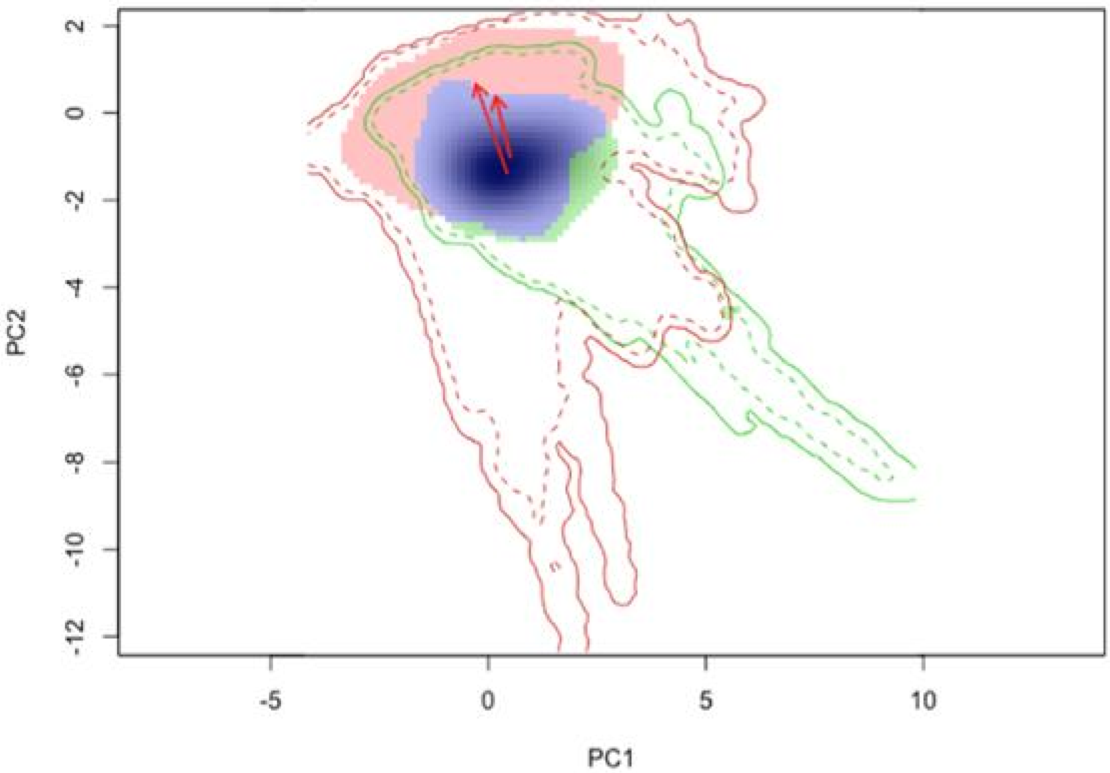

Figure 3. Niche dynamics of *Tuta absoluta*, comparing native (green) and invaded (red) ranges based on a PCA conducted on 6 selected bioclimatic variables. Unfilled areas are shown in green, stable areas in blue, and expansion areas in red. Solid and dashed lines represent the results using 100% and 90%, respectively, of the available occurrence and pseudo-absence data to delineate the native niche (green lines) and the invasive niche (red lines). Solid and dashed contour lines respectively represent the extent of 100% (I100) and 90% (I90) of available environmental conditions that exists in the native (green) and invaded (red) ranges. The red solid arrow indicates the difference (distance and direction) between the native and the invasive niche centroid. Red dashed arrow represents the difference between the centroids of the native and the invasive environmental background extent. The densities of occurrences in the native range are displayed using gray shading.

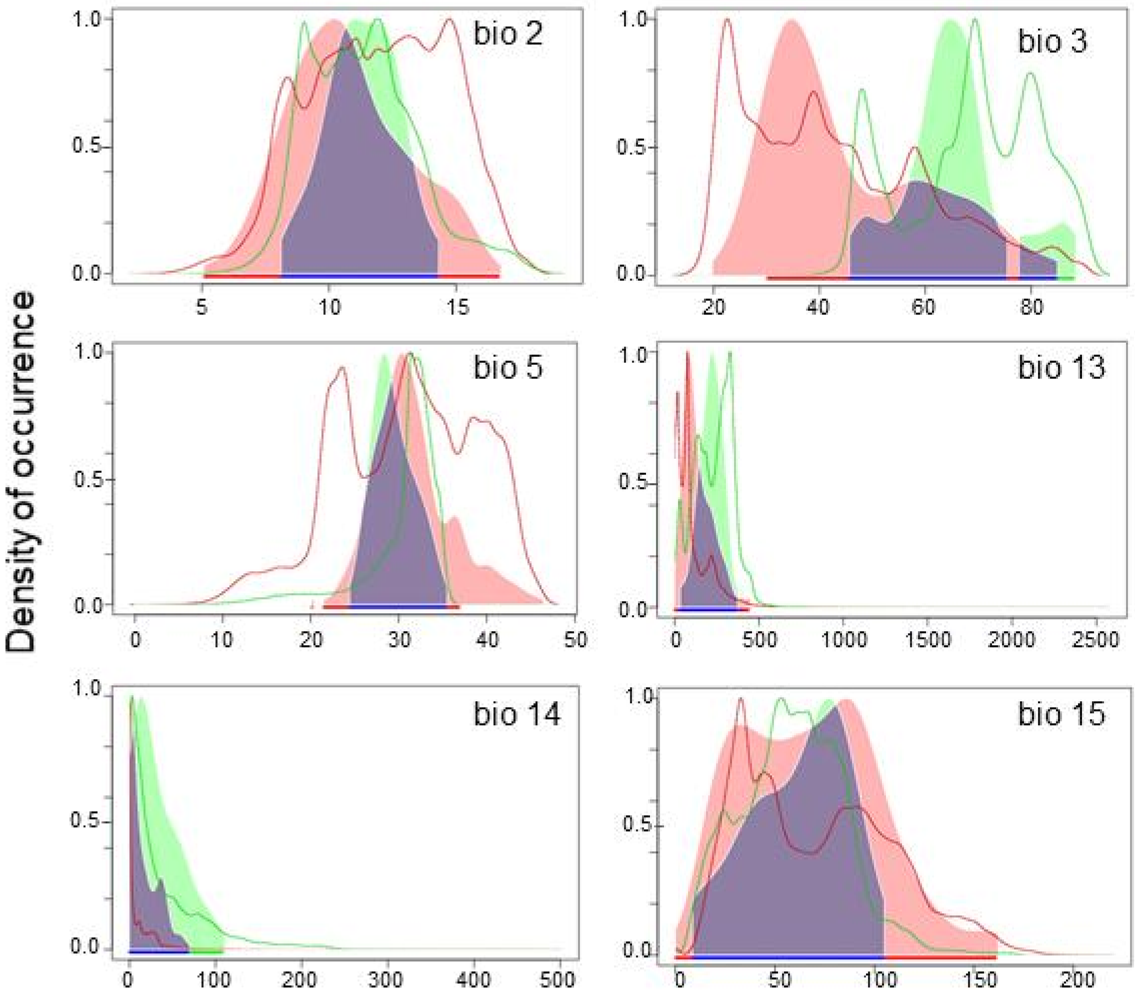

Figure 4. Niche dynamics along the gradient of each variable. The Y-axis represent the density of occurrence for a given value of each bioclimatic variable in the X-axis. Unfilling, stability and expansion areas are shown in green, blue, and red, respectively. Filled and unfilled contour lines respectively represent the extent of 100% and 90% of available environmental conditions that exists in the native (green) and invaded (red) ranges. bio2 = temperature seasonality (ºC); bio3 = isothermality (ºC); bio5 = maximum temperature of warmest month (ºC); bio13 = precipitation of wettest month (mm); bio14 = precipitation of driest month (mm); bio15 = precipitation seasonality (mm).

4. CHAPTER 2: ECOLOGICAL NICHE MODELS OF *Tuta absoluta* IN ITS NATIVE AND INVADED RANGES

ABSTRACT

Understanding invasive species' distribution and the stage of invasion are critical to develop reasonable management for different regions. Therefore, this study aimed to compare ecological niche models (ENMs) based on different distributions and determine the current invasion stage of *Tuta absoluta*. Reciprocal ecological niche models were constructed, using occurrence records from the (i) native range (South America), (ii) invaded range (Europe, Africa and Asia), and (iii) native and invaded ranges pooled (Global). The potential distribution of *T. absoluta* changed significantly based on the ranges of occurrence data used to fit the ENMs, as demonstrated by reciprocal predictions. Additionally, the models indicate that *T. absoluta* has not yet colonized all suitable regions with suitable climate in Europe, Africa, and Asia with a suitable climate. Moreover, ENMs based on invasive range may be more reliable than native models when realized niche shifts are driven by niche expansion. Most of the *T. absoluta* occurrences are in quasi-equilibrium state, but a considerable number of populations are presumably sink populations. Caution is warranted when using the source population to estimate invasion potential.

Keywords: biological invasion, climatic niche, ecological niche model, invasive species, niche shift.

1. INTRODUCTION

Invasive species pose a serious threat to agriculture, ecosystems, and economies worldwide (Paini et al. 2016). As such, numerous international agreements have been made to prevent its introduction and spread (Shine et al. 2000). Identifying areas where alien species are likely to establish and spread is essential for preventing or halting invasions, providing a great opportunity to mitigate their negative effects. Once a species has established itself in an introduced range, eradication is extremely difficult (Parkes and Panetta 2009). A more appropriate and recommended strategy is to implement spatially oriented management according to the different invasion stages (Terblanche et al. 2016, Shackleton et al. 2017). This approach requires understanding species' distribution, stage of invasion and the driving factors affecting its distribution.

Ecological niche models (ENMs) have emerged as a powerful tool to study biological invasions (Peterson et al. 2011). Correlative ENMs are built on the core principle of predicting species' realized niches based on species occurrence and environmental data. These models have been effectively implemented to predict the occurrence and spread of species in response to environmental variables (Kumar et al. 2014, Tonnang et al. 2017, Santana et al. 2019). ENMs assume that the ecological niche of the species is conserved across space and time, and that the species has occupied all potentially suitable environments and is in quasi-equilibrium state. However, these assumptions are generally violated in cases of ongoing invasions by exotic species (Guisan et al. 2013, Eckert et al. 2020, Pili et al. 2020, Liu et al. 2022).

The classical approach in ENM involves the calibration in native range and transferring to invaded ranges. However, realized niches of an invasive species may differ significantly between its native and invaded ranges (Guisan et al. 2014), such as due to niche shifting during invasions, resulting in poor model transferability. Another approach involves building ENMs using occurrence records from invaded range, which may incorporate phenotypic changes and resembles the fundamental niche (Urban et al. 2007). However, it assumes that species are in environmental equilibrium, which is rarely true in the case of invasive species. Conversely, one strategy to mitigate the impact of this assumption is pooling data from a species' native and invaded ranges (Escobar et al. 2014, Zhu et al. 2017, Eckert et al. 2020).

The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is among the most frequently mentioned invasive species causing significant losses to tomato crops worldwide (Campos et al. 2017, Biondi et al. 2018). Understand its current stages of invasion and predict the potential distribution is essential to implement spatially oriented management strategy and set different control objectives for areas with different stage of invasion.

Therefore, to support the development of spatially explicit management strategies for *Tuta absoluta* (Lepidoptera: Gelechiidae), this study assessed (i) whether the predictions depend on the geographic origin of occurrence records; (ii) its ecological niche in the invaded range in comparison with the global and native niche; (iii) the geographic distribution and the invasion stage of *T. absoluta*.

2. MATERIAL AND METHODS

Species and Climate Data

The occurrence records and climate data used in the first chapter of this thesis were employed here to build the ENMs. These occurrence records comprise 411 data points spanning 80 countries and 5 continents (Asia, Africa, North America, South America, and Europe). After thinning, occurrence records were reduced to a total of 198 data points (global range), of which 32 were within the native range and 166 within the invasive range.

Climate data comprises 6 uncorrelated bioclimatic variables for 1970-2000 with a spatial resolution of ~10 km (5 arc-minutes): bio2 = temperature seasonality; bio3 = isothermality; bio5 = maximum temperature of warmest month; bio13 = precipitation of wettest month; bio14 = precipitation of driest month; bio15 = precipitation seasonality, (Fick and Hijmans 2017). The same Bioclim variables were used for all ENMs to enable direct model comparisons and to permit comparing the relative contributions of each variable in each particular model.

Niche modelling

The realized niche of *Tuta absoluta* was modeled using Maxent (version. 3.4.4). Maxent uses environmental variable to tentatively separate sites where a species is present from background locations (Phillips et al. 2006). Moreover, Maxent has shown to produce reliable predictions with presence-only data, and generally demonstrates superior accuracy compared to many other ENM algorithms (González-Irusta et al. 2015).

Three separated models were constructed, using occurrence records in the (i) native range (South America), (ii) invaded range (Europe, Africa and Asia), and (iii) all occurrences (Global).

A total of 10.000 background points were generated for each ENM by means of random sampling within a 300-km buffer area around all species occurrence data points. Randomly generated absence points located <10 km from a presence point were then removed.

Occurrence data was split into calibration (70%) and validation (30%) datasets. Ten runs were performed for each model. Model accuracy was assessed using the area under the receiver operating characteristic curve (AUC) and the True Skill Statistics. The AUC ranges from 0 to 1, where 0.5 is no better than random and 1.0 is a perfect score. TSS ranges from -1 to +1, with -1 representing 100% wrong predictions, +1 representing perfect prediction, and 0 random fit.

The analysis were carried out using the *dismo* package in R v4.2.1. The logistic output format was used, resulting in habitat suitability values ranging from 0 (unsuitable) to 1 (suitable). The default settings were used to reduce overfitting (Phillips and Dudík 2008).

Invasion Stage

Predictions for observed presences were extracted and compared to the invasive model (ENMinvasive) and the global model (ENMglobal) to inform the current stage of invasion of the species. By comparing the results, it was possible to determine if invasive species were found inside or outside of their respective regional and global habitats. For this purpose, the theoretical framework proposed by Gallien et al. (2012) was implemented. According to this framework, if the species is only observed (i) within the regional model, it suggests adaptation to the novel climate, (ii) within both models, it is a “stabilizing” population, (iii) only within the global model, it is likely to be a colonizing population, and (iv) outside of both niches, it most likely refers to a "sink" population (Gallien et al. 2012).

3. RESULTS

ENM based on native occurrences

The average AUC for the ENM $_{\text{native}}$ was 0.953 ± 0.016. Overall, this model failed to predict occurrence on several regions. The native model failed to predict occurrences on the Mediterranean Basin, Western Europe and Eastern Europe, most of the occurrence in Southern Asia, Eastern Asia, and north of Western Asia, but predict well occurrence records on South-East Asia. In Africa, this model failed to predict on Western Asia, but predict most of the occurrences in Central, Eastern and Southern Asia. In the native range, the model predicted well on most of the region in South America with higher suitability in Southeast Brazil.

ENM based on invasive occurrences

The average AUC for the ENM $_{\text{invasive}}$ was 0.953 ± 0.016. The model accurately predicted most known occurrences of *T. absoluta*. This model predicted occurrence along most of the Mediterranean Basin, large areas on Southern, Western, Eastern Europe and, but did not predicted areas on Northern Europe.

In Africa, potential new habitats were predicted on Central Africa and some small areas on West Africa, but the model failed to predict several occurrences on the South region, and some occurrences at the northern part of West and East regions. Additionally, in Asia, the model predicted a small area on Western Asia, and large areas on Central, Eastern and Southern Asia. In the native range, the model predicted well on most of the region in South America with higher suitability in Southeast Brazil.

ENM based on all occurrences

The average AUC for the ENM $_{global}$ was 0.758 ± 0.015. Overall, the model accurately predicted most known presence records of *T. absoluta*. Similar to the invasive model, ENM $_{global}$ predicted occurrence along most of the Mediterranean Basin, large areas on Southern, Western, Eastern Europe and, but also predicted large areas on Northern Europe. In Africa, the model predicted suitability in Central Africa, West Africa, and small spots on the South of the continent. In Asia, the model predicted a small spot on Western Asia, and large areas on Central and Eastern Asia. and low suitability on Southern Asia. In the native range, the model predicted well on most of the region in Brazil, showing low suitability for the North region. Additionally, showed some spots of high suitability on coastal areas on Uruguay, Argentina, Chile, Peru, Ecuador, and Venezuela.

Invasion Stage

Most of the *T. absoluta* occurrences presented high suitability in both invasive and global models (upper right quadrant). A considerable number of populations are presumably sink populations, that is, low suitability in the invasive and global model (lower left quadrant). Few populations presented high suitability in the invasive model and low suitability in the global model (the upper left quadrant), indicating they are adapting. Finally, few populations presented low suitability in the invasive model but high suitability in the global model, indicating colonization (lower left quadrant) (Fig 4a).

4. DISCUSSION

This study predicted the potential distribution of *T. absoluta* under current climate conditions. Compared to previous models for this pest, this model used the most updated occurrence records (up to July 2022). ENM models based on native, invasive and the entire global range were also compared, and the current stage of invasion of *T. absoluta* was characterized based on a novel theoretical framework.

The classic ENM approach relies on comparing climate and species' native distribution, which assumes niche conservatism during the invasion, and therefore models can be effective in predicting invasion in the exotic range. However, the species may not maintain their native realized niches when introduced to locations beyond their native geographic ranges, especially due to evidences of climatic niche shift during invasions (Broennimann et al. 2007, Medley 2010, Pili et al. 2020). Therefore, the species may be able to occupy a larger or different portion of the fundamental niche beyond the native distribution. This may pose significant uncertainty to distribution models that rely only on occurrence records and environmental data from a local region. The current predicted distribution of *T. absoluta* is spanning a wider range than reported in previous works, which might be the result of intraspecific adaptations between populations. Climatic adaptations have been reported in several works conducted in different regions worldwide (Machekano et al. 2018, Tarusikirwa et al. 2020, Campos et al. 2021, Li et al. 2021, Tabikha 2022).

Reciprocal predictions of ENMs showed that the potential distribution of *T. absoluta* varied substantially depending on the ranges of occurrence records used to fit ENMs. In this sense, using only native occurrence records seem not to be the best model approach to predict the potential distribution of *T. absoluta*, since models based on this data underestimated the potential distribution of *T. absoluta* at coarse scale. The main cause of underprediction is possibly the realized niche shift due to niche expansion. ENMs based on native range arguably provide unreliable predictions when realized niche shifts are predominantly due to niche expansion (Strubbe et al. 2013, Tingley et al. 2016, Zhu et al. 2017). Therefore, in Europe, Africa, and Asia, where there are evidence of niche expansion and colonization of extremely novel climates (Machekano et al. 2018, Tarusikirwa et al. 2020, Campos et al. 2021, Li et al. 2021, Tabikha 2022), the native-range ENM under-predicted the current extent of distribution. The results of reciprocal predictions of *T. absoluta* highlight the risk associated with fitting ENM to species populations that are not in equilibrium (Elith et al. 2010). Alternatively, fitting ENMs with invasive range data can be useful to identify changes in a species' realized niche that occur during invasion (Urban et al. 2007). But the data must also be considered with caution, especially on recent and ongoing invasions, since the occurrence records represent only a subset of the suitable environment and therefore may underestimate the potential distribution as well. Combining native and invasive range data (global model) is a more reliable approach to reduce the influence of non-equilibrium. However, when the aim is to capture ecological niche shift or expansion during the invasion, the pooled model may be too broad to capture the distribution.

Following Gallien et al. (2012), the upper right quadrant of Figure 4 represents high suitability in both native and global habitat. and can be interpreted as quasi-equilibrium. The upper left quadrant depicts high suitability in native model, but low suitability in the global model, demonstrating local adaption. Lower right quadrant depicts high suitability in the global model, but low suitability in the local model, which is interpreted as regional colonization. Lower left represents low suitability in both the local and global model, which can be assumed as sink populations. In this work, most of the populations are in a quasi-equilibrium state, which is not a surprise considering the great dispersal ability and adaptability of *T. absoluta* (Machekano et al. 2018, Tarusikirwa et al. 2020, Li et al. 2021, Tabikha 2022). Additionally, several populations fall into the lower left quadrant, which indicates they cannot although the ENM focuses on ecological data, biotic and anthropogenic factors cannot be neglected. These factors can alter the course of invasions and facilitate or hamper the spread and establishment processes. As *T. absoluta* continues to spread worldwide and pose significant threat to tomato industry, early prevention is recommended prior to its establishment. To prevent/slow the ongoing spread of *T. absoluta*, efforts should be concentrated in the regions considered highly suitable for its establishment.

7. ACKNOWLEDGMENTS

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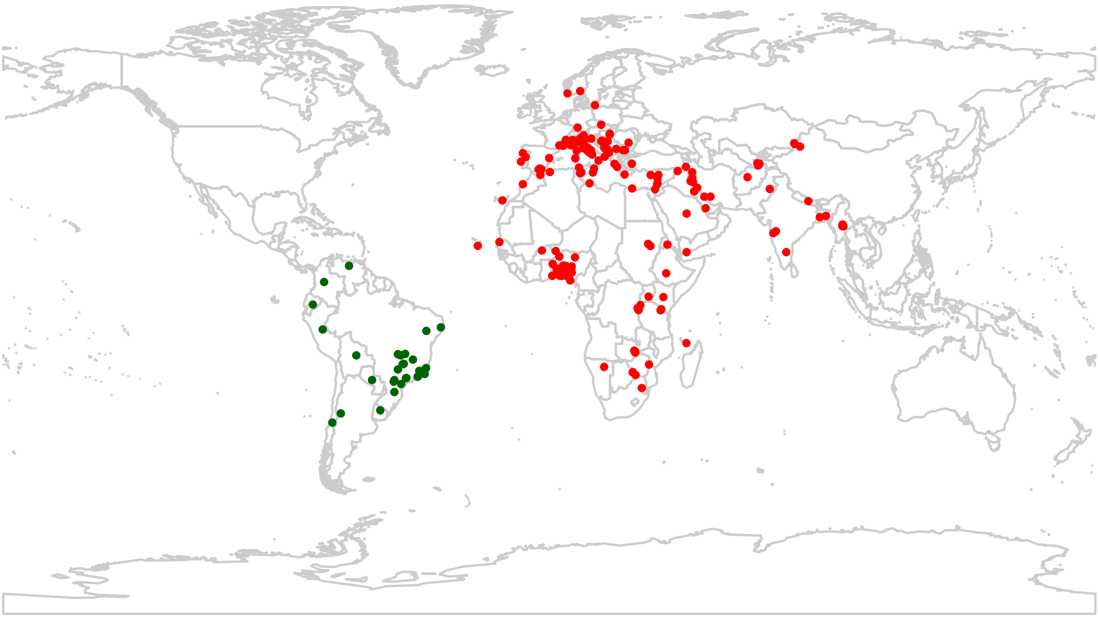

Figure 1. Occurrence records of *Tuta absoluta* in the native (green dots) and invasive (red) ranges.

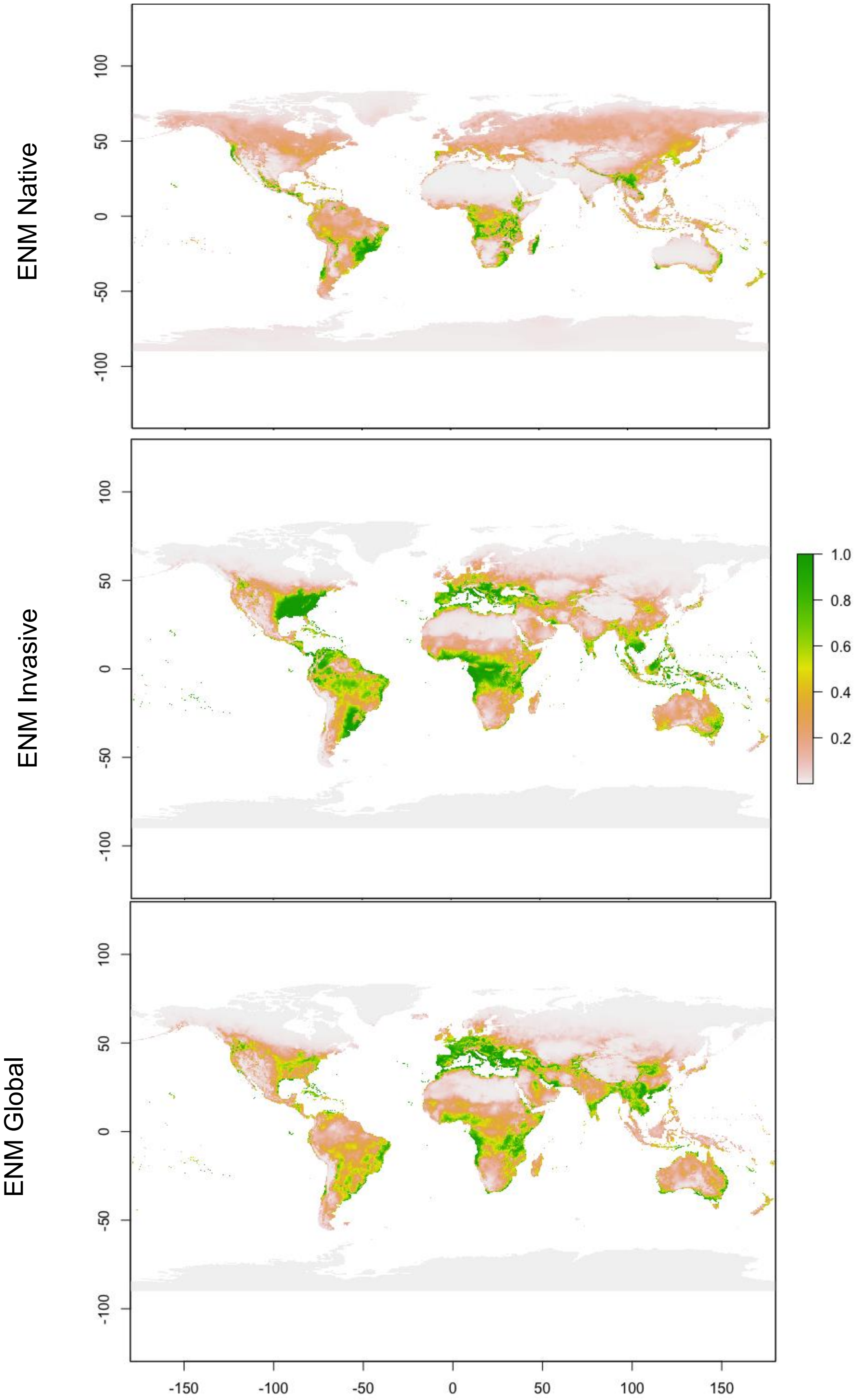

Figure 2. Reciprocal projections of ecological niche models based on data from native, invaded, and global ranges of *Tuta absoluta*.

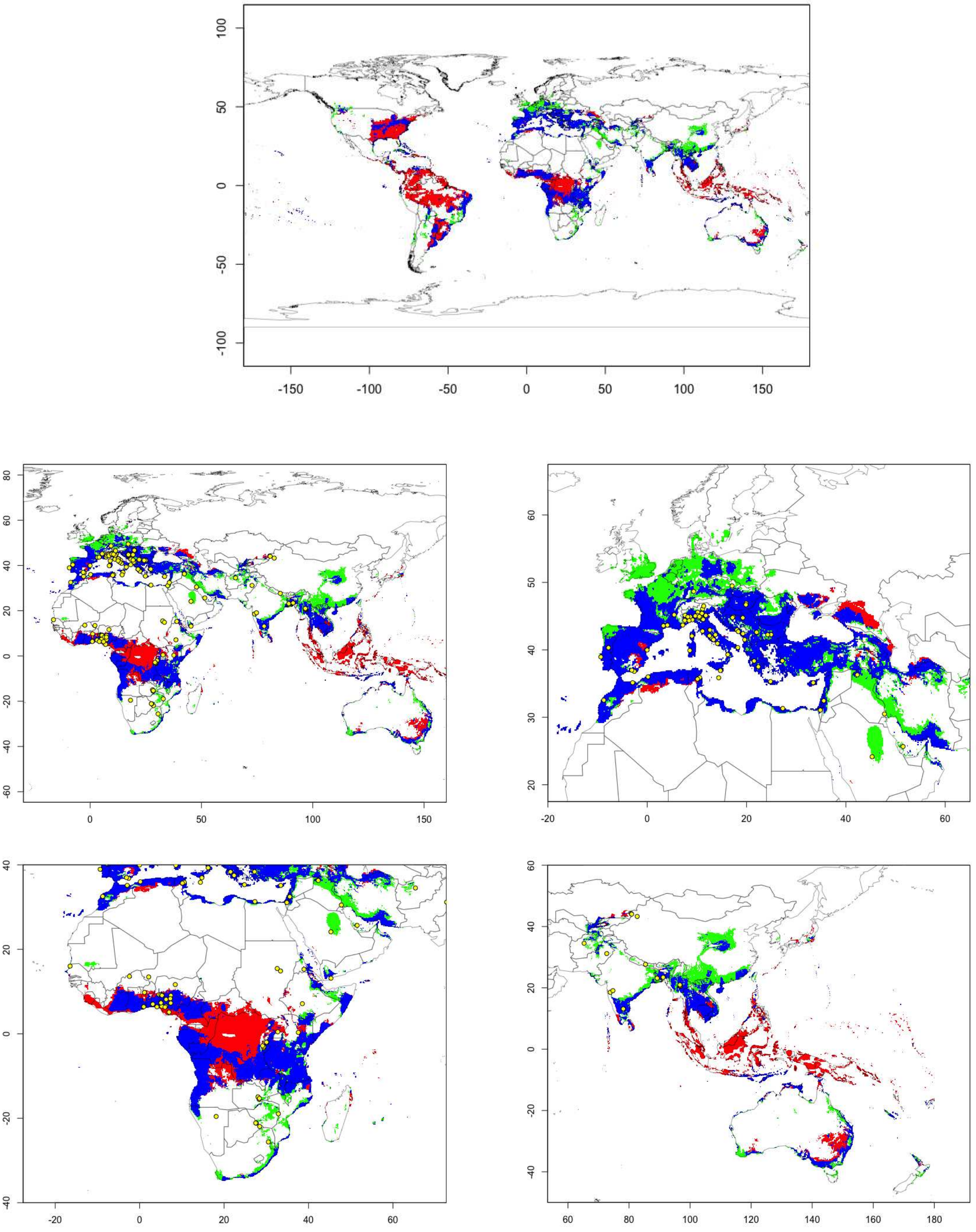

Figure 3. Maps show niche stability, expansion and unfillling. Green depicts unfilling, blue represents stability and red is expansion. Yellow dots represent occurrence records of *Tuta absoluta*.

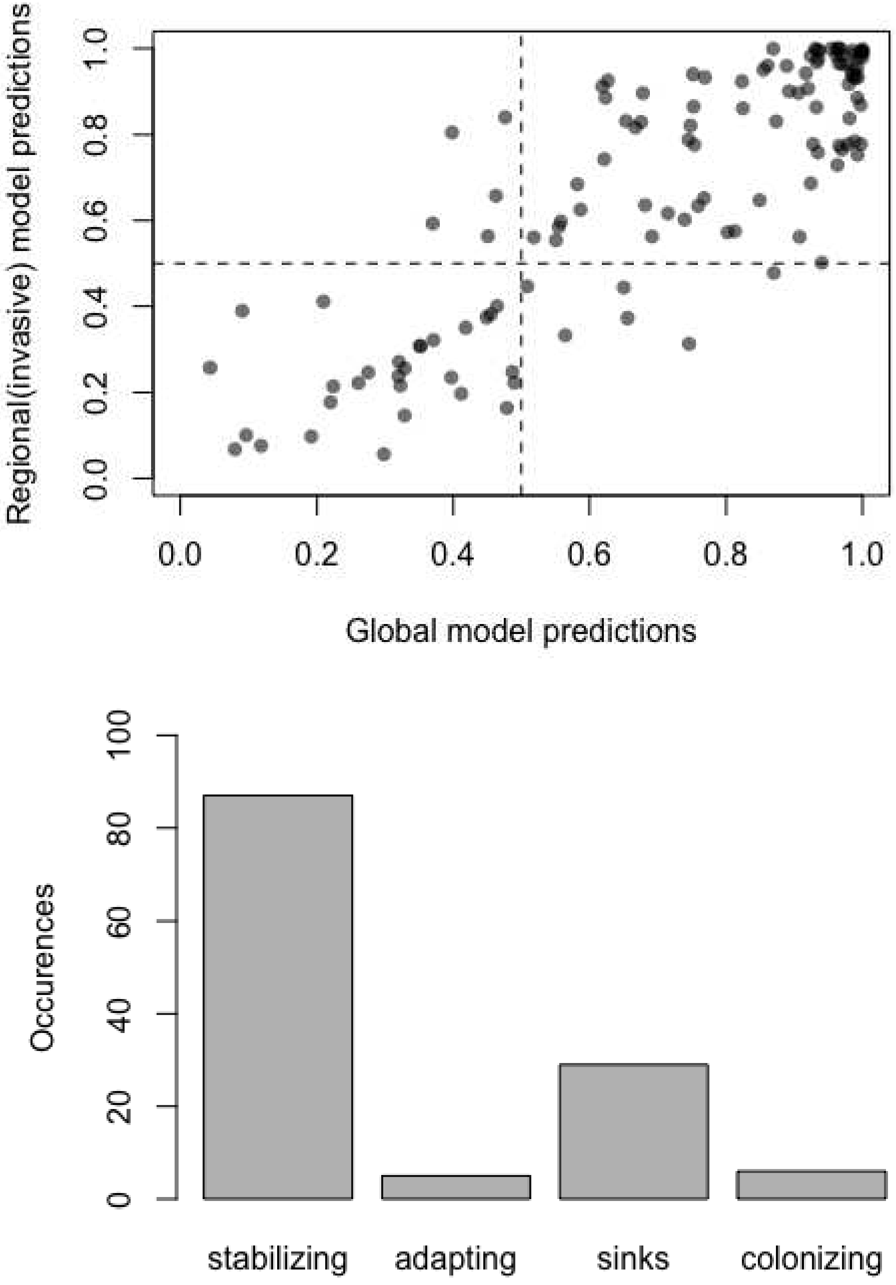

Figure 4. Scatterplot and histograms of observed presence points of *Tuta absoluta* comparing the probabilities predicted by the regional and the global model predictions.

5. CHAPTER 3: LETHAL AND SUBLETHAL EFFECTS OF AN ESSENTIAL OIL-BASED EMULSION OF PATCHOULI, *Pogostemon cablin* (LAMIACEAE), ON THE TOMATO LEAFMINER

ABSTRACT

There has been an excitement toward novel eco-friendly alternatives to pest management, particularly formulations based on essential oils (EOs). Here, the biological activity of an EO-based emulsion derived from patchouli *Pogostemon cablin* was assessed against *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), a devastating and invasive pest in tomato crops worldwide. Laboratory bioassays were carried out to determine and compare lethal doses, lethal times, oviposition of treated individuals, and oviposition of *T. absoluta* on treated leaves of tomato to pure patchouli essential oil or its emulsion containing 18% of oil. The estimated LD_{50} was 9.86 (6.95–12.5) for the EO and 14.0 (12.1–16.0) for the EO-based emulsion. Oviposition was reduced in adults derived from the second instar treated with LD_{10} by 78.5 (EO) and 85.4% (emulsion). The EO and its emulsion conferred similar avoidance to adults when sprayed on tomato leaves. Therefore, both formulations present similar lethal and sublethal effects against *T. absoluta*. This study demonstrated a remarkable potential of an emulsion containing 18% of *P. cablin* oil to be employed for *T. absoluta* management on tomato crops. Further studies are needed to assess and guarantee open field applications.

Keywords: acute toxicity, biorational insecticide, integrated pest management, plant-based pesticide.

1. INTRODUCTION

The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is an important pest of tomato crops in Brazil and Europe (Guedes and Picanço 2012, Campos et al. 2017, Biondi et al. 2018). The larvae cause crop yield losses due to feeding activity on leaves, stems, flowers, and fruits (Silva et al. 2011, Campos et al. 2017). In Brazil, *T. absoluta* was first reported in 1979 and two years later, it was already present in the central tomato-producing regions of the country, causing severe yield losses (Muszinski et al. 1982, Guedes and Picanço 2012, Galdino et al. 2015). The tomato leafminer is native to South America, and its invasion and spread in Europe in 2006 changed its importance to a significant threat to global tomato production (Desneux et al. 2011, Guedes and Picanço 2012). Currently, *T. absoluta* is found in approximately 80 countries (EPPO 2007).

Pest resistance against current insecticides and increased concern regarding the collateral effects of pesticides on human health and the environment are driving the search for novel alternatives to pest control (Sousa et al. 2017). Essential oils (EOs) have been considered an alternative in this sense, as they are derived from medicinal and aromatic plants, which are considered eco-friendly due to their low persistence in the environment and lower toxicity to non-target organisms, in addition to having biological activity against several pests (Athanassiou et al. 2018, Pavoni et al. 2020, Lucia and Guzmán 2021). However, water insolubility, chemical instability, high volatility, and short residual activity due to degradation by temperature and light impair its use (Pavoni et al. 2020).

The development of EO-based emulsion may be an alternative to overcome the drawbacks of EO since this formulation confers small particle size, controlled release in the environment and increased penetration in the target pest (Liu et al. 2011, Werdin González et al. 2014, Athanassiou et al. 2018, Rocha et al. 2018, Pavoni et al. 2020, Santos et al. 2022). These characteristics protect the active ingredients from degradation and may also increase efficacy as per smaller particle size and higher solubility and mobility than pure EO (Montefuscoli et al. 2014, Werdin González et al. 2015).

Several studies showed the biological activity of essential oils derived from *Pogostemon cablin* against urban and crop pests (Ga'al et al. 2018, Rocha et al. 2018, Feng et al. 2019, Lima Santos et al. 2022, Santos et al. 2022). Besides the noted lethal effect on numerous insect species (Lima Santos et al. 2022), several sublethal effects have been attributed to this EO, such as impairment of reproduction and feeding (Santos et al. 2022), impairment of behavioral traits such as impair behavioral traits such as displacement and speed on some ant species (Rocha et al. 2018), increased walking activity (Rocha et al. 2018, Santos et al. 2022), and histopathological changes in the midgut (Ga'al et al. 2018, Santos et al. 2022). In addition, repellent effect was also observed at some concentrations of EO and its main compound (patchoulol) (Feng et al. 2019).

However, to our knowledge, there are no studies regarding patchouli emulsion to control *T. absoluta*. Thus, this work aimed to determine the lethal and sublethal effects of patchouli essential oil emulsion for the tomato leafminer.

2. MATERIAL AND METHODS

Insects

The insects used in this work came from laboratory colonies maintained at the Integrated Pest Management Laboratory of the Federal University of Viçosa. The colonies were reared as described by Silva et al. (2011). The populations were reared in a laboratory at 25 ± 0.5 °C, relative humidity of 75 ± 5% and 12 h photophase. The larvae were fed tomato leaves ('Aguamiel') grown in a greenhouse without any pesticide treatment.

Emulsion

The emulsion was composed of 36% Tween 80 (surfactant), 36% ethanol (95% PA; co-surfactant), 18% *Pogostemon cablin* essential oil (oil phase) and 10% ultrapure water (aqueous phase). This emulsion was prepared as described by (Santos et al. 2022). After preparation, the emulsion was stored in a 200 mL amber bottle at 25°C in the dark for 24 h for complete homogenization. The main compounds present in this emulsion were patchoulol (43.05%), α-Guaiene (16.06%), and α-Bulnesene (13.69%) (Santos et al. 2022). The emulsion had a microparticle size of 3.73 ± 3.70 µm (mean ±

SD), conductivity of 0.0472 ± 0.0353 mS/cm, pH (7.68 ± 0.35), and zeta potential of –20.27 ± 5.81 mV (Santos et al. 2022) .

Bioassays

Bioassays were conducted to determine: (i) lethal doses, (ii) lethal times, (iii) oviposition and (iv) oviposition preference of *T. absoluta* individuals exposed to the essential oil and its emulsion.

Treatments were diluted in acetone (99.9% purity). The control treatment consisted of acetone only. Previous tests showed that acetone, the surfactant and co-surfactant present in the microemulsion, did not influence the mortality of *T. absoluta.*

Dose-response curve

Serial dilutions of patchouli EO and its emulsion were performed to obtain doses of 5, 10, 15, 20 and 30 µg of EO per mg of insect and 5, 10, 15, 20, 25 and 30 µg of emulsion per mg of insect.

A total of six replicates were performed for each dose. The experimental unit consisted of Petri dishes (6 × 1.5 cm) containing 10-second instar *T. absoluta* and untreated tomato leaflets (cultivar 'Aguamiel') for feeding.

Patchouli essential oil and emulsion were applied by topical application of 0.5 µL of the treatment in the dorsal region of the insects with the aid of a micro syringe (Hamilton®, 10µL). Then, the plates were sealed with plastic film and placed in B.O.D at 25 ± 2 °C, 70 ± 10% RH and photophase for 12 hours. Mortality was assessed 72 hours after application. In the assessments, the insects were touched with the bristles of a brush, and those that did not move were considered dead.

Time-mortality bioassay

In the time-mortality bioassay, we used the LD_{90} for the emulsion, with acetone as a control treatment. Four replicates were used, each consisting of 10-second instar of *T. absoluta*. A tomato leaf was provided for feeding. Topical application was performed as described in the determination of the dose-response curve.

Mortality assessment was performed every 10 minutes until 2 h, every 1 h until 12 h, and then every 12 h until 72 h. Individuals that did not move after being touched by the bristles of a brush were considered dead.

Oviposition Rate

Second instar *T. absoluta* was subjected to LD10 of essential oil and emulsion by topical application. The surviving individuals that reached the pupal stage were sexed (GENÇ 2016), and individual couples were placed in separate cages until emergence. A tomato leaf and a cotton cloth moistened with honey were placed inside each cage. To maintain turgidity, a bevel cut was made on the tomato leaf petiole, then placed in a glass bottle. Four replicates were used, each with one couple. The oviposition of *T. absoluta* females, derived from second instar larvae treated with the LD_{10}, was evaluated after 72h.

Oviposition Preference

Tomato leaves were sprayed with 0.1% v/v Patchouli EO or its emulsion and the control treatment with pure acetone. A total of eight replicates were performed, each consisting of a cage (40 × 40 × 40 cm) containing 10 couples of *T. absoluta* and a leaf treated with one of the treatments. The cages were maintained at room temperature. The number of eggs in each of the treatments was evaluated after 24 h with the aid of a magnifying glass (40x).

Statistical analyses

All statistical analyses were performed in the R software version 4.2.1 (R. Core Team 2022). Mortality data were submitted to PROBIT analysis using the ecotox package (Hlina 2021). Models with $p > 0.05$ were accepted by the chi-square goodness-of-fit test (χ^2). LC_{50} and LC_{90}, as well as their 95% confidence intervals, were calculated.

Time mortality was analysed using Kaplan–Meier estimators in the survival package (Therneau et al. 2022). LT_{50} and its 95% confidence intervals were calculated. Curves and LT_{50} were compared using the Log-rank test with Bonferroni correction.

Oviposition rate, and oviposition data were fitted to generalized linear models (GLM) using the lme4 package (Bates et al. 2015), with treatment as the fixed effect and error distribution accordingly. Oviposition rate was fitted to the negative binomial model and oviposition preference was initially fitted to the Poisson error distribution, but as overdispersion was detected, this data was refitted to quasi-Poisson. Model fit was checked using the 'performance' package (Lüdecke et al. 2021), and means were compared using least-square means at $\alpha = 0.05$ (package 'emmeans') (Lenth et al. 2023).

3. RESULTS

Dose-mortality bioassay

Tuta absoluta presented similar susceptibility to the EO and EO-based emulsion. Estimated dose-response curves for the essential oil ($\chi^2_3 = 5.82$, $p = 0.12$) and the EO-based emulsion (($\chi^2_5 = 2.37$, $p = 0.67$) showed similar toxicity to *T. absoluta* based on overlapping 95% confidence intervals of the LD_{50} (Figure 1). The LD_{50} for the EO was 9.86 (6.95 – 12.50) and for the emulsion was 14.0 (12.1 – 16.0) µg per mg of insect. The estimated LD_{90} was 21.7 (16.4 – 38.7) for the EO and 36.2 (29.5- 49.7) µg per mg of the insect for the emulsion (Figure 2).

Time-mortality bioassay

Survival of second instar *T. absoluta* exposed to LD_{90} of the EO-based emulsion reduced according to time. High mortality was observed during the first hour of assessment, indicating this is a fast-acting pesticide. The time necessary to decrease half of the population (LT_{50}) was 3.00 ± 0.08 hours. The lethal time for the pure essential oil could not be calculated because all individuals died within the first 10 minutes of evaluation.

Oviposition

Oviposition of adult females exposed to the EO and EO-based formulation at the sublethal concentration (LD_{10}) were negatively affected when compared to second instar larvae that received only acetone (control) ($\chi^2{}_9 = 37.95$, $p < 0.001$). The average number of eggs of females exposed to LD_{10} during the second instar was 5.75 ± 0.48 for the EO-base emulsion, 8.50 ± 0.87 for the EO, and 39.50 ± 1.71 eggs per plant for control treatment after 72 hours of oviposition.

Oviposition Preference

When exposed to sprayed leaves in a free-choice bioassay, females of *T. absoluta* preferred to oviposit on the control compared to the EO and EO-based emulsion ($F_{2,\,21} = 7.60$, $p = 0.003$). The average number of eggs on sprayed tomato leaves was 9.88 ± 1.55 for the EO, 7.50 ± 1.46 for EO-based emulsion, and 18.38 ± 3.05 eggs per female for control treatment after 24 hours of oviposition.

4. DISCUSSION

Innovative approaches that effectively reduce risks and hazards without losing efficacy and feasibility are of great appeal to attend agricultural concerns, as currently employed molecules are undoubtedly showing numerous drawbacks that have accelerated the replacement process. Therefore, essential oils have emerged as a promising, safe, and environmentally sustainable option for pest control (Lucia and Guzmán 2021). However, several characteristics restrict the practical applications of this type of molecule, most notably their high volatility, low water solubility, and low chemical stability (Gierer et al. 2019, Ramakrishnan et al. 2019, Upadhayay et al. 2020, Zhu et al. 2020).

This study demonstrated that an EO-based emulsion of patchouli showed similar lethal and sublethal effects in comparison with the pure EO for *T. absoluta*. The EO-based emulsion was formulated in a micro-scale emulsion, which has been assumed to be a promising alternative to overcome the main drawback associated with the handling, storage and application of essential oils (Barradas and de Holanda e Silva 2020, Lucia and Guzmán 2021). Formulation of oil-in-water emulsions confer more stability and availability of lipophilic molecules such as essential oils (Lucia and Guzmán 2021), ensuring sustained and controlled release of the active ingredients, solubilization of lipophilic substances, suitability for different ways of administration, protection from degradation, controlled volatilization, and reduction of side effects and dose (Barradas and de Holanda e Silva 2020).

The estimated lethal doses (LD50 and LD90) for the patchouli EO and its emulsion containing 18% of EO were equivalent. Thus, the emulsion has potential to be employed for the control of *T. absoluta* since it had a similar toxicity with 5.5 times less active ingredient. Probably, the advantages related to the use of an emulsion-based formulation conferred this equivalent toxicity between the two formulations.

In our study, it was not possible to quantify the lethal time for the pure essential oil since all individuals died within the first 10 minutes of assessment. Its then can be assumed that the TL50 for the pure essential oil is at most equal to 10 minutes, indicating that this compound has an extremely fast action. Based on this assumption, the emulsion would have a higher TL50 than the pure essential oil, that is, it has a comparatively slower action. However, the TL50 for the emulsion is only 3h, which is also very fast acting, and considering the active ingredient savings and overcoming of several drawbacks conferred by the emulsion formulation, this slight slower action becomes negligible.

Second instar *T. absoluta* exposed to LD_{10} of the patchouli essential oil and its emulsion presented similar responses on the oviposition of emerging females. Both formulations significantly reduced the average number of eggs laid by females on tomato plants. In fact, this substances are known to be capable of causing effects to various organs and compromise feeding (Shahzad and Manzoor 2021, Santos et al. 2022). In a recent study, Santos et al. (2022) observed several damages on the midgut of *Hypothenemus hampei* as a result of larval exposure to sublethal doses of essential oil and emulsion of *P. cablin*. Moreover, these authors associated the reduced oviposition of adults emerged from treated larva because of lower feeding during larval development. EOs are also known to affect reproduction due to changes in the structure and number of gametes produced, resulting in failed fertilization and unviability of eggs (Alves et al. 2014, Cruz et al. 2015).

In the free choice test, the mean numbers of eggs laid on tomato leaves treated with *P. cablin* EO and its emulsion were significantly lower than on control plants (acetone only), indicating both formulations conferred avoidance to oviposition. After exposing female adults of sweet potato whitefly, *Bemisia tabaci* biotype B, to plants sprayed with *P. cablin* oil, (Yang et al. 2010) observed a similar response. Reduced oviposition is a typical result of adults staying avoid settling on plants.

This study reveals that the essential oil of *P. cablin* and its emulsion, containing 18% of oil, present similar lethal and sublethal effects to *T. absoluta*. Both formulations presented appreciable toxicity against this leafminer,. Furthermore, larvae exposed to sublethal doses have its oviposition impaired at adult stage. When sprayed on tomato leaves, the EO and its emulsion also confer repellence to adults.

9. ACKNOWLEDGMENTS

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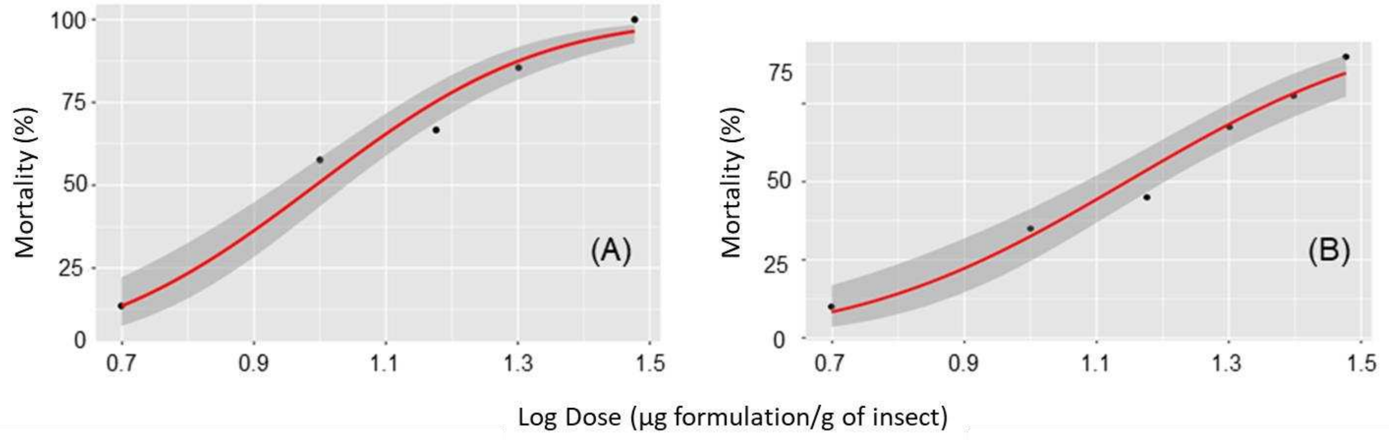

Treatment	n (number of insects)	LD50 (CI95%) – µg/mg	LD90 (CI95%) – µg/mg	slope	χ^2	*P*
Essential oil of patchouli	200	9.86 (6.95 – 12.5)	21.7 (16.4 – 38.7)	3.74	5.82	0.12
EO-based emulsion	240	14.0 (12.1 – 16.0)	36.2 (29.5 – 49.7)	3.10	2.37	0.67

Figure 1. Dose response curve for second instar larvae of *Tuta absoluta* exposed to the (A) essential oil of patchouli and the (B) EO-based emulsion (18%). Shaded areas depict the 95% CIs.

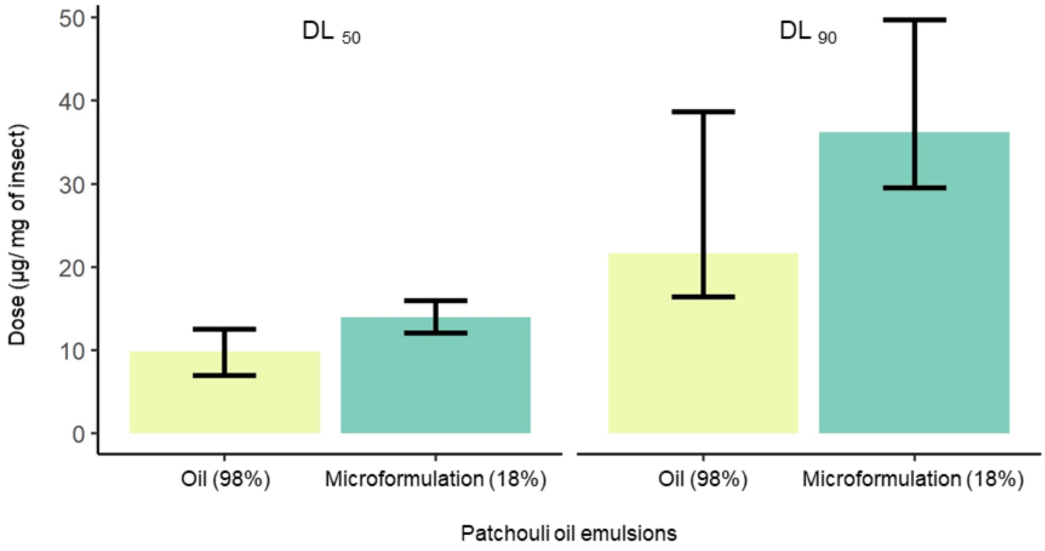

Figure 2. Lethal doses (LD50 and LD90) for second instar larvae of *Tuta absoluta* exposed to the essential oil (EO) of patchouli and the EO-base emulsion (18%).

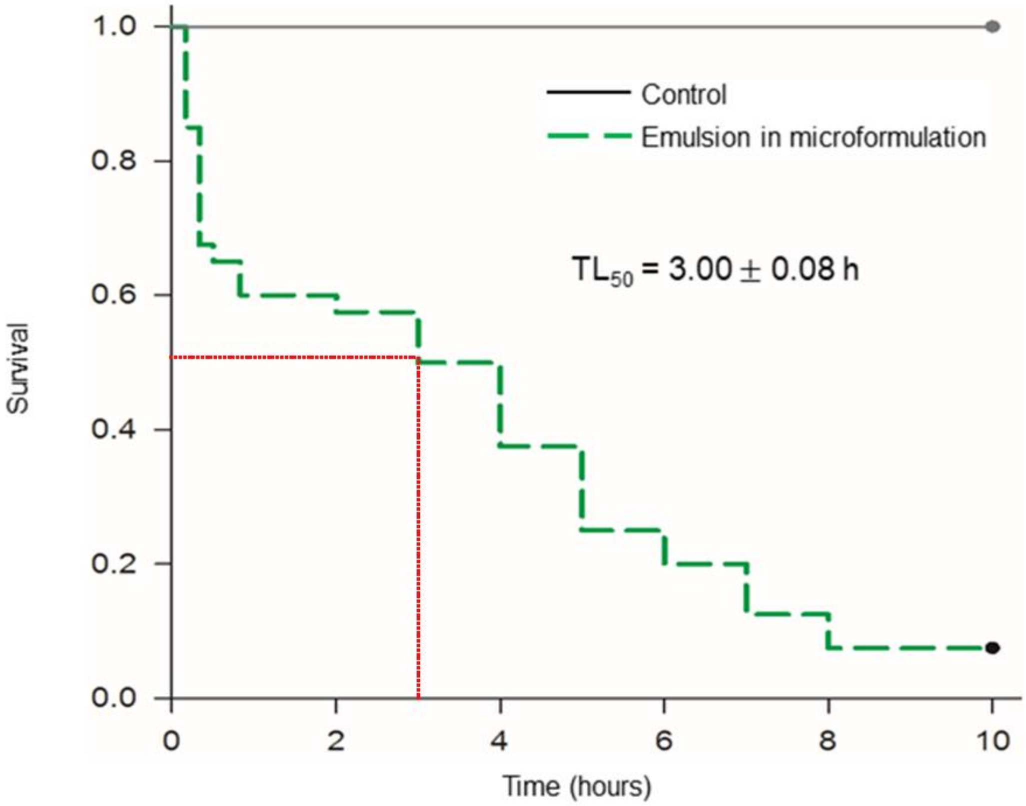

Figure 3. Survival curve for second instar larvae of *Tuta absoluta* exposed to the LD90 of the essential oil emulsion (18%). Dotted line indicates the LT50. The Kaplan–Meier survival analysis was performed to determine statistical differences between the curves.

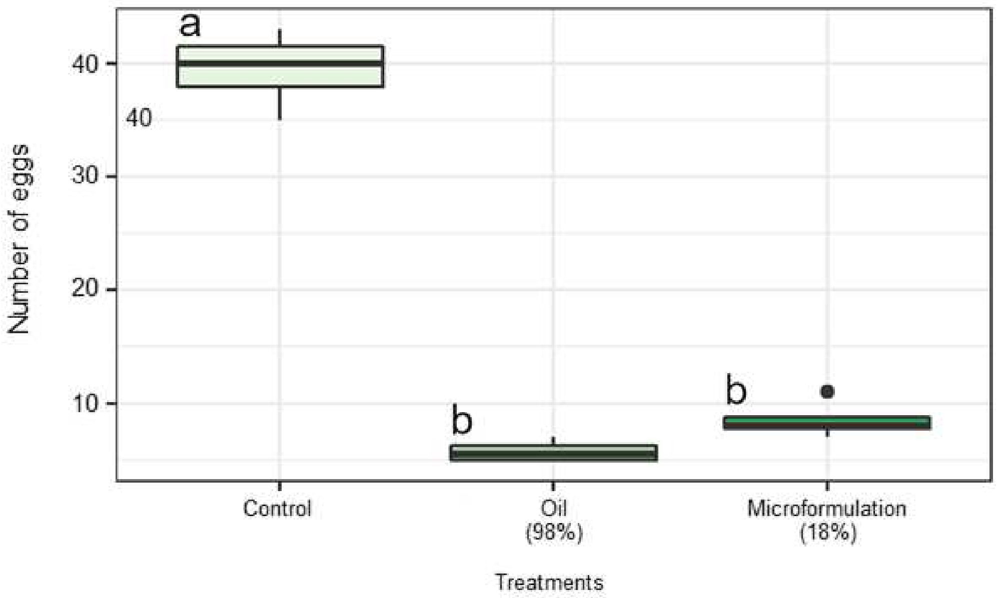

Figure 4. Oviposition of *Tuta absoluta* females submitted to acetone (Control), LD10 of patchouli essential oil and emulsion containing 18% of the oil during second instar. The treatments followed by the same letter are not significantly different according to the Tukey´s test (α = 0.05).

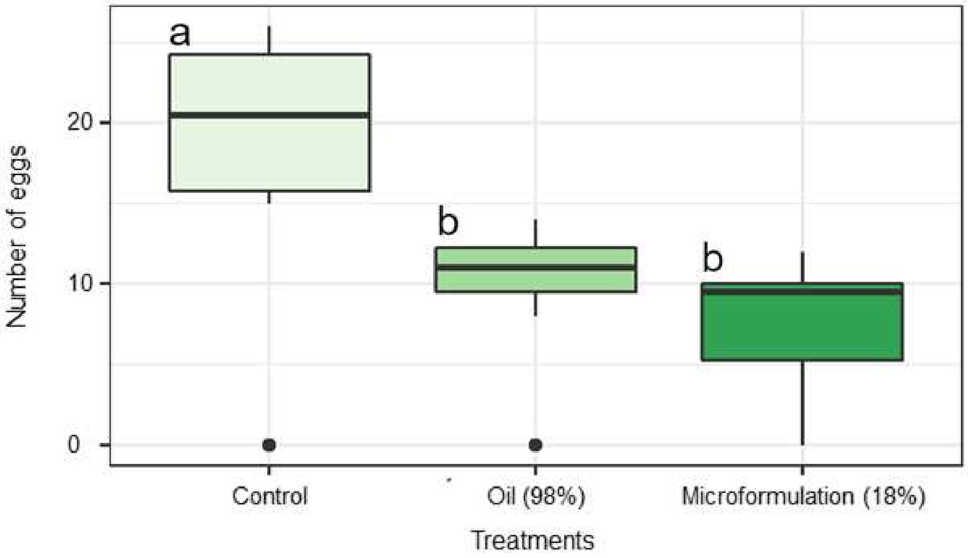

Figure 5. Oviposition preference of *Tuta absoluta* in tomato leaves sprayed with the control (acetone), 0.1% of patchouli essential oil, or 0.1% of the emulsion containing 18% of the essential oil, in free choice bioassay after 24 hours. The treatments followed by the same letter did not differ according to the Tukey´s test (α = 0.05).

6. GENERAL CONCLUSIONS

This study has provided evidence that *T. absoluta* has inhabited nearly all suitable climatic habitats in the invaded region that resemble its native range. Additionally, evidence was found that *T. absoluta* overcame bioclimatic obstacles and expanded its climatic range during the invasion process. Moreover, niche expansion is attributed as the primary cause of niche shift in this pest´s invaded range.

Reciprocal predictions showed that the potential distribution of *T. absoluta* changed significantly based on the source of occurrence records. According to these models, *T. absoluta* has not yet colonized all suitable climate-regions in Europe, Africa, and Asia. The majority of *T. absoluta* occurrences are in quasi-equilibrium, however a significant number of populations are apparently sink populations. Therefore, caution must be taken when selecting occurrence points for niche modeling studies.

The estimated LD_{50} for the EO of *P. cablin* and its emulsion was similar. Oviposition was reduced in adults derived from the second instar exposed to sublethal dose of EO or its emulsion. Both formulations conferred similar avoidance to adults when sprayed on tomato leaves.

Thus, this thesis contributed to the climatic niche, geographic distribution, and management of *T. absoluta* wordwide, and can be a starting point for future niche modeling studies and biosecurity protocols.