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Evidence of rapid spread and establishment of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in semi-arid Botswana

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Abstract

Background: *Tuta absoluta* (Meyrick), a major invasive pest of Solanaceous plants, was recently detected in Botswana. Abiotic and biotic factors, together with a suite of population demographic traits are likely key for species propensity and invasion success. First, we determined the movement of *T. absoluta* from its core detection centre to new invasion areas using pheromone baiting and established likely biotic dispersal drivers. Second, we measured thermal tolerance vis critical thermal limits and lower and upper lethal limits to determine how these traits shape population establishment.

Results: We detected *T. absoluta* in all 67 pristine sites across nine districts of Botswana. Within-district trap catches varied between cultivated and wild hosts but were generally not statistically significant ($P > 0.001$). We report three major wild host plants for *T. absoluta* as biotic dispersal drivers: *Solanum coccineum* (Jacq.), *Solanum supinum* (Dunal) and *Solanum aculeatissimum* (Jacq.). *Solanum coccineum* and *S. supinum* were omnipresent, while *S. aculeatissimum* distribution was sporadic. Thermal tolerance assays showed larvae were more heat tolerant, with a higher critical thermal maxima (CT_{max}) than adults ($P < 0.001$), whereas the adults were more tolerant to cold with a significantly lower ($P < 0.001$) critical thermal minima (CT_{min}) compared to larvae. The upper lethal temperatures ranged from 37–43 °C, whereas the lower lethal temperatures ranged from − 1 to − 12 °C for 0–100% mortality, respectively. In the light of prevailing environmental (habitat) temperatures (T_{hab}), warming temperature (7.29 °C) and thermal safety margin (22.39 °C) were relatively high.

Conclusion: *Tuta absoluta* may not be under abiotic physiological or biotic constraint that could limit its geographical range extension within Botswana. The ubiquity of wild Solanaceous plants with the bridgehead of year-round intensive monocultures of Solanaceous crops within a favourable climatic framework may mean that environmental suitability aided the rapid spread of *T. absoluta*.

Keywords: Tomato leaf miner, Insect invasion, Thermal tolerance, Global change, Solanaceous plants

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Background

Invasive species are a major threat to agroecosystems and global change [1, 2] and increased global connectivity [3] has drastically increased the diversity and magnitude of such invasions especially in the hot-dry Afrotropical region. Tomato leaf miner, (*Tuta absoluta*) (Meyrick) (Lepidoptera: Gelechiidae), is one of the most destructive insect pests of tomatoes globally [2, 4]. It is of South American origin and was first detected in Spain in 2006 [5, 6] before rapidly spreading and establishing in novel environments in the Mediterranean Basin, Europe, Middle East, South Asia (India), north, east and west Africa [5–9] and recently Southern Africa [10–12]. Because of its high reproductive potential, multivoltinism and potential to acclimatize to different climatic conditions [1], *T. absoluta* is currently considered a key limiting phytosanitary factor affecting the global Solanaceous crops value chain [13].

The larvae of *T. absoluta* feeds on all aerial parts of the plants including the fruits, resulting in significant yield losses and cosmetic damages as well as secondary infection [14, 15]. Characteristic larval mesophyll mining also compromises photosynthetic capacity of crops significantly reducing yields [14]. In the absence of control, yield losses ranging 80–100% have been reported in open and protected tomato fields [5]. A cost–benefit analysis has shown a significant increase in cost of production through high use of insecticides [2, 16], increased tomato market prices as farmers try to recover the high production cost, spatial prohibition of tomato seedlings and fruits trade [17] culminating into overall increased food and nutrition insecurity [18].

In tropical sub-Saharan Africa, irrigated tomatoes are an essential component of horticulture, a major pillar of sustainable development, with a significant contribution to food and nutritional security as well as household source of income especially for resource-poor farmers [18]. However, a major constraint to growing field horticultural crops in Southern Africa is the reduction in yield and quality caused by insect pests [19]. The potential invasion of Southern Africa by *T. absoluta* has already been described [1, 3, 6] with models based on its invasion history and global warming [20]. However, there are no reports based on field data on its thermal fitness and how this correlates with availability and distribution biotic resources, e.g. wild host plant species. Although *T. absoluta* survival on wild Solanaceae, Amaranthaceae, Fabaceae, Chenopodiaceae and Asteraceae plant families was reported, no report has so far combined this knowledge with its on-going invasive movement in the light of prevailing climate data.

For an invasive species to be established, it first has to overcome several environmental barriers [21] including

transport, introduction, population establishment and spread [22]. Upon introduction into a novel environment, high propagule pressure [23], species genetic and demographic characteristics [24] and physiological tolerance allow the establishment and habitat permeability [3]. Climate synchrony should exist between introduced areas' and species' environmental stress tolerance to allow successful spread during transience and niche occupation post-invasion [3, 25]. As such, physiologists often use species' thermal tolerance assays as proxy for determining potential for establishment of invasive species. Similarly, it has also been clear from modelling studies, that even when propagule material is high, environmental suitability remains an overriding factor for invasive species successful establishment [3, 23, 26]. Indeed, physiological assays have found use in niche modelling and invasive species risk assessments to determine critical risk invasion areas [27, 28]. *Tuta absoluta* is known to respond naturally to rapidly changing environments [29]. This is characteristic of successful invaders, which should inherently possess high basal and plastic physiological tolerance, including rapid genetic adaptive shifts [30]. Nevertheless [3], also show that native environmental heterogeneity may contribute to species invasive success. This means, species coming from a more heterogeneous environment may likely cope with a changing novel environment through phenotypic adjustment, compared to those coming from a more stable environment.

Temperature is the most important abiotic factor exerting direct and indirect effects on *T. absoluta* population dynamics [1] and consequently invasion success [31, 32]. Therefore, temperature forms a first abiotic 'ecological filter' [33] for successful invasion in a new environment [34], and failure to mount any compensatory mechanisms against it may result in the species failing to establish [35, 36]. The proximity of the environmental temperatures to species thermal physiological limits can therefore indicate species vulnerability and dispersal fitness [31]. Species introduced into habitats close to their thermal tolerance limits are more affected by environmental temperature [37] than those introduced into habitats far from their thermal tolerance limits.

Insects have been reported to experience multiple overlapping abiotic and biotic stressors such as temperature, starvation and desiccation in the wild [3, 38, 39]. Hence, an understanding of bioecology of invasive species is of paramount importance in enlightening mechanisms underlying the successful spread and establishment of invasive alien species [1, 40]. This will also involve determining how the invasive species may respond to native wild host plants. The availability and distribution of alternative wild (non-cultivated) host plants play a significant inoculum sink–source role across the novel landscapes

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[6]. Since its detection in Zambia [41], South Africa [10, 42] and Botswana [12], no work has documented *T. absoluta* spread and establishment across the biotic and abiotic frontiers. Here, we ought to establish whether *T. absoluta* was indeed spreading and elucidate the major environmental drivers to successful establishment in Botswana. We measured its thermal tolerance vis limits to activity (critical thermal minima [CT_{min}] and critical thermal maxima [CT_{max}]) and lethal limits (lower and upper lethal limits [LLT] and [ULT], respectively) and compared this with prevailing ambient climatic environment. Second, we investigated wild Solanaceous host diversity and linked this to *T. absoluta* invasion. To date, data on *T. absoluta* invasion potential in tropical climates have only been derived from modelling [1, 2]. No studies have looked at *T. absoluta* physiological thermal tolerance limits with field climate data to test the possible role of climate on its range expansion and spread. Similarly, no study has coupled physiological tolerance and its interaction with host availability on *T. absoluta* invasion pathway. The objective of this study was therefore to investigate whether *T absoluta* has spread and established from its core detection site across other pristine districts of Botswana, since its first detection [12]. Such information is important for pest risk assessments, niche modelling and may aid in developing phytosanitary regulations for effective invasive pest management.

Methods

Insect trapping and sites

Following the detection of *T. absoluta* at Genesis farm (S21.14776; E27.64744), Matshelagabedi village in the North East District of Botswana December 2016 [12], a follow-up surveillance trapping was conducted across 9 of the 10 districts of Botswana (Fig. 1). Traps were not set in Kgalagadi as it is largely part of the Kalahari Desert with very minimal vegetation, human settlement and agricultural activity. A total of 201 (67 sites with 3 traps per site) yellow delta traps (Chempac-Progressive-Agricare®) (Suider Paarl, South Africa) equipped with sticky pads were placed ~1 m above ground in tomato fields (cultivated host) and open forests (wild hosts) in each of the study districts during the hot-rainy summer season when the wild hosts were flourishing. High temperature, high relative humidity [1] and presence of the host [2] were reported to possibly enhance its propensity to spread. The major male-attracting synthetic sex pheromone (3E,8Z, 11Z)-3,8,11-tetradecatrienyl acetate (TDTA) loaded on grey rubber dispensers at a dosage of 110 μg per lure, (*Tuta absoluta*-optima PH-937-OPTI Russel IPM, Flintshire, UK) was used. Trap
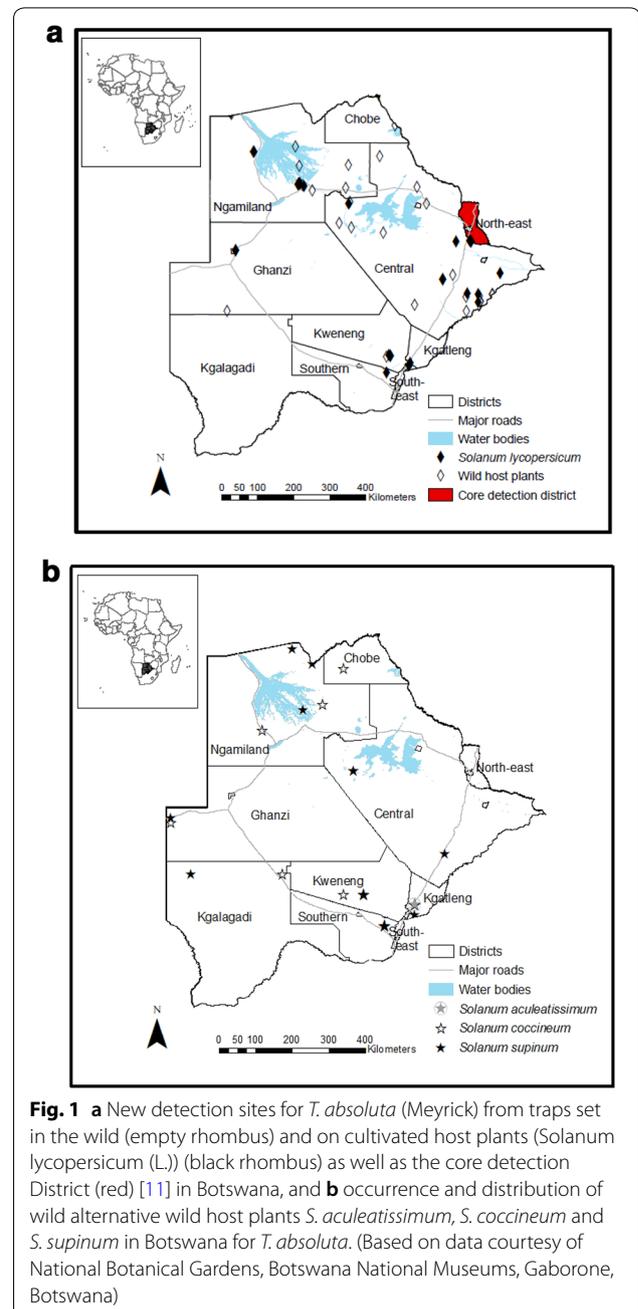

Fig. 1 **a** New detection sites for *T. absoluta* (Meyrick) from traps set in the wild (empty rhombus) and on cultivated host plants (Solanum lycopersicum (L.)) (black rhombus) as well as the core detection District (red) [11] in Botswana, and **b** occurrence and distribution of wild alternative wild host plants *S. aculeatissimum, S. coccineum* and *S. supinum* in Botswana for *T. absoluta*. (Based on data courtesy of National Botanical Gardens, Botswana National Museums, Gaborone, Botswana)

catch data were collected after ~30 days, and trapped moths were counted using dyed pointers (chopsticks dipped in insect dye) and mechanical (tally) counters following gross morphological identification [43]. Global Positioning System (GPS) points were recorded for each trapping site using a Garmin® (GPSMAP 62 model, Olathe, USA). Climate data for the sampling areas were obtained from the Meteorological Department, Ministry of Environment, Wildlife and Tourism (MEWT), Republic of Botswana.

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Basal thermal tolerance experiments
Insect culture
Larvae were collected on damaged tomato fruits into insect cages (BugDorm®, MegaView Science Co., Ltd. Taiwan) from Noka farm (North East District) (S21.12860; E27.48830), with a general temperature range of 3.4–35.5 °C; mean, mean minimum and monthly temperature range of 20.5–22.6 °C, 11.9–13.3 and 29.1–30.4 °C, respectively [44]. These were allowed to pupate in the laboratory in climate chambers Memmert® climate chambers (HPP 260, Memmert GmbH + Co.KG, Germany) set at 25 ± 1 °C, 65 ± 5% relative humidity (RH) and 12L–12D photoperiod. This laboratory rearing temperature closely approximated mean annual temperature from the environment from which the specimens were collected. Eclosed *T. absoluta* adults were placed in 25-cm³ clean cages, where they fed on 10% sucrose solution *ad libitum* using the cotton dental wick source method (a feeding apparatus for liquid-feeding insects; insects suck the liquid from a wet cotton wick that draws the solution through capillarity) and provided with organically produced tomato-fruiting plants to lay eggs. Experiments were conducted using fourth instar F_1 generation larvae and freshly emerged unsexed adults (± 2 days old). Sex was not considered a factor in our experiments since it has been reported not to affect thermal tolerance traits in some related species (e.g. [45–47]).

Lethal temperature assays
Lethal temperatures were determined using established methods as outlined in [48]. Upper and lower lethal temperatures (ULTs and LLTs) were determined using direct plunge protocol at 2-h duration at temperatures that elicited 0–100% mortality. Ten insects were placed in 60-ml polypropylene vials with gauzed lids and placed in a 33 × 22 cm ziplock bag, replicated three times. This was then plunged into a Merck® water bath (Modderfontein, South Africa) filled with 99.9% circulating ethanol. For ULT, tiny wet filter paper was suspended in each vial to maintain benign humidity and prevent desiccation-related mortality. Following treatment (ULT and LLT), test insects were placed at 25 ± 1 °C and 65 ± 5% RH in Memmert® climate chambers for 24 h before scoring survival. All insects had access to food and water *ad libitum* during the 24-h recovery period. Survival was defined as the ability to coordinate muscle response to stimuli such as gentle prodding, or normal behaviours such as feeding, flying or mating [48, 49].

Critical thermal limits (CTLs)
CTLs were assayed using a programmable waterbath (LAUDA Ecogold® RE 2025, Lauda-Königshofen, Germany) connected to a transparent double-jacketed chamber as outlined by [45]. A thermocouple (type K 36SWG) connected to a digital thermometer (Fluke 54 series IIB) was inserted into the central organ pipe (control chamber) to record chamber temperature. A total of ten test insects replicated three times to yield 30 replications per treatment were used in these experiments. Test insects were individually placed into the organ pipes of the double-jacketed chamber connected to a programmable water bath filled with 1:1 water: propylene glycol to allow for subzero temperatures [50]. Both CT_{max} and (CT_{min} experiments started from an ambient set point temperature of 25 °C from which temperature was ramped up (CT_{max}) or down (CT_{min}) at 0.25 °C/min until CTLs were recorded. Although it is likely faster than natural diurnal heating or cooling rates in the wild [45], this ramping rate was chosen as a compromise between ecological relevance and maximum throughput (see also discussions in [45, 51]). In this study, we defined CTLs as the temperature at which each individual insect lost coordinated muscle function and the ability to respond to mild stimuli (e.g. prodding with a thermally inert object).

Data analyses
New detection sites and the distribution of wild Solanaceous host plants were presented on maps (ArcGIS, ArcMap 10.2.2). Trap catch and thermal tolerance data analyses were carried out in STATISTICA, version 13.2 (Statsoft Inc., Tulsa, Oklahoma) and R version 3.3.0 [52]. CTLs met the linear model assumptions of constant variance and normal errors; therefore, they were analysed using one-way ANOVA in STATISTICA. LLT and ULT assays results did not meet the assumptions of ANOVA, and thus, they were analysed using generalized linear models (GLM) assuming a binomial distribution and a logit link function in R. Tukey–Kramer's *post hoc* tests were used to separate statistically heterogeneous means.

Warming tolerance (WT) and the thermal safety margin (TSM) of *T. absoluta* under Botswana conditions were calculated as outlined by [53]:

$$WT = CT_{max} - T_{hab} \quad [53]$$

$$\text{and,} \quad TSM = T_{opt} - T_{hab} \quad [53]$$

where CT_{max} = critical thermal maximum for *T. absoluta* adult (the migratory stage), T_{hab} = habitat temperature—Botswana mean annual temperature for 2015/16. T_{opt} = optimum temperature for *T. absoluta.*

Results
The spread of *T. absoluta* in Botswana
Apart from North East District, the area of *T. absoluta* first detection [12], the species was recorded in eight other districts (Fig. 1a). Moths were detected both in

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the wild (forests, grazing lands and national parks distant from agroecosystems) and on cultivated solanaceous crops; mainly tomato *Solanum lycopersicum* (L.). We detected *T. absoluta* in areas such as Moremi Island (Okavango Delta) more than 200 km from the nearest human settlements and agricultural activities and bordered by Moremi and Chobe Game Reserves) (Fig. 1a). Surveillance results support our hypotheses that *T. absoluta* spread and successfully established across Botswana (Fig. 1a).

Tuta absoluta wild host plants belonging to the Solanaceae family showed a cosmopolitan distribution (Fig. 1b). Wild host species diversity showed three dominant species; *Solanum aculeatissimum* (Jacq.), *Solanum coccineum* (Jacq.) and *Solanum supinum* (Dunal). *Solanum supinum* was the most widely distributed, occurring in all districts except only in Chobe, North-East and South-East and was found on the Moremi Island of the Okavango Delta (Fig. 1b) giving credence to the occurrence of *T. absoluta* in such a remote area. *Solanum coccineum* had more sporadic distribution, occurring in Chobe, Ngamiland, Ghanzi, Kgalagadi, Kweneng districts and the surrounding areas of the Okavango Delta. However, *S. aculeatissimum* was only found in Kgatleng district (Fig. 1b).

Moths abundance in wild and cultivated hosts

Large numbers of *T. absoluta* moths were captured in all districts, in both cultivated and wild hosts. The cultivated host, *S. lycopersicum* hosted significantly higher numbers ($P < 0.001$) (Table 1) than the wild host plants within districts, especially in Kweneng and Central districts (Fig. 2). Inter-district populations were also generally not significantly different within the same host type (Fig. 2). Overall, in the wild host plants, we recorded a grand mean of 411.1 ± 13.38 moths/trap/month from the cultivated *S. lycopersicum* which was significantly higher ($P < 0.001$) (Table 1) than 187.4 ± 12.21 moths/

Table 1 Differences in mean moth trap catches between cultivated *S. lycopersicum* and wild hosts and different districts in Botswana

Effect	SS	DF	MS	F	P value
District	443,092	8	55,387	3.5151	< 0.001
Host type	406,792	1	406,792	25.8168	< 0.0001
District*host	206,503	8	25,813	1.6382	> 0.05
Error	756,328	48	15,757		

Tests of significance were done using factorial ANOVA and Tukey's HSD test was used to separate statistically significant means at 95% CI

DF Degrees of freedom, *SS* sum of squares, *MS* mean sum of squares, *F* Fisher–Snedecor test statistic
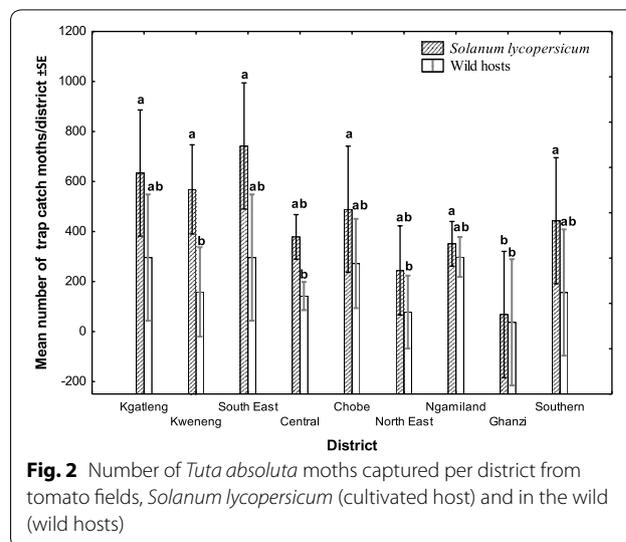

Fig. 2 Number of *Tuta absoluta* moths captured per district from tomato fields, *Solanum lycopersicum* (cultivated host) and in the wild (wild hosts)
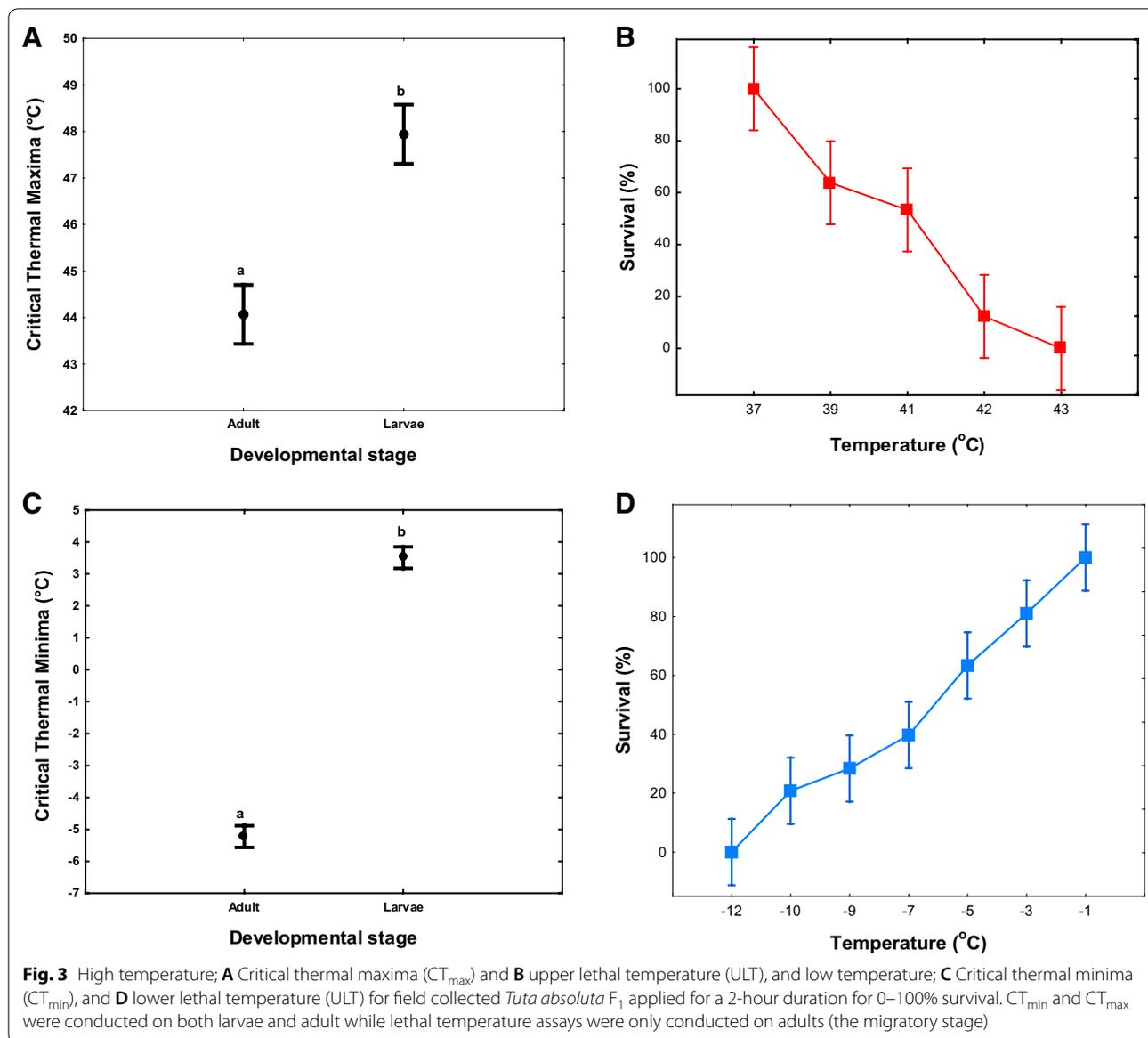
trap/month recorded from the wild hosts. High numbers were recorded on *S. lycopersicum* in Central, South-East, Chobe, Kgatleng and Southern districts and in tunnels compared to open fields in other districts. There were no significant interaction effects between the host plant and the district ($P > 0.05$) (Table 1) signifying that in each district host type was not a significant factor affecting abundance (trap catches).

Basal thermal tolerance

Both life stages of *T. absoluta* showed relatively high temperature tolerance although the larvae had significantly higher (47.9 ± 1.25 °C) CT_{max} than the adult (44.1 ± 0.43 °C) (Fig. 3A). The highest temperature where *T. absoluta* could not survive (ULT_0) was 43.0 °C, while the highest temperature for 100% survival (ULT_{100}) was 37 °C (for a 2-h stressful high-temperature exposure). There were significant differences ($\chi^2 = 107.29$, df $= 4$, $P < 0.001$) in survival between test temperatures, again signifying the role of temperature severity and duration in its survival (Fig. 3B). However, on low temperature tolerance, the adult had a significantly lower CT_{min} (-5.2 ± 0.23 °C) than the larvae (3.5 ± 0.07 °C) (Fig. 3C), and the LLTs ranged from -12.0 to -1.0 °C for LLT_0 and LLT_{100}, respectively, based on a 2-h duration at stressful low temperature (Fig. 3D). There were significant differences ($\chi^2 = 163.73$, df $= 6$, $P < 0.001$) in survival between the low test temperatures, implying that survival was determined by both temperature severity and duration of exposure.

Climate data and basal thermal tolerance

Field temperature data from eight districts of Botswana in 2015/2016 seasons (period post-first detection prior

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Fig. 3 High temperature; **A** Critical thermal maxima (CT_{max}) and **B** upper lethal temperature (ULT), and low temperature; **C** Critical thermal minima (CT_{min}), and **D** lower lethal temperature (ULT) for field collected *Tuta absoluta* F_1 applied for a 2-hour duration for 0–100% survival. CT_{min} and CT_{max} were conducted on both larvae and adult while lethal temperature assays were only conducted on adults (the migratory stage)

to and during establishment and spread of *T. absoluta*) are shown in Fig. 4a and b. The mean monthly maximum temperatures ranged from a low of 22.3 °C (Kweneng district) to a high of 37.4 °C. (South-East district) (Fig. 4a). Highest maximum field temperatures were below *T. absoluta* CT_{max} by about 6 °C (adults) and above 10 °C (larvae). Relating ULTs to the field maximum temperature data showed that the *T. absoluta* ULT_0 of 43 °C (Fig. 4a) was well above the highest maximum temperatures recorded in nature (37.4 °C; Fig. 4a), implying that *T. absoluta* was not under high-temperature-related physiological stress that could limit its spread and establishment.

The mean monthly minimum temperatures ranged from a low of 1.1 °C (Kweneng district) to a high of 21.3 °C in December 2015 (Ngamiland district) (Fig. 4b). The lowest minimum field temperatures were above *T. absoluta* adult CT_{min} by about 6 °C (adult) and below that of the larvae by about 2.4 °C (see Fig. 4b). This implied that the minimum field temperatures were not physiologically constraining survival of *T. absoluta* adult but the larvae. Adult *T. absoluta* LLT_0 was − 12.0 °C, while LLT_{100} was − 1.0 °C for a 2-h stressful low-temperature exposure (see Fig. 3D). Both temperatures fell well below the most extreme low temperatures recorded in the environment (see Fig. 4b), implying that adult *T. absoluta*
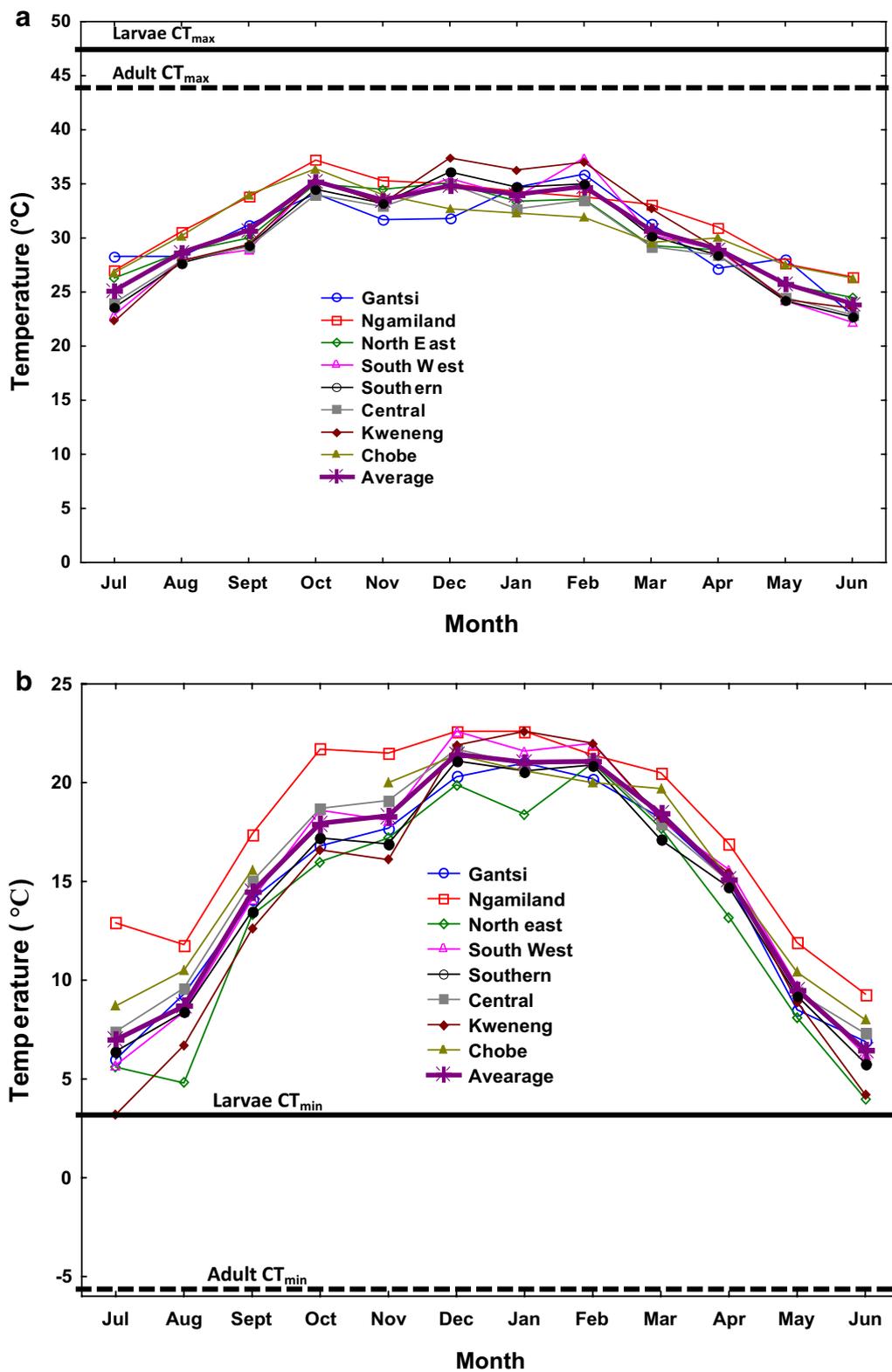
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Fig. 4 Field temperatures, **a** mean monthly maximum temperatures and **b** mean monthly minimum temperatures for eight districts of Botswana in 2015/16 season related to *T. absoluta* CT_{max} and CT_{min}, respectively. Horizontal lines denote CT_{min} and CT_{max} for larvae (continuous) and adult (dotted)

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may not be under diurnal low-temperature physiological stress.

Warming tolerance (WT) and thermal safety margin (TSM)

The annual mean temperature for Botswana in 2015/2016 was 22.71 °C considered in this study as the habitat temperature (T_{hab}), and the optimum temperature for *T. absoluta* performance and population growth is 30 °C [54] considered as T_{opt}. The adult CT_{max} was recorded as 44.1 °C (see "Basal thermal tolerance" section). Based on these data, the warming tolerance (WT) and the thermal safety margin (TSM) of *T. absoluta* under Botswana conditions were calculated according to [53]:

$$WT = 44.1\ ^{\circ}C - 22.7\ ^{\circ}C$$
$$WT = 22.39\ ^{\circ}C$$

and similarly,

$$TSM = 30\ ^{\circ}C - 22.71\ ^{\circ}C$$
$$TSM = 7.29\ ^{\circ}C$$

Discussion

Following its first invasion in Botswana in December 2016 [12], our results confirm that *T. absoluta* has spread and successfully established in almost all districts of Botswana, thus potentially eliciting widespread economic damage to Solanaceous crops. Although *T. absoluta* was first recorded in North east district of Botswana, evidence from this work suggest its rapid and wide extension of its distribution horizons with new records reported in various districts in the country within an 8-month period (January to August 2017) (Fig. 1). Indeed, this trend is not unusual for the species [2]. The species has been reported to spread at a rate of ~ 800 km/year aided through wind currents and plant material belonging to families Amaranthaceae, Convolvuceae, Fabaceae, Malvaceae and Solanaceae identified through volatile cues by female moths for egg laying [2]. Therefore, the observed rapid spread and successful niche establishment may be directly linked to the reported availability of host plants in the wild [3], climate suitability and physiological thermal tolerances [26]. These characteristics are consistent with other globally invasive economic insect pest species, e.g. *Chilo partellus* (Swinhoe) [55], *Bactrocera dorsalis* (Hendel) [56], *Ceratitis capitata* (Wiedemann) [57] and *Drosophila suzuki* (Matsumura) [58]. Our results associated *T. absoluta* with a wide range of cultivated and wild host plants [as in example 2, 59], consistent with polyphagic characteristic of many invasive species [22]. *Tuta absoluta* thermal activity physiological thresholds examined here also suggest that there is a conducive climate niche across the country and that species activity and

hence invasion may not be constrained by temperature. Our survey showed Botswana hosts wild solanaceous plants: *S. aculeatissimum*, *S. coccineum* and *S. supinum*, which are all suitable hosts to *T. absoluta* [see 2, 15]. Amongst these wild host plants, *S. supinum* was the most widely distributed, occurring in all districts of the country, while *S. coccineum* and *S. aculeatissimum* distribution was sporadic. Therefore, it is highly likely that these wild host plants provide biotic resources, (food and shelter) supporting the invasion pathway of *T. absoluta* in Botswana. Although tomato is the preferred host for *T. absoluta,* the species can switch hosts from cultivated to wild as a survival strategy, a notion supported by [5] and [60]. Such availability of biotic resources and suitable environmental conditions are also known to impair diapausing in *T. absoluta* larvae [1] resulting in increased breeding propagule pressure even under less favourable climate conditions, with implications on niche invasion success.

Short-distance dispersal (adjacent field to field or field to tunnels) of *T. absoluta* is known to be facilitated by wind especially soon after introduction [13] with moths capable of active flights of up to 100 km [59], a characteristic that may aid the species' dispersal [2, 32, 61]. Pressure distribution from the Indian Ocean was reported to traditionally create strong east-westerly air masses in the Southern African region [62]. This supports the possible movement of *T. absoluta* through wind currents from the north-east district (core detection district) to the central, southern and western parts of the country. On the other hand, long-distance dispersal may occur through open tomato trade, markets and other related activities [32]. These attributes together may to a larger extent have promoted the spread and establishment of *T. absoluta* propagule moths which could easily locate either cultivated or wild hosts during dispersal. However, the detection of *T. absoluta* in Moremi Island (Fig. 1a); (~ 200 km from human settlements and agroecosystems) suggests that wind and wild host plants might have played a more significant role in its invasion success.

High populations of *T. absoluta* were recorded on *S. lycopersicum* in Central, South-East, Chobe, Kgatleng and Southern districts (Fig. 2) where production of tomatoes is done in tunnels. The reason may be that the moths were contained within tunnels and hence highly concentrated resulting in the observed high trap catches. Amongst these districts, South-East recorded the highest moth catches. The district is a horticultural hotspot with high concentration and prolonged availability of the cultivated host plants (tomato, green and red pepper) which hosts *T. absoluta*. Since production of tomatoes is carried out throughout the year in this district, the tunnels also act as inoculum reservoirs that form bridgeheads for

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further introduction and reinfestation of outdoor cultivated and wild host plants [1–3]. Similarly, relatively high *T. absoluta* moths were recorded in the wild (Fig. 2) signifying its ability to survive outside the cultivated host plant ranges (agroecosystems). This therefore nullifies the possibility of controlled production of Solanaceous crops as a management measure against *T. absoluta*, as has been the case, e.g. *Pectinophora gossypiella* (Saunders) in cotton [63].

Native environmental heterogeneity may also contribute to invasion success [3]. Propagules from a more heterogeneously stressful environment are more adaptable to multiple stressful conditions [64] and, together with other factors, may work synergistically towards the succession of ecological filters [reviewed in 3]. Climate matching between the native and novel environment is known to aid invasion success of invasive alien species [30, 65, 66]. Interestingly, African biotic and climatic conditions are closely related to *T. absoluta's* native region [1]. Insect species have specific optimum temperatures at which they optimally perform and develop [31, 37]. In addition, lower and upper developmental thresholds mark the temperatures beyond which they cannot perform and develop [31, 37, 67]. As such, basal environmental stress tolerance, phenotypic plasticity and rapid genetic adaptive shifts are key to invasive species establishment [30]. *Tuta absoluta* tolerance to temperature and relative humidity versus typical Botswana climate [68] may form the primary characteristics defining its range expansion [1, 37, 68]. Prior predictions using climatic suitability indices defined the eco-climatic index (EI) of Botswana to fall within 20–50, classified as high risk of establishment for *T. absoluta* [1]. Our results are thus in agreement with this prediction. Climatic conditions (chiefly temperature) are known to significantly influence generation numbers of multivoltine insects, with higher temperatures facilitating faster degree day accumulation and shorter generation times [69]. At an optimum temperature of 30 °C, the life cycle of *T. absoluta* ranges approximately 26 days [53] accounting to ~12 generations per year [2]. Global warming comes with increased mean temperatures and variability thereof and is reported to increase insect metabolism [70]. With African temperatures projected to increase, future populations of this pest may likely increase in tropical relative to temperate regions [1]. Botswana is arid to semi-arid with mean monthly maximum temperatures recorded in 2015/2016 season ranging 23.6 to 35.1 °C (Fig. 4a). Given that the optimum temperature for *T. absoluta* is 30 °C [54], a TSM of 7.29 °C was relatively high [37, 53]. This signifies that *T. absoluta* can tolerate an increase in atmospheric temperature of 7.29 °C from current Botswana ambient environmental temperatures of 22.71 °C

(T_{hab}) before its population growth and general performance can drop to critical levels. This is a considerably high TSM compared to most tropical species whose TSM is ~0 °C [53]. This, coupled with a wider WT (22.39 °C), further supports that Botswana environmental temperatures were conducive for the performance, rapid spread and establishment of *T. absoluta*. The lower and upper developmental threshold for *T. absoluta* is ~14 and 34.6 °C, respectively [54], translating to a wide thermal window (~20.6 °C) which is known to optimize key insect activity and life-sustaining behaviours such as development, mating and dispersal [3, 55], and may potentially facilitate the invasion pathway of *T. absoluta*. Thus, conducive climatic conditions might have chiefly facilitated the rapid accumulation of degree days hence culminating into shorter generation time. This high reproductive capacity may also have contributed to its increased invasion success in novel environments in the country [as in 1].

Improved environmental tolerance and thermal plasticity are the key contributing factors towards invasion success of invasive alien species into a novel environment [30, 39, 71]. Lower and upper lethal temperatures (LLT and ULTs) for *T. absoluta* adults ranged from −1 to −12 °C and 37 to 43 °C respectively for 2 h treatments. In addition, the CT_{max} for larvae and adults were 47.9 ± 1.25 and 44.1 ± 0.43 and CT_{min} were 3.5 ± 0.07 and -5.2 ± 0.23 respectively. Field temperature recorded during 2015/2016 season show that highest maximum temperatures were below both ULT and CT_{max} for both *T. absoluta* larvae and adults. In addition, LLTs and CT_{min} for adults were relatively lower than the lowest minimum field temperatures (Fig. 4b). This, added to the high TSM and WT, indicates that *T. absoluta* may not be at risk of cold and heat stress both of which has an implication on the invasion succession pathway. These results supports that *T. absoluta* is highly temperature tolerant at both extremes and may survive in arid/semi-arid sub-Saharan Africa whenever hosts plants are available. Its high basal thermal tolerance, coupled by favourable climates in Botswana (Fig. 4a and b), may mean that *T. absoluta* survives all-year-round temperature conditions, in the absence of diapause, a characteristic likely aiding successful establishment. Furthermore [38], showed rapid cold hardening may also aid invasion success in insects, and indeed *T. absoluta* has been shown to rapidly cold-harden [see 2], a phenomenon likely aiding the invasion pathway. The absence of native coevolved natural enemies has also been reported to promote invasion success in novel environments [5, 64]. It is highly likely that the rapid spread and establishment of *T. absoluta* in Botswana may have been facilitated by the absence of biological control agents. We thus recommend that native fortuitous

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natural enemies need be identified and promoted coupled with a campaign against the instinctive overuse of pesticides by small scale farmers [19] to preserve potential native natural enemies, reduce cost of production and protect public health. Further work needs to determine *T. absoluta* insecticide resistance to establish a controlled effective spraying program, coupled with the identified effective natural enemies to establish an efficacious tailor-made integrated pest management (IPM) program. Overall, an area-wide approach to *T. absoluta* management is recommended, and one that involves a coordinated Southern African region, to prevent further spread and establishment of the species [2].

Conclusion

Current results support the rapid spread and establishment of *T. absoluta* in Botswana following its first detection. This continued invasion by *T. absoluta* in tropical climates is a real concern for the horticultural industry, as well as African food and nutrition security. Host plant availability, climate suitability and high thermal tolerance may to a larger extent have contributed to the successful invasion, rapid spread and establishment of *T. absoluta* in the semi-arid tropical Botswana. In addition, intensive monocultures, continuous irrigation and unrestricted trade of Solanaceous crops coupled with strong winds and a lack of natural enemies may also be contributory factors. Furthermore, absence of efficient and coordinated area-wide management practices may have exacerbated the successful rapid invasion. A significant long-term management strategy would be necessary to optimize surveillance and monitoring of *T. absoluta* in the region for developing sustainable management options. Similarly, introduction of egg-targeting parasitoids (*Trichogramma spp.*) and predators as well as larval parasitoids (mostly belonging to Braconidae families) and predators (Miridae) [2, 14] could improve management of African suppression programmes, more especially in non-agroecosystem and natural environments.

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