



Distribution, degree of damage and risk of spread of *Trioza erytreae* (Hemiptera: Triozidae) in Kenya

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Abstract

The African citrus triozid (ACT), *Trioza erytreae* Del Guercio, is a destructive pest particularly on citrus, and vectors, “*Candidatus*” *Liberibacter africanus* (CLaf), which is the causal agent of the African citrus greening disease. Our study seeks to establish the distribution and host-plant relationship of ACT across citrus production areas in Kenya. We also modelled the risk of spread using the maximum entropy modelling algorithm with known occurrence data. Our results infer that ACT is widely distributed and causes severe damage to four alternative host plants belonging to the family Rutaceae. The adults, immature stages (eggs and nymphs), galls and the percentage of infested leaves were significantly higher in shaded than unshaded trees. However, adult ACTs preferred Kenyan highlands to Victoria Lake and coastal regions. The average area under the curve of the model predictions was 0.97, indicating an optimal model performance. The environmental variables that most influenced the prediction were the precipitation of wettest quarter, precipitation of wettest month, mean diurnal range, temperature seasonality and mean temperature of the coldest quarter. The current prediction of ACT exceeded its existing range, especially in the Western, Nyanza, Central, Rift valley and Eastern regions of Kenya. The model predicted a contraction of suitable habitats for a potential spread in 2040 with an inland shift to higher altitudes in the cooler regions. The potential for further expansion to climatically suitable areas was more pronounced for the 2080 forecast. These findings provide relevant information to improve monitoring/surveillance and designing IPM strategies to limit its spread and damage.

KEYWORDS

African citrus triozid, climate change, damage levels, integrated pest management, risk assessment

Sétamou, Ekesi and Borgemeister equally contributed to the manuscript.

1 | INTRODUCTION

Citrus spp. (Sapindales, Rutaceae) includes some of the world's major fruit crops recognized for global availability and contribution to food and nutritional security (Liu, Heying, & Tanumihardjo, 2012). Citrus ranks first internationally in trade value among all fruits (UNCTAD, 2013). The most commonly known species of commercial importance are sweet orange (*Citrus sinensis* (L.) Osbeck), lemon (*Citrus limon* (L.) Osbeck), lime (*Citrus aurantifolia* (Christm.) Swingle), grapefruit (*Citrus paradisi* (Macfad.) and mandarin orange (*Citrus reticulata* (Blanco)) (FAOSTAT, 2018). Sweet orange is the main species, cultivated globally, and represents more than 65% of the total citrus output (FAOSTAT, 2018; Khamis et al., 2017). Annual global production of citrus was 146,429,018 tonnes in 2016, with sweet orange cultivars contributing to more than half of the world's total approximately 85,233 tonnes produced from 7,268 ha of land in Kenya (FAOSTAT, 2018). Although the majority of these fruits produced are consumed locally as fresh products, a smaller quantity of the Kenyan citrus is processed into juices, jam and marmalades (MMA, 2008). Yet, local market demand is so high that the production is currently supplemented by imports from South Africa and Egypt, the leading citrus producers in Africa (Chadwick, 2017; MTI, 2017), which represent 5%–21% of the domestic consumption (MMA, 2008; Tschirley, Muendo, & Weber, 2004).

Citrus greening disease is associated with three nonculturable Gram-negative bacterial strains belonging to "*Candidatus*" Liberibacter, identified through 16S rDNA sequence analysis (Bové, 2006). The main bacteria species are "*Candidatus*" Liberibacter africanus (CLaf), from Africa, "*Candidatus*" Liberibacter asiaticus (CLas), originally from Asia, and "*Candidatus*" Liberibacter americanus (CLam), from Brazil. Asian form of citrus greening or Huanglongbing (HLB) is associated with CLas that has largely displaced CLam in Brazil while CLaf is the causal agent of the African citrus greening disease (ACGD; Cocuzza et al., 2017). These phloem-limited greening pathogens are transmitted from infected to uninfected plants through grafting or by citrus psyllids (Gottwald, 2010). "*Candidatus* Liberibacter africanus" is transmitted mainly by the African citrus triozid (ACT) *Trioza erytreae* Del Guercio prevalent in Africa (Ajene et al., 2019; Aubert, 1987; Khamis et al., 2017) and more recently in Europe (Cocuzza et al., 2017; Hernández, 2003; Moll & Vuuren, 1977), while CLas and CLam are transmitted by the Asian citrus psyllid *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Liviidae) prevalent in Asia and America (Ammar, Ramos, Hall, Dawson, & Shatters, 2016; Chiyaka, Singer, Halbert, Morris, & Bruggen, 2012). The main symptoms of ACGD-infected trees include yellow shoots, leaves with blotchy mottle, small lopsided fruits with a curved central core and bitter taste, whereas infected branches show twig die-back and affected trees progressively decline and eventually die (Lee et al., 2015). Currently, there is no known cure for both forms of the disease (Gottwald, 2010), hampering citrus production in Kenya,

particularly in the highlands (Ekesi, 2012). However, efforts to manage the disease vectors include use of quarantine measures, introduction of natural enemies, chemical control and removal of infested/infected trees (Cocuzza et al., 2017; Van den Berg, 1990).

African citrus triozid, native to Africa, was detected for the first time in Kenya in 1922 (Khamis et al., 2017; Waterston, 1922). It is the only species of triozids (Hemiptera: Triozidae) that attacks citrus and induces pit-like galls on leaves (Cocuzza et al., 2017; Hodkinson, 1984, 1984). Although direct damage from ACT feeding can be significant, the economic importance of the pest stems from its ability to vector CLaf (Aidoo, Tanga, Khamis, et al., 2018; Aubert, 1987) and CLas (Ajene et al., 2019). Currently, ACT is a major pest categorized as an "A1" quarantine pest by CABI (2004).

The seasonal population fluctuations of ACT follow the flushing rhythm of the citrus host (Cook, Maqutu, & Vuuren, 2014). However, flush abundance is an inconsistent indicator of the mean density of *T. erytreae* per flush shoot as stated for *D. citri* a close relative of ACT (Hall, Hentz, & Adair, 2008). Large infestations of adult *T. erytreae* in citrus orchards can occur at any time of the year, depending on the environmental factors and flush availability (Catling, 1972; Cook et al., 2014; Green & Catling, 1971; Samways, 1987). The females lay their eggs exclusively on newly emerged flush shoots on which immature life stages of ACT complete their development. The adults can live up to three months and even under drought conditions can still survive on their host plants (Van den Berg, 1990). During the citrus off-season, alternative hosts are essential breeding sites for ACT. In South Africa, four such Rutaceae alternative hosts, namely *Clausena anisata* (Willd.) Hook. f. ex Benth., *Vepris lanceolata* (Lam.) G. Don, *Zanthoxylum capense* (Thunb.) Harv. and *Orcia* sp., were reported (Aidoo, Tanga, Paris, et al., 2018; Van den Berg, 1990) and recommended similar investigations in other pest-affected areas. In addition, *T. erytreae* population fluctuation is driven by various climatic factors including temperature, vapour pressure deficit, rainfall and light (Cook et al., 2014).

Better understanding of the biotic and abiotic factors influencing the biology and population dynamics of ACT could facilitate the development of models to predict the spread of the pest and develop appropriate control strategies. Despite ACT status as a major pest and disease vector of citrus in Africa, there is scant information on its distribution, abundance, infestations in different citrus-growing areas of East Africa, and prediction of potential areas at risk of possible invasion. Hence, modelling the current distribution and forecasting areas at risk of ACT invasion are central for the development of its management strategies and spread prevention plans. Various species distribution models (SDS) have been used to describe and estimate the ecological pattern and areas at risk of pest invasion across time and space (Elith & Leathwick, 2009). Maximum entropy (MaxEnt; Phillips, Anderson, & Schapire, 2006) is one such model widely used to project current and future distribution of pests at different time periods (Elith & Leathwick, 2009) because of its better predictive performance compared to other modelling algorithms (Elith et al., 2006) even with reduced numbers of samples (Pearson, Raxworthy, Nakamura, & Townsend, 2007). In addition, MaxEnt

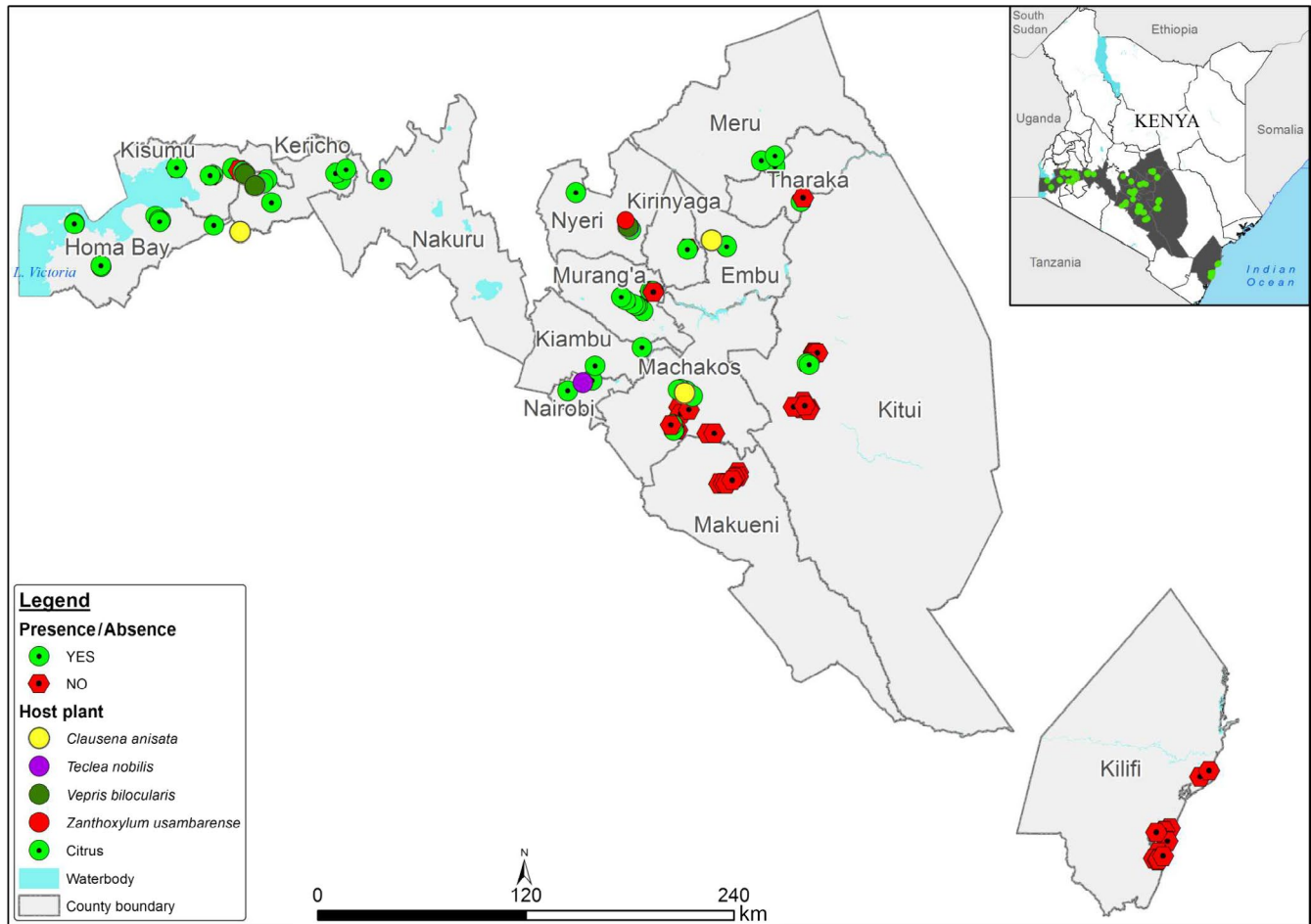


FIGURE 1 Map showing sites where *Trioza erytreae* was sampled and alternative host plants [Colour figure can be viewed at wileyonlinelibrary.com]

models perform better when presence- or absence-only data are available (Phillips et al., 2006). Knowledge of the geographical distribution, abundance, pest damage, the number of individuals present, when, and why they are found at a given location is essential for the development of appropriate and effective management strategies. Understanding the distribution of insects is crucial because it fills the knowledge gap of the biology and ecology of the species and enhances the development of reliable sampling plans (Binns & Nyrop, 1992) that are often prerequisites for the implementation of effective IPM strategies. Hence, our goal was to evaluate ACT's biological parameters including its distribution, population densities and damage levels in different citrus-growing regions of Kenya to inform on the development of appropriate IPM strategies. We also attempted a prediction of suitable climatic areas for ACT invasion.

2 | MATERIALS AND METHODS

2.1 | Data collection

To determine the geographical distribution, population densities, leaf damage levels (galls) and climatic areas suitable for ACT, field surveys were conducted from December 2015 to April 2018 in the

different citrus-growing regions of Kenya (Figure 1). During these surveys, data were collected on numbers of ACT adults and immature stages (eggs and nymphs), and percentage of leaves showing galls symptoms. Sampling was carried out in home gardens, commercial and small-scale orchards in the high-, mid- and lowlands to cover a wide range of altitudinal breadth (Figure 1). In total, data collected from 30 orchards spread across 11 counties were used for our analysis: Nairobi (2), Murranga'a (2), Kirinyag'a (1), Meru (2) Nyeri (1), Embu (3), Kericho (5), Kisumu (2), Tharaka (1), Machakos (2) and Homa Bay (9). The sites selected in the present study were based on the availability and accessibility of citrus orchards and being major production areas in the country. In each county, at least one orchard from different sub-counties was selected. However, the sampling technique used was the same for each orchard. In each orchard, ten trees were randomly selected within the orchard, that is five trees under shade and five unshaded trees (in the open). A tree was considered "shaded" when the canopy received full shade from the canopy of another tree (taller one), and "unshaded" when a tree was fully exposed in the open and was directly exposed to the sun. In addition, ACT abundance and degree of damage were determined along a defined transect, namely coastal (Kilifi County), highlands (Kericho Country) and Victoria Lake (Homa Bay County) regions.

The orchards in the coast, highlands and around Victoria Lake regions had elevations ranging from 10 to 100 m, 1,100 to 1,300 m and 1,300 to 2,316 m, respectively. In each region, five orchards were randomly selected, and the procedure described above was followed for sampling.

The survey was conducted when there were profuse flush shoots based on the description by Cifuentes-Arenas, Goes, Miranda, Beattie, and Lopes (2018) namely phase 1 (emergence) consisting of one stage (V1), phase 2 (development) consisting of two stages (V1 and V2), phase 3 (maturation) consisting of two stages (V4 and V5) and phase 6 (Dormancy) consisting of only one stage (V6). Each groove was visited once. We followed the general procedure outlined by Sétamou, Flores, French, and Hall (2008) with slight modifications. The canopy of each tree was divided into four cardinal points (Northeast [NE], Northwest [NW], Southeast [SE] and Southwest [SW]) using a hand-held analog plastic compass (Suunto-A10 NH measuring $56 \times 104 \times 10$ mm with 2.5° and 2° accuracy and resolution, respectively). In each quadrant, five flush shoots as described by Catling (1969) and Sétamou et al. (2008) were randomly selected, that is NE, NW, SE and SW for a total of 20 flush shoots per tree. The number of ACT galls per shoot, number of leaves per shoot, number of leaves with ACT galls (triozid pits), number of all the developmental stages, host plant type, geographical locations, host plant species, and the environment (shaded/unshaded) of the tree were recorded for each location. At least 10 shoots from each of the alternative host plants were randomly sampled and counted for adults, immature stages (eggs and nymphs) and galls. The occurrence of immature stages (eggs and nymphs) and/or galls of ACT in each of the sites was an indication of infestation, as reported in previous studies using galls per shoot as a reasonable proxy for ACT presence (Aubert, 1987).

2.2 | Data analysis

The data on percentage flush shoots with triozyd galls/pits and the number of ACT adults and immature stages (eggs and nymphs) on the different citrus cultivars namely Citrumelo (*Citroncirus* spp.), Lemon (*C. limon*), Tangerine (*C. tangerina*), "Washington navel" and "Valencia" (both *C. sinensis*) were analysed using nested mixed model which takes into account all the random factors associated with hierarchical sampling. This was followed by an analysis of deviance using the chi-square distribution. Akaike information criteria (AIC) was used to confirm the accuracy of the model (Cifuentes-Arenas et al., 2018). When significant, means were separated using Tukey's HSD. Shade and unshade, and cultivar (host species) were the treatments. Trees were considered as replicates because they were independent units, whereas quadrants were sub-samples. For the alternative host plants, count numbers of ACT developmental stages and galls per shoot on different alternative host sampled were $\log(x' = \log(x + 1))$ transformed and subjected to analysis of variance (ANOVA) followed by Student-Newman-Keuls (SNK) test. Analyses were conducted in R software (R Development Core Team, 2008).

2.3 | Model development

To predict the full ecological range of ACT, we fit its geographic expansion models using MaxEnt based on presently available occurrence data and climate data for Kenya downloaded from the Bioclim data set (Fick & Hijmans, 2017). To minimize multicollinearity among predictor variables (Merow, Smith, & Silander, 2013) and also reduce overfitting and underfitting of the suitability map of the species (Kuhn, 2008; USGS, 2004), we performed a Pearson correlation test between all the predictors (Bioclim variables) and elevation data from the United States Geological Survey 30m SRTM data set using the find correlation function in caret package in R Statistical Software (version 3.4.4). From the Pearson correlation analysis, at a threshold of $r > 0.7$ (Dormann et al., 2013), the number of bioclimatic variables was reduced from 19 to five, namely Bio2 (Mean Diurnal Range), Bio4 (Temperature Seasonality), Bio11 (Mean Temperature of Coldest Quarter), Bio13 (Precipitation of the Wettest Month) and Bio16 (Precipitation of the Wettest Quarter), which were least correlated were selected for running the final MaxEnt model.

For simulation of the ACT distribution, current climatic conditions at 1-km grid resolution from the Bioclim data set were used (Fick & Hijmans, 2017). This data set contains grids of temperature, rainfall and derived bioclimatic summary variables, which represent annual trends, seasonality and limiting environmental factors. For running the MaxEnt model, the presence data and the six predictor variables were used with 30% of the presence samples used for testing and the remaining 70% used for validation. For prediction of distribution under future climatic condition simulations, down-scaled global climate models (GCMs) HadGEM2-ES data, based on the Representative Concentration Pathways Scenarios, Fifth Assessment Report (RCPs-AR5; IPCC, 2013) future year 2055 (mean over 2041–2070) were considered. We used future climate simulations from Bioclim to project future scenarios, and due to the absence of vegetation projection, we assumed vegetation and topography to be unchanged over the projection period. The same six variables were used to run the MaxEnt models for future scenarios to generate the suitability maps.

3 | RESULTS

3.1 | Distribution, abundance and damage levels

African citrus triozyd was found in all citrus-growing areas sampled except Makueni and Kilifi counties (Figure 1). Our results show that ACT was widely distributed and caused severe damage to four alternative host plants belonging to the Rutaceae family. The sites surveyed in Makueni and Kilifi had elevations ranging from 1,000 to 1,100 and 20 to 300 m above sea level (m. a. s. l.), respectively. The other citrus-growing sites visited had elevations ranging from 10 to 2,315 m. a. s. l. There were significant differences between the citrus cultivars and the mean number of eggs, nymphs, adults and percentage leaves infested with galls (eggs: $F = 14.106$, $df = 4$, $p < 0.0001$, nymphs: $F = 3.869$, $df = 4$, $p = 0.0042$, adults: $F = 3.927$,

TABLE 1 Number of *Trioza erytreae* and infestation on shoots of five citrus cultivars selected from different compass quadrants

Cultivar	Eggs	Nymphs	Adults	Galls	% Infested leaves
Lemon	15.55 ± 3.67b	35.02 ± 6.33b	0.87 ± 0.21b	155.06 ± 12.53b	20.28 ± 1.1b
Tangerine	0.00 ± 0.00c	0.61 ± 0.10d	0.00 ± 0.00d	223.59 ± 44.2a	22.83 ± 2.46b
Valencia	12.85 ± 5.87b	36.82 ± 7.2ab	1.29 ± 0.39a	143.27 ± 17.56b	18.1 ± 2.46c
Washington navel	32.54 ± 4.96a	18.67 ± 2.82c	0.80 ± 0.20b	124.99 ± 8.73b	18.51 ± 1.45c
Citrumelo	45.7 ± 14.04a	128.2 ± 25.84a	0.30 ± 0.20c	258.93 ± 39.62a	36.19 ± 2.90a

Note: Across each host plant species (column), means followed by different letters are significantly different (Tukey's HSD).

$df = 4$, $p = 0.004$ and percentage leaves infested with galls: $F = 4.079$, $df = 4$, $p = 0.0032$). However, galls counted on the different cultivars showed significant level of variation ($F = 1.154$, $df = 4$, $p = 0.0187$; Tables 1 and 2). All stages (ACT), galls and percentage leaves infested with galls significantly varied between shaded and unshaded trees (eggs: $F = 12.917$, $df = 1$, $p = 0.0003$, nymphs: $F = 9.295$, $df = 1$, $p = 0.0023$, adults: $F = 4.927$, $df = 1$, $p = 0.026$; Figure 2). Also, the number of galls and percentage leaves infested with galls was significantly higher in the shaded trees than unshaded ones (galls: $F = 42.655$, $df = 1$, $p < 0.0001$, percentage leaves infested with galls: $F = 53.039$, $df = 1$, $p < 0.0001$). The mean number of eggs, nymphs and galls did not significantly differ among the different ACTs alternative host plants (Table 3).

The results clearly showed that ACT (all stages) varied across the different regions. The mean numbers of adults and developmental stages were significantly and consistently higher in the Kenyan highlands compared to the orchards in the coastal and Victoria Lake regions (eggs: $F = 71.015$, $df = 2$, $p < 0.0001$; nymphs: $F = 128.77$, $df = 2$, $p < 0.0001$; adults: $F = 80.033$, $df = 2$, $p < 0.0001$; galls: $F = 136.49$, $df = 2$, $p < 0.0001$; Table 4 and Figure 3).

3.2 | Current and future scenarios

Model predictions indicate that rainfall conditions were more important than other variables in creating the map. The possible future distribution map based on the current climate and occurrence data of ACT is shown in Figure 4a. The model predicts most areas

in the Western, Nyanza, Rift valley and Central regions to be unsuitable habitats for ACT. In addition, some few areas in the coastal and Eastern regions were predicted with low possibility of an ACT spread.

The two future predictions showed variable results (Figure 4b,c). The 2040 climate change model (4b) predicts a contraction in suitable climate areas while the 2080 prediction (Figure 4c) an expansion of the pest's ecological niche. For the 2040 scenario, there was a substantial reduction in the suitable habitat areas for ACT throughout the counties with a noticeable shift, particularly in the Eastern and coastal regions. A similar observation was made in most of the counties in Rift valley and Central regions of Kenya. Moreover, for the 2040 scenario, there was an inland shift of the potential distribution range of ACT in the Western, Nyanza and Central regions. In some parts of Rift valley and Eastern regions, there was a decline in areas suitable for ACT in the 2040 prediction. There was a considerable expansion of potentially suitable climate areas under the 2080 scenario, particularly in the regions.

The model performance for ACT was better than random, with a training area under the curve (AUC) and test values of 0.946 and 0.926, respectively, for the current scenario (Figure 5). The 2040 prediction gave 0.939 and 0.929 for training and test data, respectively, while 0.936 and 0.956 were recorded for training and test data for the 2080 scenario; hence, the model performed well in predicting the potential habitats of the pest. A maximum training sensitivity plots specificity threshold value of 1.720 from the 10th percentile training presence occurrence of the psyllids was recorded. Among

TABLE 2 Nested analysis of variance of African citrus triozid infestation levels and densities as affected by citrus host plant, site, tree and canopy quadrant in Kenya

Source of variation	No. of eggs	No. of nymphs	No. of adults	No. of galls	% Leaves infested
	% Variance component (random effects)				
Random effects					
Sub-county	19.24	30.56	16.52	23.84	22.57
Quadrant	0.35	0	0.52	1.22	0.91
Tree	0.25	3.26	0.93	1.23	1.48
Residual	80.16	56.18	82.07	73.7	75.05
Fixed effects					
Cultivar (error ddf)	249.33	471.16	229.49	215.57	235.17
Environment (error ddf)	1,054.13	1,060.48	1,066.73	1,068.90	1,068.88

Note: Variance components are unbiased estimates obtained using linear mixed model in R software (*lme4* package). errorddf = denominator (error) degree of freedom.

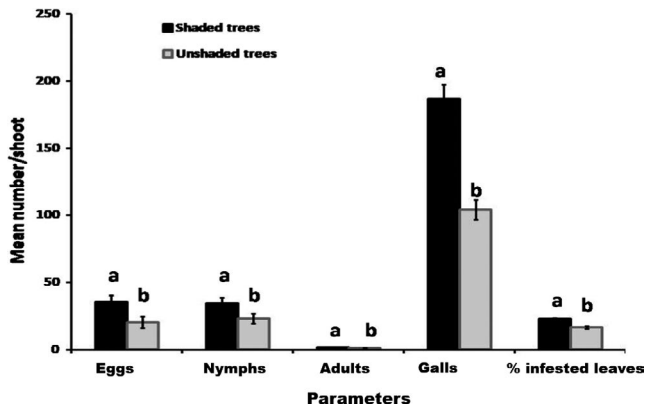


FIGURE 2 Mean number of *Trioza erytreae* and infestation levels on shaded and unshaded citrus tree

the climatic variables, the percentage contribution varied from each other (Table 5). Precipitation of the wettest quarter contributed to 77.8% of the current, 53.1% to 2040 and 50.0% to 2080 scenarios, while precipitation of the wettest month contributed 8.6%, 30.5% and 38.2% for current, 2040 and 2080 distribution of ACT, respectively. These two factors explain about 86%, 83% and 88% for the current, 2040 and 2080 models, respectively. Elevation contributed to 6.5%, 5.3% and 6.0% for current, 2040 and 2080 scenarios, respectively. Mean temperature of the coldest quarter contributed the least with 0%, 0.2% and 0% for current, 2040 and 2080 predictions, respectively (Table 5).

TABLE 3 Number of *Trioza erytreae* and level of damage on alternate host plants

Parameters	Host plants			
	<i>Clausena anisata</i>	<i>Teclea nobilis</i>	<i>Vepris bilocularis</i>	<i>Zanthoxylum usambarense</i>
Eggs	146.29 ± 18.11	106.05 ± 14.04	81.70 ± 13.04	90.50 ± 16.24
Nymphs	72.36 ± 15.11	63.20 ± 14.84	40.02 ± 9.09	78.90 ± 17.21
Adults	2.12 ± 0.42a	1.75 ± 0.45ab	1.20 ± 0.30ab	0.30 ± 0.15b
Galls	123.40 ± 21.18	75.70 ± 19.21	72.48 ± 14.48	66.70 ± 9.79

Note: Within each row, means followed by different letters are significantly different while means without letters are not significantly different (Tukey's HSD). Parameters: eggs, nymphs and galls are not significantly different across host plants.

TABLE 4 Nested analysis of variance of ACT infestation levels and densities as affected by transect (highlands, coastal, Victoria Lake regions)

Source of variation	No. of eggs	No. of nymphs	No. of adults	No. of galls
	% Variance component (random effects)			
Random effects				
Tree	7.55	2.277	12.042	3.277
Quadrant	0.19	0	1.46	0.352
Cultivar	21.19	31.04	23.64	3.759
Environment	7.54	18.471	0.551	2.337
Residual	63.55	48.213	63.082	89.28
Fixed effects				
Site (error ddf)	591.97	594.56	584.16	499.31

Note: Variance components are unbiased estimates obtained using linear mixed model in R software (*lme4* package). errorddf = denominator (error) degree of freedom.

4 | DISCUSSION

4.1 | African citrus triozid distribution, abundance and damage levels

Adults, eggs, nymphs and damage symptoms of ACT appear to be widely distributed in Kenya, and the pest seems to be more prevalent in lower temperatures. In the hot and humid Makueni and Kilifi Counties, no adult ACT, immature stages or symptomatic leaves were recorded in all the orchards visited. A combination of factors including suitable habitats, host plant, natural enemies, diseases and heritable traits has been reported to influence the distribution and establishment of a species in a new area (Wallner, 1987). This can further be explained by the fact that ACT eggs are highly vulnerable to desiccation and as such might not have been able to hatch, develop and establish in these dry habitats where temperatures were high with low relative humidity (Green & Catling, 1971). This suggests that, in addition to elevation, other factors can influence ACT's distribution and abundance. Citrus farms in Kilifi County were not infested by ACT, possibly because of the prevailing high temperatures as reported above. However, these areas are perfectly suitable for *D. citri*, ACT's Asian counterpart, which is more adapted to warmer climates as shown in recent invasions in Kenya and Tanzania (Rwomushana et al., 2017; Shimwela et al., 2016).

During our field survey, it was observed on several occasions that ACTs activities were higher in the Southeast quadrant of the

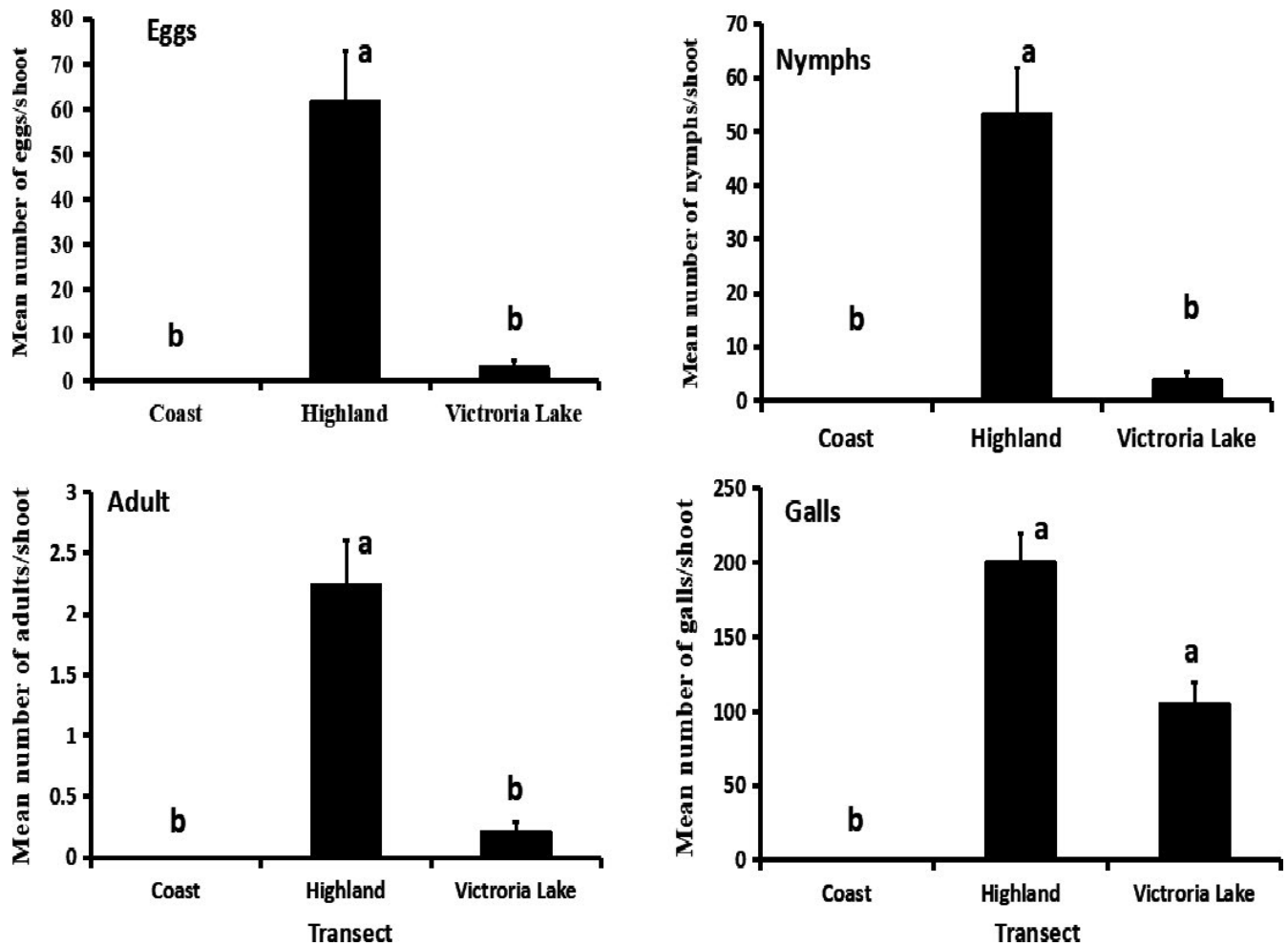


FIGURE 3 Distribution of *Trioza erythrae* adults and developmental stages along the coastal, highlands (Kericho county) and Lake Victoria (Homa Bay) regions in Kenya

tree. Directional preference of ACTs in citrus orchards has previously been reported in Spain where the south-facing sides of the citrus trees were preferred by ACT relative to other directions, though the authors did not examine the canopy quadrant of the trees (Cocuzza et al., 2017). Considerable high numbers of adults, galls per shoot and percentage infested leaves were observed in the SE quadrant, which corroborates findings by Sétamou et al. (2008), who reported similar findings on *D. citri* in citrus groves. The authors speculated that, at the latitude in South Texas where the study was conducted, the SE side groves and tree canopy were more illuminated than other sides. However, further investigation is warranted to clearly elucidate our observation and the preference of SE side of trees and groves by both ACT and *D. citri*.

An earlier study reported that ACT prefers leaves of lemon over other host plants for reproduction (Aidoo, Tanga, Paris, et al., 2018; Moran, 1968; Moran & Buchan, 1975). However, we found higher mean numbers of ACT immature stages (eggs and nymphs), galls and infested leaves on citrumelo than on the other cultivars, which might be partially attributed to volatiles produced by citrumelo. This is consistent with results of Fancelli et al. (2018) who demonstrated a positive relationship between host plant volatiles and attraction

of *D. citri* to its preferred host plants. Additional studies to address ACT-citrumelo volatiles and their attraction are crucial to understanding the underlying mechanisms involved in their preference for feeding and oviposition on this host and for the development of attractants for ACT. Although volatiles have been implicated in the attraction of psyllids for feeding and reproduction, other factors such as the nutritional status of the host plant cannot be overlooked. For instance, Sétamou, Graça, and Sandoval (2016) observed that *D. citri*, when raised on different host plants, showed considerable variation in terms of feeding and reproductive preferences.

Apart from these, several other factors are well documented to strongly influence the abundance of ACT, key among them are availability of young soft shoots and the quality of the host plant (Cocuzza et al., 2017). Similarly, studies on ACT population dynamics revealed that peak population densities coincided with the flushing of the citrus tree (Cook et al., 2014). In addition, ACT can disperse and identify new flush shoots over more than 500 m (Van den Berg & Deacon, 1988). It is worth noting that, in the absence of a suitable foliage, ACT can only survive for a few hours (Catling, 1973) before dying from desiccation (Van den Berg & Deacon, 1988). The densities of different ACT immature stages and damage levels (galls

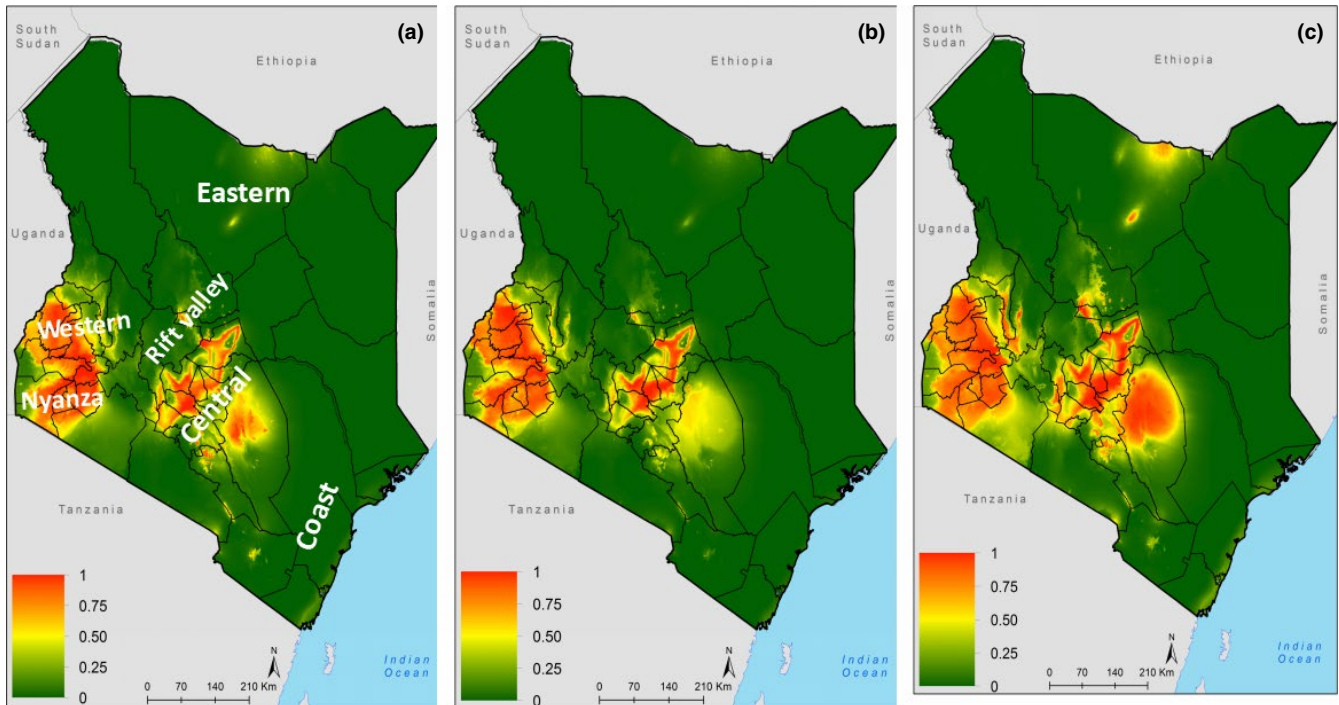


FIGURE 4 Map showing the current suitable (warm) and unsuitable (green) climate areas at risk of *Trioza erythrae* incursion; current scenario (a), future scenarios 2040 (b) and 2080 (c). According to the potential distributional index in the legend: 1 represents optimal suitable conditions for establishment; 0.75 represents highly suitable conditions for establishment; 0.50 represents suitable conditions for establishment; 0.25 represents marginal conditions for establishment; and 0 represents unsuitable conditions for establishment [Colour figure can be viewed at wileyonlinelibrary.com]

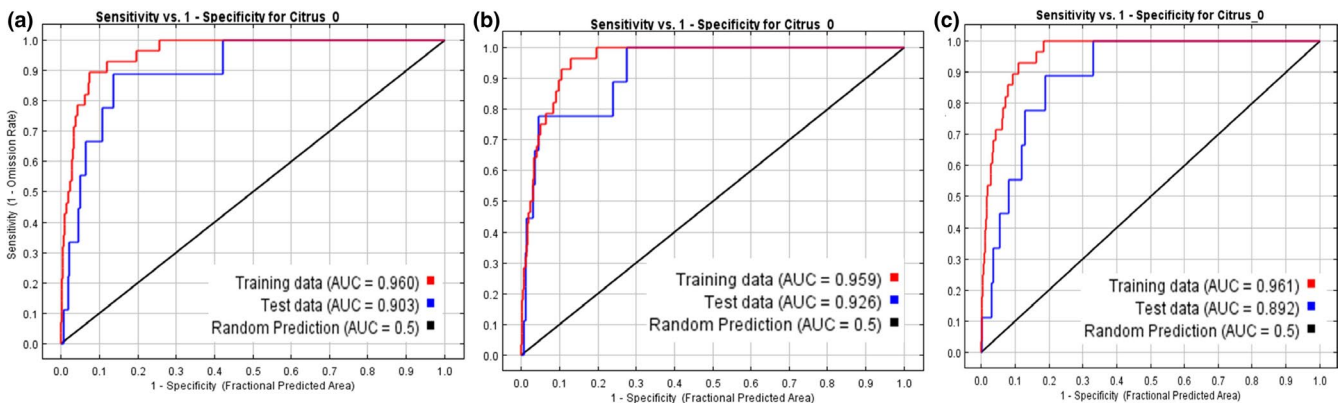


FIGURE 5 ROC curve and area under the curve value under the current period for a (current), b (2040) and c (2080) [Colour figure can be viewed at wileyonlinelibrary.com]

per shoot and infested leaves) were significantly higher in shaded than unshaded trees when compared across the citrus cultivars and canopy quadrants. This is probably attributed to greater exposure to sunlight and consequently higher temperatures in unshaded trees. Both ACGD and ACT favour cooler and moist climates, which for the latter are more suitable for oviposition and the development of the immature stages (Catling, 1973; Schwarz & Green, 1970).

Additional psyllid species were also recorded on *Stephania abyssinica* (Quart. -Dill. & A.Rich.) (Menispermaceae) during the spatial survey. There was a difficulty in identifying the species due to

contradictory reports associated with the identity of psyllids on *S. abyssinica*. However, from molecular research by Khamis et al. (2017), these psyllid species on *S. abyssinica* were grouped into ACT. Similarly, Kalyebi et al. (2015) claimed to have found ACT on *S. abyssinica* in Uganda based purely on presence of pit galls. Moreover, a study by Abate (1988) on identity and bionomics of insect vectors of tristeza and greening diseases of citrus in Ethiopia found and grouped psyllids on *S. abyssinica* and other non-rutaceae plants into ACT. Contrarily, a study by Label et al. (2007) separated these psyllids from ACT as undescribed species. Also, a study on Afrotropical

Environmental variables	Per cent contribution			Permutation importance		
	Current	2040	2080	Current	2040	2080
Precipitation of wettest quarter (mm)	77.8	53.1	50	88.7	27.5	56.8
Precipitation of wettest month (mm)	8.6	30.5	38.2	0.5	48.6	23.7
Elevation (m)	6.5	5.3	6	0.7	0	0.6
Mean diurnal range (mean of monthly (max temp – min temp)) (°C)	6.1	9.8	5.5	9	19.1	16.1
Temperature seasonality (standard deviation*100) (°C)	0.9	1	0.2	1.1	2	2.7
Mean temperature of coldest quarter (°C)	0	0.2	0	0	2.7	0.2

TABLE 5 Estimates of contribution and permutation importance of environmental variables in MaxEnt modelling of *Trioza erytreae*

jumping plant lice of the Triozidae family (Homoptera: Psylloidea) notes *T. catlingi* Hollis and *T. menispermicola* Hollis on *S. abyssinica* (Hollis, 1984). Specifically, Aubert, Garnier, Cassin, and Bertin (1988) put *Trioza* spp. described on *S. abyssinica* into a different psylla species. Also, a recent study by Aidoo, Tanga, Khamis, et al. (2018) confirmed that ACTs reproduction was confined to rutaceous alternative host plants. This clearly suggests that this is likely a morphologically near identical psyllid to ACT but quite possibly not the same species, or a subspecies only infesting this host plant. However, this requires further investigation.

From our survey data, *T. erytreae* population levels significantly varied across the coast, highlands and Victoria Lake regions. Densities of adults, immature stages and galls were significantly higher in the highlands compared to those in Victoria Lake and coastal regions. Our observation could be attributed to different climatic conditions across the regions. Higher temperatures and prolonged drought periods are associated with high mortality rates in ACT (Green & Catling, 1971; Van der Merwe, 1941).

4.2 | Current and future scenarios

Species distribution models have been extensively used to describe a range of applied and theoretical ecological issues (Peterson et al., 2011). Although there are many available techniques, MaxEnt is widely used (Elith et al., 2006). We used ACT presence-only data to model the current and future potential habitats under different climate change scenarios. Although rainfall appears to be the key factor limiting ACT's distribution, high temperatures prevent its establishment, particularly in the Kenyan lowlands. Temperature and precipitation are known to influence species distributions at broad scales (Weins, 2011). In addition, the distribution of ACT and the pathogen it transmits are restricted to cool habitats that are below 30°C (Bové, 2006; Cocuzza et al., 2017). High temperature coupled with low humidity has been shown to increase ACT egg and nymphal mortality (Samways, 1987).

The abundance of ACTs in the Kenyan highlands suggests a shift of citrus production from lowlands to highlands due to its ability to adapt to low temperatures. However, the recent introduction of *D. citri* in the Kenyan lowlands (Roberts, Steenkamp, & Pietersen, 2015; Rwomushana et al., 2017) puts this recommendation into question. Similarly, a recent study in Ethiopia by Ajene et al. (2019) showed CLAs in field populations of *T. erytreae* indicating a potential spread of both citrus greening pathogens (CLaf and CLAs). Although CLAs vectored by ACT has not been reported in Kenya, management strategies to curb the introduction and spread of CLAs by ACTs to the Kenyan high- and midlands due to a rise in international trade through introduction and exchange of plant materials require an urgent attention (Siverio et al., 2017). A follow-up study on ACTs distribution in mainland Europe a year after an initial survey showed a rapid rise in the distribution range of the pests posing a serious threat to the citrus-growing regions in Europe (Arenas-Arenas, Duran-Vila, Quinto, & Hervalejo, 2019). A similar study is required for ACT in Kenya.

Our results indicate a possible change in the current and future distributions of ACT. As the climate changes, some areas that are presently suitable for the pest and/or where ACT occurs may become unsuitable. Our findings suggest that the areas not suitable for ACT incursion could be suitable for ACT invasion and vice versa. The model accurately predicted many suitable habitats at risk of possible spread. For instance, our model accurately predicted Bungoma County which was not covered by the present survey as suitable climate areas. This agrees with an earlier study by Kilalo et al. (2009) which reported the highest percentage orchard infestations in Bungoma County. However, the ability of a species to establish outside its distributional range depends on a wide variety of other factors: natural enemies (predators, parasitoids and fungi), vegetation of the area, and presence of its host plant, as well as anthropogenic activities. All these factors need to be further investigated to better understand the ecology and potential risk of spread of this devastating pest across different citrus agroecosystems.

5 | CONCLUSION

The present study highlights the importance of citrus cultivars susceptibility to ACT and their influence on the distribution of the pest within the tree canopy with more shaded trees prone to heavy ACTs attack than unshaded ones. The reasons for higher preference for shaded trees remain largely unknown, although studies have shown that *T. erytrae* is sensitive to hot, dry condition and favours cool, moist areas, which might warrant closer attention. This implies that ACTs are cool tolerant, which explains why they were predominantly distributed in the highlands of Kenya compared to Lake Victoria and the coastal regions of Kenya. However, the proportion of the regions predicted to be climatically suitable for ACT is slightly broader for the future scenario, suggesting that the pest will be more tolerant to a wider range of climatic conditions over time towards the coastal plains. This raises major concerns for the regional horticulture industry as *D. citri* has been recently reported in the region, which tend to have high invasive powers and probably higher potential to out-compete ACT. This implies that ACT and *D. citri* are of significant concern to biosecurity agencies in the uninvaded regions. These concerns are further compounded by low phytosanitary skills in the region. However, our findings provide important information to enhance monitoring/surveillance and to design local, regional and national-level phytosanitary and integrated pest management strategies to curb the spread and potential establishment of these species in Kenya and beyond.

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CONFLICT OF INTEREST

The authors have declared that there exists no conflict of interest.

AUTHORS' CONTRIBUTIONS

OFA, SA, CB, SE, SFM, FK, IR and CMT conceived the idea and contributed to subsequent reading. OFA wrote the first draft. OFA, BR, AA and CB contributed to data collection and proofreading. OFA,

JK and CB involved in data analysis and contributed to subsequent reading.

ETHICAL APPROVAL

This study was not undertaken in national parks or any protected areas. It was carried out in home gardens, commercial and small-scale citrus orchards, which were potentially infested by ACT. No specific permission was required for these experiments or collections due to the studies not involving endangered or protected species. This article does not contain any studies with human participants or animals performed by any of the authors.

INFORMED CONSENT

Informed consent was obtained from all the participants involved in the study.

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