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The Asian Citrus Psyllid (*Diaphorina citri*) in Africa: using MaxEnt to predict current and future climatic suitability, with a focus on potential invasion routes

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The Asian Citrus Psyllid (ACP) (*Diaphorina citri* Kuwayama, 1908) (Hemiptera: Psyllidae) is a major citrus pest. The species has been introduced to West and East Africa, but has not yet spread to southern Africa, where it could have a devastating impact on citrus farming and livelihoods. A proactive response is key to mitigating the species' impacts, particularly the ongoing monitoring of potential invasion routes and entry points into South Africa. Species distribution models (SDMs) were developed under current and future climates for ACP in Africa, and these models were used to (1) determine where the species likely poses a threat, (2) identify potential invasion routes into South Africa, and (3) assess how these factors will be affected under climate change. The SDMs indicated that there is an almost contiguous band of suitable climate along the east coast of Africa that joins the species' current range in East Africa to South Africa, and under aggressive climate change a potential route of invasion through Namibia and Botswana. Much of South Africa is climatically suitable for the species, but under climate change, climatically suitable areas are likely to shift further inland. The spread of ACP into South Africa is unlikely to be prevented, but the outputs of the present models will inform monitoring activities and assist with preparations to respond to this predicted biological invasion.

INTRODUCTION

Diaphorina citri (Kuwayama, 1908) (Hemiptera: Psyllidae), commonly referred to as the Asian Citrus Psyllid (ACP), is a major agricultural pest of citrus globally (Grafton-Cardwell et al. 2013; Hall et al. 2013) (Figure 1; Figure 2). The psyllid is native to Asia, but currently has a large invasive distribution, particularly in North and South America and West and East Africa. The psyllid is a vector of multiple species of phloem-limited bacteria, *Candidatus Liberibacter* spp., which cause citrus greening disease (Huanglongbing; HLB) (Stelinski, 2019). The three known bacterial strains associated with HLB are "africanus" (CLaf), "americanus" (CLam), and "asiaticus" (CLas), where the last-mentioned is the most damaging and widespread (Andrade et al. 2020). The disease results in chlorosis, defoliation, preharvest fruit drop, and twig dieback; ultimately causing reduced fruit quality and yield (McCollum and Baldwin 2016) (Figure 3 a and b). There is currently no effective treatment for HLB (Li et al. 2021).

Huanglongbing is arguably the most damaging disease of citrus globally, causing substantial economic losses (Gottwald 2010; Alvarez et al. 2016). Citrus growers in Florida (United States of America), for example, recorded a 91% decrease in citrus yields since *D. citri* was first reported in the state in 2005 (Graham et al. 2020; Volpe et al. 2024), with over 90% of citrus trees affected by HLB (Ferrarezi et al. 2020). In 2003–2004 the state produced 250 million boxes (USDA 2023b). This reduced to 169 million boxes in 2004–2005, and to 15.85 million boxes in 2023 (USDA 2023a).

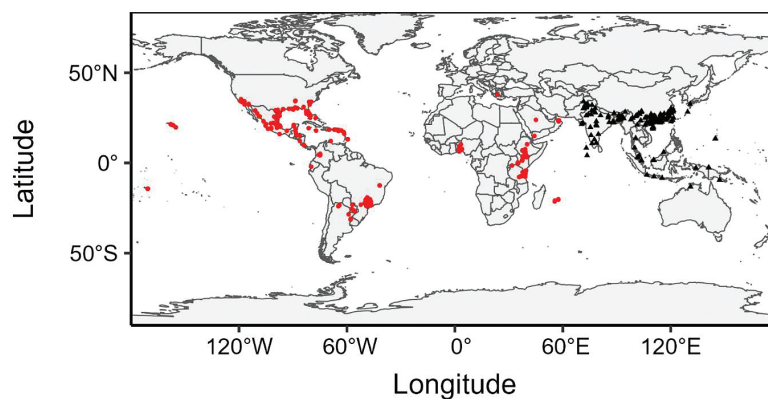


Figure 1: The global distribution of *Diaphorina citri*, as sourced from the literature, Global Biodiversity Information Facility (GBIF), and field surveys conducted by Citrus Research International (CRI) (Table S1). Invaded range localities are shown as red circles, and native range localities as black triangles.

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SUPPLEMENTARY MATERIAL

Supplementary figures and
tables are available for the
article in separate documents.



Figure 2: Habitus, lateral view of a female *Diaphorina citri* Kuwayama. Photo credit: EV Mauda.

Similar reports exist for citrus industries in Brazil (Bassanezi et al. 2020; Belasque et al. 2010; Ferrarezi et al. 2020) and China (Yang et al. 2006; Zhou 2020).

Diaphorina citri is present in Africa, and has been recorded in Tanzania (Shimwela et al. 2016), Kenya (Rwomushana et al. 2017), Ethiopia (Ajene et al. 2020), Nigeria (Oke et al. 2020), Ghana (Aidoo et al. 2023), and the Republic of Benin (Sétamou et al. 2023). Additionally, HLB has been reported in Kenya and Ethiopia (Saponari et al. 2010; Roberts et al. 2017; Ajene et al. 2020). The spread of the psyllid across these African countries has been attributed to its dispersal ability, the movement of plant material via traded citrus such as rootstock seedlings and grafts, and the transport of eggs and immatures on the alternative host *Berberis koenigii* (L.) (Curry tree) (Rwomushana et al. 2017). The relatively rapid southward spread of the psyllid towards South Africa raises serious concerns related to the socio-economic importance of citrus (Shimwela et al. 2016), especially considering that the southern African citrus industry is worth over R30 billion (US\$1.58 billion) per annum (CGA 2022). The South African citrus industry is closely monitoring the spread of *D. citri* in Africa, as its entry into the country will be economically devastating if proactive measures are not implemented timeously. An additional concern is that there is a triozid native to Africa, the African citrus triozid (ACT), *Triozia erytrae* (Del Guercio 1918) (Hemiptera: Triozidae), which occurs predominantly in the Afrotropical regions (Hollis 1984). *Triozia erytrae* is also capable of vectoring the CLas bacterial strain under laboratory conditions (Reynaud et al. 2022), which may accelerate the spread of HLB in South Africa following the possible arrival of *D. citri* and the potential spread of the bacteria from one host to another.

A number of recent studies have applied species distribution models (SDMs) to predict the geographic areas that are most climatically suitable for *D. citri* under both current and future climate conditions (Aurambout et al. 2009; Narouei-Khandan et al. 2016; Wang et al. 2019, 2020; Aidoo et al. 2022; Rodríguez-Aguilar et al. 2023). The aims of the present investigation were to build updated MaxEnt SDMs that include more recent validated occurrence records from both online repositories (Global Biodiversity Information Facility; GBIF, and the published literature) and field surveys in Africa and Brazil. This work aimed to predict possible invasion routes into South Africa, and how these routes might change between the present and the year 2070 under two climate change scenarios. Including future climate projections into the SDM analyses can offer insights into how entry routes and priority areas might change over time, necessitating the need for adaptive biosecurity (Lemic et al. 2024). Realised niches of *D. citri* were also compared in its native and invaded ranges to gain a better understanding of the insect's ability to expand its distribution in invaded habitats. The ability to predict potential *D. citri* invasion routes and climatic barriers offers the South African citrus industry the ability to

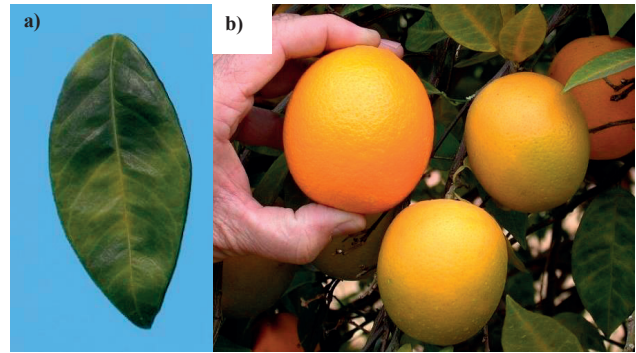


Figure 3: a) Leaf and b) fruit symptoms caused by HLB infection. Photo credits: Peter Stephen.

take proactive steps to minimise losses, and to focus control strategies in the country's high-risk areas.

MATERIALS AND METHODS

Species occurrence records

A total of 802 global occurrence records for *Diaphorina citri* (native and introduced range) were sourced from the literature ($n = 507$), the Global Biodiversity Information Facility ($n = 216$), and from the field records ($n = 79$) of researchers at Citrus Research International (CRI) (Figure 1, Table S1). All duplicate occurrence records were removed, and to avoid pseudo-replication, only one presence record per 2.5 min grid cell was retained using the `gridSample()` function in the `dismo v1.3-14` package (Hijmans et al. 2023a) in R v4.3.1 (Valavi et al. 2019) (R Core Team 2023). The thinned dataset comprised 566 occurrence records, which were used for model calibration. Spatial autocorrelation may result in biased models, since sites that are geographically close have a higher probability of sharing a similar climate. This may violate the assumption of independence (Legendre 1993). The degree of spatial autocorrelation on the entire distribution was therefore tested using the `cv spatial_autocor()` function in the `blockCV v3.1.3` package (Valavi et al. 2019).

Environmental predictors

Current global climate data for the standard 19 variables were downloaded from the WorldClim ver. 2.1 database (<https://www.worldclim.org/data/bioclim.html>) (Fick and Hijmans 2017) using the `worldclim global()` function in the `geodata v0.5-8` package (Hijmans et al. 2023b). This dataset contains the annual and seasonal means and variations in temperature and precipitation over the years 1970–2000. Future climate data for the same variables were downloaded for the years 2021–2040, 2041–2060, and 2061–2080 using the `cmip6_world()` function in the `geodata` package (Hijmans et al. 2023b). The resolution for all climate data was set to 2.5 min, and future climate data were downloaded for both Representation Concentration Pathway 4.5 (RCP4.5; $ssp = 245$) and RCP8.5 ($ssp = 585$). The RCP values indicate the predicted increase in greenhouse gases in the atmosphere (Fick and Hijmans 2017).

To select uncorrelated climatic variables, pairwise Pearson's correlation coefficients were calculated for all predictors, and those that were not highly correlated ($r < 0.7$) were selected (Figure S1) (Capinha and Anastácio 2011). The reduced set of uncorrelated variables were further passed through a collinearity test using the `vifstep()` function in the `usdm v1.1-18` package (Naimi et al. 2014), retaining predictors with a variance inflation factor (VIF) < 5 . Four climatic variables were used for modelling, and comprised annual mean temperature (bio1), temperature annual range (bio7), annual precipitation (bio12), and precipitation of the coldest quarter (bio19) (Fick and Hijmans 2017) (Figure S2; Table S2).

Although adult *D. citri* can become cold acclimated over winter periods, the species is more suited to warmer conditions, with an optimal developmental temperature range of 24–28 °C (Hall et al. 2013). Experimental evidence suggests that the psyllid is more suited to a higher relative humidity (RH), producing fewer eggs if RH drops below 40% (Skelley and Hoy 2004). The selected climate variables are therefore biologically relevant and have been used as inputs in various combinations across other *D. citri* modelling studies (Narouei-Khandan et al. 2016; Wang et al. 2020; Aidoo et al. 2022). Catling (1969) found that vapour pressure deficit (VPD) was significantly correlated with *T. erytraeae* density, and that it was a better indicator of species abundance than rainfall. This might also be a factor to consider for ACP abundance predictions, although this kind of data may not be available at the scales required for modelling purposes.

Model calibration

MaxEnt v3.4.3 (Phillips et al. 2006, 2017) was implemented via the dismo (Hijmans et al. 2023a) and megaSDM (Shipley et al. 2022) R packages. The MaxEnt (maximum entropy) modelling algorithm uses only confirmed presence data, not true absences, and is currently one of the most popular choices in species distribution modelling studies due to its high prediction performance and broad applicability (Merow et al. 2013; Phillips et al. 2017). The method has also been used previously to accurately predict the presence of invasive species (Ward 2007; Sutton and Martin 2022).

Since MaxEnt is a presence-only model, background points need to be generated and included in model building (Phillips et al. 2006). Selecting background points in SDM analyses is a long-debated issue, as the method chosen can have a significant impact on a model's performance (Van Der Wal et al. 2009). Background points need to be carefully selected such that they are drawn from areas where the target species has not been recorded, and that are on the boundary of climatic suitability (Jiménez-Valverde et al. 2011). Köppen-Geiger climate zones were selected that contained at least one occurrence record for *D. citri* across its entire distribution, and 10 000 random background points were selected from these geographic areas using the spatSample() function in the terra v 1.7-39 package (Hijmans et al. 2023c).

Taxon-specific parameter tuning is important to optimise MaxEnt model complexity to avoid overly complex models that may underperform when transferred in space and/or time (Elith et al. 2011; Merow et al. 2013; Sutton and Martin 2022). To identify optimal parameter settings, model tuning was carried out using the ENMevaluate() function in the ENMeval package (Kass et al. 2021). Model tuning selects the most appropriate feature classes (FC) and regularisation multiplier (RM) to avoid overfitting and maximise model sensitivity (Radosavljevic and Anderson 2014). The 4-fold spatial block partitioning technique was selected with the FC combinations L (linear), Q (quadratic), H (hinge), and LQH, with RM set at 1, 2, 4, 6, and 8. A total of 20 MaxEnt models were specified, and the best model was selected based on five metrics: namely (1) overall parsimony/corrected Akaike Information Criterion (AICc), (2) overfitting (difference in the area under the curve between the training and testing data) (AUC_{diff}), (3) discriminatory ability (area under the curve for the test data) (AUC_{test}), (4) the Continuous Boyce Index (CBI_{test}), and (5) 10% omission rates (OR_{10}) (Table S3). Our final model comprised the FC combination LQH, and RM = 6 (Figure S3 and Table 1), and was generated using MaxEnt v3.4.3 in R using the MaxEntModel() function in the megaSDM v2 package (Shipley et al. 2022). Models were trained using data from both the native and invaded ranges of *D. citri*. Model calibration using a combination of both native and invaded range data may provide a more accurate depiction of a species' realised niche,

and therefore its potential to spread (Mau-Crimmins et al. 2006; Trethowan et al. 2011).

Climatic suitability projections were obtained using the MaxEntProj() function in the megaSDM package, where the future climate scenarios for the years 2010, 2030, 2050, and 2070 were incorporated, as detailed above, using the optimal model selected (LQH6). Maps for each time period were generated using the createTimeMaps() function in the megaSDM package.

To account for potential issues with the extrapolation of predictions into novel environmental spaces (Elith and Leathwick 2009; Yates et al. 2018), a Multivariate Environmental Similarity Surfaces (MESS) (Elith et al. 2010) map was generated for Africa using the mess() function in the dismo package (Hijmans et al. 2023a). A MESS analysis provides an indication of the climatic similarity of the set of presence points used to calibrate MaxEnt models to any given point in the geographic area of interest (Guillaumot et al. 2020), thereby estimating potential prediction uncertainty (i.e. extrapolation). Negative MESS values indicate geographic areas with climates that fall outside the range used to calibrate models (extrapolation space; MESS-), while MESS values between 0 and 100 indicate areas with climates that fall within the range of those used in model calibration (interpolation space; MESS+) (Elith et al. 2010).

Niche overlap

Realised niche overlap between the native ($n = 202$) and invaded ($n = 364$) range of *D. citri* (Figure 1) was analysed by running a principal component analysis (PCA) on the selected four climatic variables for both distribution ranges using the prcomp() function in the stats package (R Core Team 2023). This was followed by the generation of convex hull spatial polygons using the geom_convexhull() function in the ggConvexHull (Martin 2023) package and SpatialPolygons() function in the sp package (Pebesma et al. 2023). Overlapping areas were calculated using the gIntersection() function in the rgeos package (Bivand et al. 2023). The percentage overlap between the native and invaded range polygons was treated as an indication of the degree of niche overlap. Confidence intervals (95%) were calculated using the summarySE() function in the Rmisc R package (Hope 2022) to test which climatic variables were responsible for explaining the differences in climatic niche between the native versus introduced range.

RESULTS

Model evaluation

The optimal MaxEnt model (FC = LQH, RM = 6) yielded a discriminatory power greater than 0.75 ($AUC_{test} = 0.81 \pm 0.07$), a low level of overfitting ($AUC_{diff} = 0.08 \pm 0.06$), an omission rate near 10% ($OR_{10} = 0.11 \pm 0.14$), and a Continuous Boyce Index value close to 1 ($CBI = 0.95 \pm 0.04$) (Figure S3; Table S3). The MESS map for Africa supported a low incidence of extrapolation, which strengthens the statistical confidence that can be placed in this model (Figure S4).

Current climate

Model projections for the current climate indicate moderate to high climatic suitability for *D. citri* across large parts of sub-Saharan Africa (Figure 4a). For example, much of East Africa was found to be climatically suitable for *D. citri*, with large parts of Ethiopia, Kenya, Uganda, Rwanda, Burundi, and Tanzania predicted to be highly suitable (suitability scores > 0.75). Much of central and coastal West Africa were also climatically suitable, from Guinea in the far west through to Gabon and Democratic Republic of Congo, albeit that the climatic suitability in these areas (suitability 0.60–0.80) was not as high as throughout much of East Africa. Lastly, the eastern and coastal regions of

southern Africa were found to be highly climatically suitable for *D. citri*, from southern Tanzania, through Malawi, Eswatini, and Mozambique into the eastern provinces of South Africa (e.g. the KwaZulu-Natal, Mpumalanga and Eastern Cape provinces) (Figure 4 a). Notably, the central and western parts of southern Africa were projected to be largely climatically unsuitable for *D. citri*, including areas such as: Zambia, Botswana, Angola, Namibia and the north-western region of South Africa. However, note that the predictions along the coast of Namibia have high uncertainty (Figure S4). Climatically suitable regions in Africa suggest a potential invasion route from Central Africa, moving southwards through Mozambique and Zimbabwe into South Africa (Figure 4b).

Future climate

Changes in climatic suitability between current conditions and those projected for the year 2070 suggest that large areas of Africa will remain suitable for *D. citri*, with only marginal changes over time (Figure 5a–d). The formation of small pockets of highly suitable areas may serve as invasion bridgeheads (Figure 5c and d). These pockets were evident under the more aggressive climate change scenario (RCP 8.5), appearing in Namibia, Botswana, and Angola (Figure 5d). Increased suitability in the inland regions of South Africa were higher under the moderate climate change scenario (RCP 4.5), spanning across large areas of the Mpumalanga, Free State, and Eastern Cape Provinces, Lesotho, and smaller areas in the south-western corner of the

KwaZulu-Natal Province, the southern rim of the Northern Cape Province, and patches within the Western Cape Province (Figure 5a and c; Figure S5 a and b). The RCP4.5 climate change scenario suggested a possible invasion route along the eastern margin of the African continent, into South Africa (Figure 5e), while the RCP8.5 scenario suggested an additional potential route through Namibia and Botswana, although with slightly less climatically suitable linking areas (Figure 5f).

Niche overlap

Principal components 1 (PC1) and 2 (PC2) contributed 50.5% and 26.8%, respectively, to the variance observed in the climatic data used in the MaxEnt models (Figure 6; Figure S6; Figure S7). Native and invaded range realised niches overlapped by 70%, and the invaded region occupied 14.5% outside the native range area (i.e. an indication of realised niche expansion) (Figure 6). Mean and 95% confidence interval values suggested that there were significant differences in temperature annual range and annual precipitation between the invaded and native range (Figure 7a–d). Temperature annual range in the native distribution (24.0 ± 1.0 °C) was significantly higher than the invaded range (19.3 ± 0.6 °C) (Figure 7b). Similarly, annual precipitation in the native range (1570.6 ± 98.0 mm) was significantly higher than the invaded range (1124.0 ± 56.1 mm) (Figure 7c). There was no significant difference in annual mean temperature and precipitation of the coldest quarter between the invaded and native ranges (annual mean temperature

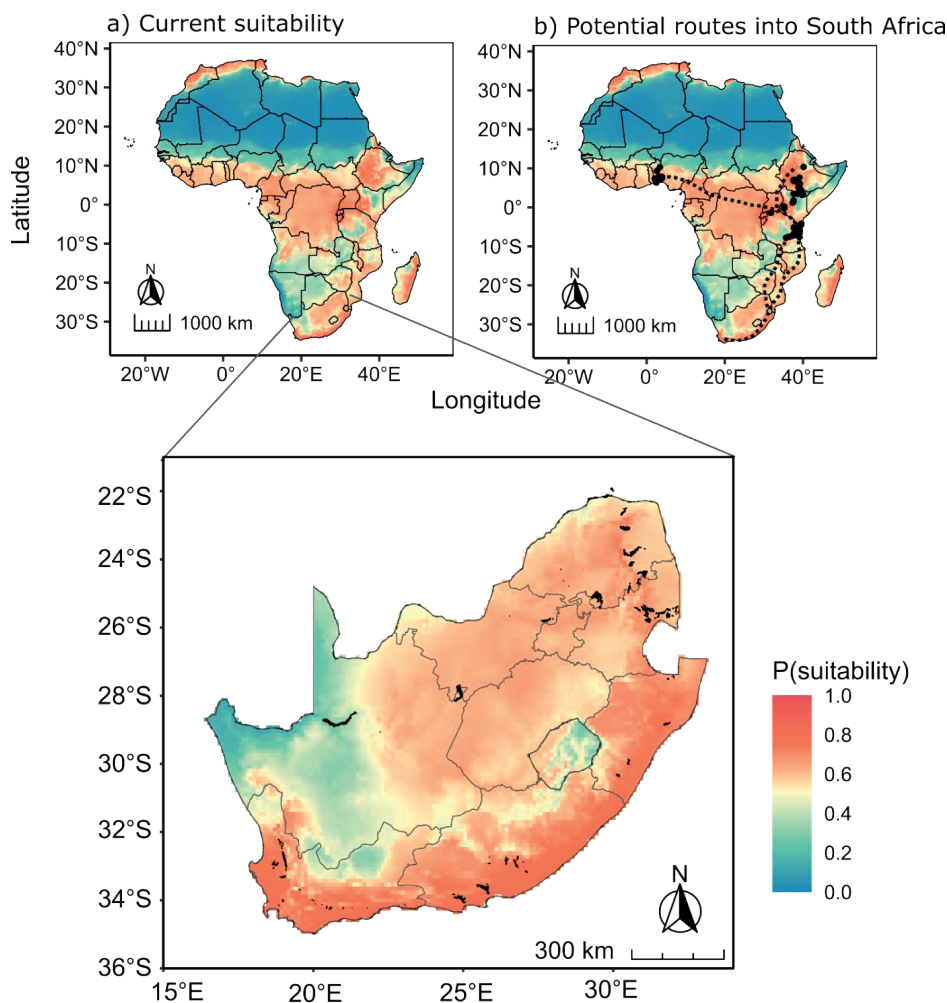


Figure 4: a and b) Projected MaxEnt climatic suitability for *Diaphorina citri* on the African continent under current climate conditions. Suitability scores closer to 1 indicate a higher probability that climatic conditions are favourable to *D. citri* in a particular geographic region. The black circles in panel b) denote confirmed presence recordings of *D. citri*, and the dotted lines indicate potential dispersal routes into South Africa through climatically suitable regions. The enlarged section stemming from panel a) shows climatic suitability for South Africa, where the overlaid areas in black denote major citrus producing areas in the country.

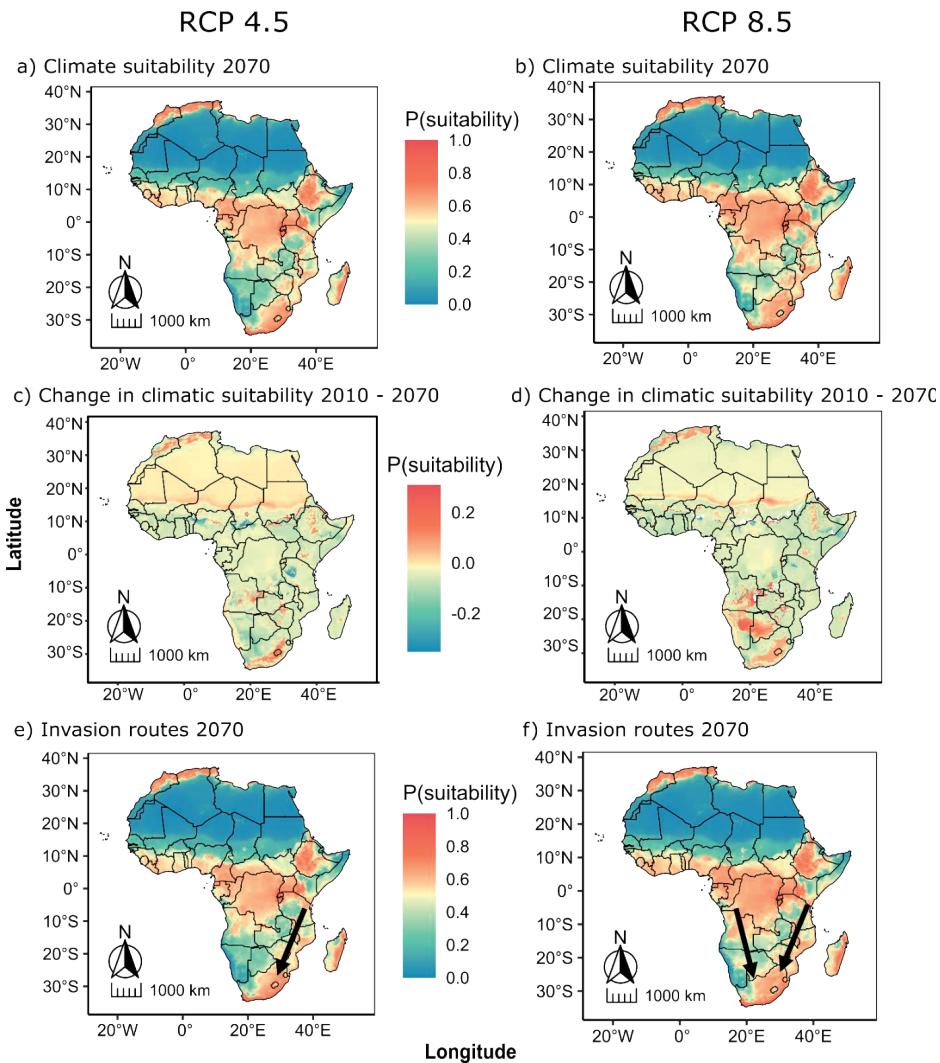


Figure 5: Predicted climatic suitability for the year 2070, under both the RCP4.5 and RCP8.5 climate change scenarios. Panels a) and b) show overall climatic suitability across the African continent, c) and d) show the change in suitability between the current and 2070 climate, and e) and f) highlight potential invasion routes into South Africa.

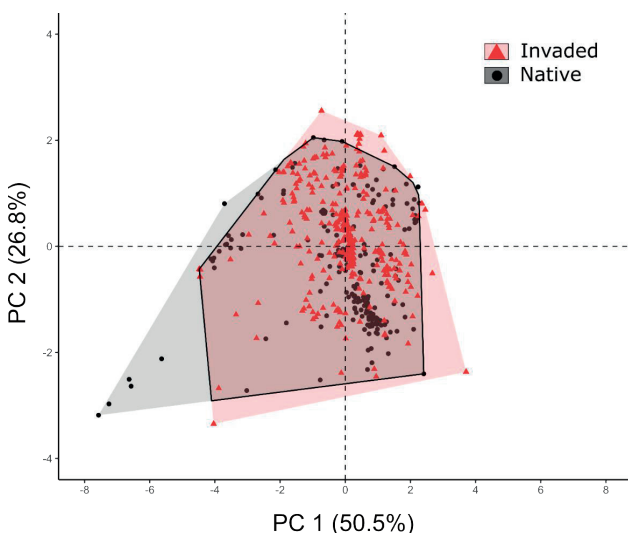


Figure 6: Principal components analysis (PCA) for the reduced climatic variables (annual mean temperature (bio1), temperature annual range (bio7), annual precipitation (bio12), and precipitation of the coldest quarter (bio19)) in the native (black circles) and invaded (red triangles) ranges, showing a high degree of niche overlap (70%), as indicated by the black-bordered polygon. The percentages shown on the axes denote the variation that each principal component is able to explain in the data.

invaded range: 21.9 ± 0.3 °C; annual mean temperature native range: 21.5 ± 0.5 °C; precipitation of the coldest quarter invaded range: 181.2 ± 16.3 mm; precipitation of the coldest quarter native range: 197.3 ± 36.2 mm) (Figure 7 a and d).

DISCUSSION

Diaphorina citri poses a major risk to citrus industries globally and has already resulted in substantial economic losses in countries including the USA, Brazil, and China. Its presence in Africa is a serious concern to citrus growers in southern Africa, as the psyllid may disperse southwards and spread if climatic conditions are favourable. South Africa is the second largest exporter of citrus worldwide after Spain (Simoes and Hidalgo 2011). The potential damage from *D. citri* can have a major detrimental impact on the country's Gross Domestic Product (GDP) and employment.

Using updated global distribution records for *D. citri*, including from recent field surveys, species distribution models (SDMs) were employed to predict potential invasion routes and entry points into South Africa, climatically suitable areas within the country, and how these factors may change leading up to the year 2070 under climate change scenarios. To date, the present work contains the most comprehensive SDM results for *D. citri* in Africa and provides a robust set of predictions that may assist in management programmes going forward.

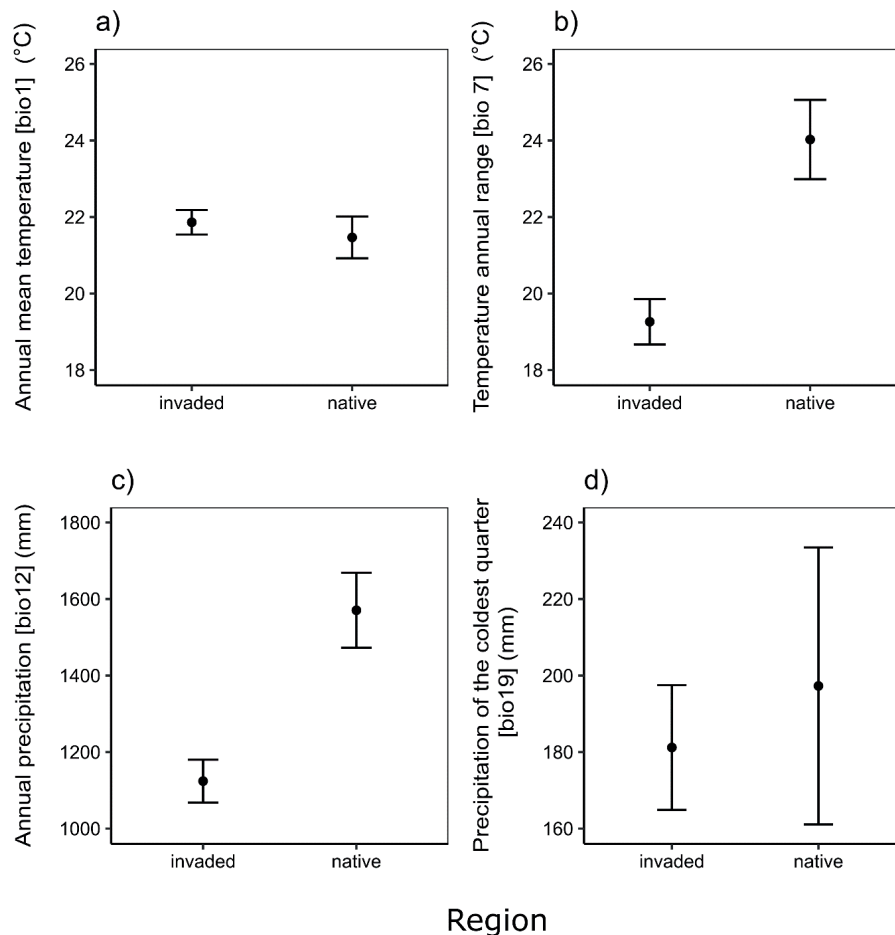


Figure 7: Means and 95% confidence intervals for each climatic variable included in the MaxEnt model, comparing the invaded to the native range. Panels show a) annual mean temperature (bio 1), b) temperature annual range (bio 7), c) annual precipitation (bio 12), and d) precipitation of the coldest quarter (bio 19).

Model projections

Current climate

The predictions presented in this work are broadly like those presented for Africa in Aidoo et al. (2022), except that the present results show higher climatic suitability over most of South Africa, while theirs reported mostly low to medium suitability in the northern regions bordering Zimbabwe and Mozambique, and along the coastal belt into the Western and Northern Cape Provinces. These differences are likely due to a greater number of distribution records in the present analyses, particularly for Africa.

Future climate

Changes in climatic suitability between current conditions and those projected for the year 2070 suggest that large areas of the African continent will remain suitable for *D. citri*, with small pockets outside South Africa likely able to serve as bridgehead populations resulting in further invasion (Bertelsmeier and Keller 2018; Morel-Journel et al. 2019). These bridgehead areas are evident under the more aggressive climate change scenario (RCP 8.5), appearing in Namibia, Botswana, and Angola. Only differences between 2070 and the current climate are shown, because those for 2030 and 2050 were qualitatively similar to 2070 (Figure S8).

An increase in suitability in the interior regions of South Africa by the year 2070 suggests a possible shift into these cooler inland areas as *D. citri* tracks climate change. The increase in inland suitability was more pronounced under the RCP4.5 scenario, suggesting that hotter temperatures and drier climates predicted under an aggressive climate change scenario in South Africa may be unfavourable to the psyllid.

Contrasting the present results, Aidoo et al. (2022) reported that the interior regions of South Africa were unsuitable under current climate conditions and would only become more favourable by the years 2030 to 2050. These differing results could be explained by a multitude of reasons, such as differing climate predictor variables, parameter configuration, choice of algorithm, and input training data quality (Li and Wang 2013; Sutton and Martin 2022). The present models also included a comprehensive occurrence record dataset, accurate cross-validation statistics, and limited extrapolation values.

Potential entry points and invasion routes

The introduction of agricultural pests to Africa has increased over time (Sileshi et al. 2019), and several that have been introduced elsewhere in Africa have subsequently spread southward and into South Africa. Notable examples include the large grain borer (Coleoptera: Bostrichidae: *Prostephanus truncatus* Horn 1878), tomato leaf miner (Lepidoptera: Gelechiidae: *Tuta absoluta* Meyrick 1917), mites (*Brevipalpus* spp. Donnadieu 1875), and fall army worm (Lepidoptera: Noctuidae: *Spodoptera frugiperda* Smith 1797) (Muatinte et al. 2014; Venter, 2017; Visser et al. 2017; Saccaggi and Ueckermann 2024). Such intra-African movement of alien species appears to be increasing (Faulkner et al. 2017a), and given sufficient time, *D. citri* is similarly likely to disperse southward into South Africa from its current invaded range in East and West Africa. Although not a citrus pest, the Asian spotted wing drosophila, *Drosophila suzukii* (Matsumura 1931) (Diptera: Drosophilidae), recently followed a similar southward dispersal route along East Africa, and was recorded for the first time in South Africa

in 2023 (IPPC, 2024). *Drosophila suzukii* is already present in four of South Africa's nine provinces.

The large area of suitable climate across most of South Africa suggests that once *D. citri* has entered the country, it may spread across all nine provinces, barring a small less suitable area in the western region of the Northern Cape Province that stretches north into Namibia. The coastal belt spanning from the KwaZulu-Natal Province southwards into the Western Cape is highly suitable for *D. citri*, posing a major threat to citrus growing regions in those areas. Stringent monitoring in the northern areas of South Africa bordering Zimbabwe and Mozambique is vital for the early detection of *D. citri*, where its spread may be facilitated by the presence of backyard trees in residential areas and abandoned citrus groves (Sétamou et al. 2022). Notably, the first records of the large grain borer, tomato leaf miner, and fall army worm were all in the north-east of South Africa (Muatinte et al. 2014; Visser et al. 2017; Venter 2017). A co-ordinated regional response to alien species is required to better manage invasions on the continent, but this will be challenging considering the relatively low proactive response capacity of most African countries (Early et al. 2016), and the potential for conflicting interests (Faulkner et al. 2020). South Africa is also connected through shipping to other parts of the world where *D. citri* is present. For example, *D. citri* occurs in Mauritius, and the shipping route that connects Durban to Port Louis could pose a high threat due to the relatively high shipping traffic, short travel time, and the environmental similarity of the two ports (Faulkner et al. 2017b). Therefore, since ports such as Durban and Maputo may also be high-risk entry points, these risks need to be assessed and mitigated with regular monitoring.

Niche expansion implications

The present analyses suggested that *D. citri* has a large degree of climatic overlap between its realised niche in its invaded and native ranges (70% climatic niche overlap). A fundamental assumption in climate matching studies is that the organism's climatic niche is conserved in its invaded range, otherwise model performance can be compromised by additional evolutionary and ecological factors that have not been accounted for (Wiens and Graham 2005; Broennimann et al. 2007; Saupe et al. 2018; Liu et al. 2020). This high degree of climatic overlap between the native and invaded range of *D. citri* indicates an increased confidence in the present models (Trethowan et al. 2011). However, approximately 14.5% of the climatic niche occupied by *D. citri* in its invaded distribution did not overlap with the climatic niche it occupies in its native distribution. For example, *D. citri* can colonise sites where annual precipitation is below 1 200 mm per year in its invaded distribution, but in its native range, it occurs in areas where annual precipitation exceeds 1 600 mm. Similarly, in its invaded range, *D. citri* occupies areas with less variability in annual temperatures (18 – 20 °C), whereas in its native distribution, annual temperature range is greater (> 24 °C). There are a variety of possible reasons for a dissimilarity between the native and invaded range niches of *D. citri*. These include the species' ability to acclimate to novel environments, an incomplete characterisation of the species' fundamental niche in the native range due to limited distribution records, biased sampling, and biological interactions (e.g. parasitism and herbivory) (Lau et al. 2008; Jiménez-Valverde et al. 2011; Liu et al. 2020; Peterson 2011; Saupe et al. 2018). Additionally, one of the limitations of correlative distribution models is that the fundamental niche of a species cannot be fully described due to the models' reliance on occurrence records only (i.e. only the realised niche is represented) (Jiménez et al. 2019).

The present MaxEnt models were calibrated using both native and invaded range occurrence records, and, as such, are likely to capture these differences in realised niches. However, it is

possible that *D. citri* will expand its thermal niche in invaded areas over time, making continued surveillance, detection and reporting of new populations vital to update and improve the present predictions of climatic suitability for the psyllid. Adaptive biosecurity measures may need to be implemented as changes in routes and entry points are detected.

Integrated pest management (IPM) implications

Area-wide management of psyllids will be required to effectively monitor and control their spread. If ACP and ACT are found to occur in the same region, efforts should be made to remove infected host trees and to correctly identify both the psyllids and the disease. Current evidence has shown that ACP spread has been faster than the disease, and that the spread of HLB followed the psyllid. For example, ACP was present in Florida for approximately 5–7 years before HLB was detected (Halbert and Manjunath 2004), and specimens collected in Tanzania tested negative for HLB when the first detection of ACP was made (Shimwela et al. 2016). Furthermore, ACP was known to occur in Brazil for more than 80 years (Lima 1942), however, HLB was only detected decades later in some states (do Carmo Teixeira et al. 2005). In the absence of HLB, *D. citri* poses a major threat in spreading African greening to citrus-growing areas that were previously free from greening and ACT. African citrus greening is vectored mainly by ACT, which is more heat-sensitive, and remains the more widespread disease especially in cooler climates in mid-altitudes. However, the presence of more heat tolerant ACP populations could facilitate an increased spread of African citrus greening, provided that the CLaf bacterium adapts to warmer conditions too.

Classical biological control of the ACP will be challenging because of the high diversity of indigenous psyllids found in southern Africa, where there are approximately 27 described *Diaphorina* species (Petty 1924; Petty 1933; Capener 1970a, 1970b, 1973). Additionally, their associated parasitoids and hyper-parasitoids could affect the efficacy of parasitoid species already used for controlling the African citrus triozid (*Trioza erytreae*) in southern Africa (Aubert and Quilici 1984; Van den Berg and Greenland 2000; Pérez-Rodríguez et al. 2019; Urbaneja-Bernat et al. 2019).

CONCLUSION

Diaphorina citri poses a major threat to the South African citrus industry, making the timeous implementation of monitoring and control measures at potential points of entry vital. The present SDM results suggested a high probability of a southward dispersal of the psyllid through Africa, which is likely to enter South Africa through Mozambique and/or Zimbabwe and spread throughout the country. Identifying possible invasion routes and high-risk areas under both current and future climatic conditions will be crucial to citrus growers and stakeholders going forward, and ongoing SDM analyses are encouraged as additional *D. citri* records become available, and more insight is uncovered regarding the insect's physiology and thermal limits. Future work would benefit from including the psyllid's dispersal ability into SDMs, and running a separate set of models for the native psyllid, *Trioza erytreae*, to investigate potential overlapping areas with *D. citri* and the possibility of the transfer of the CLas bacterial strain between host species.

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CJM van Steenderen wishes to dedicate this manuscript to his late father, Dr Ronald Adriaan van Steenderen, who tragically passed away on 24.02.2024. Ronnie was a pioneer in wastewater treatment and offered 35 years of service to the CSIR in Pretoria. His enthusiasm for science inspired his son to follow a career in Entomology, for which he will always be grateful.

DATA STATEMENT

All R scripts are available on the associated GitHub repository: https://github.com/clarkevansteenderen/ACP_AfricanEnt. Input files are stored on the CBC database and are available upon request.

CREDIT CONTRIBUTOR ROLES

CJM van Steenderen: formal analysis, investigation, data curation, methodology, software, writing – original draft, writing – review and editing, visualisation EV Mauda: resources, project administration, writing – review and editing W Kirkman: resources, project administration, writing – review and editing KT Faulkner: writing – review and editing GF Sutton: conceptualisation, methodology, software, writing – review and editing, supervision, project administration

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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