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# The potential distribution of *Bactrocera dorsalis*: considering phenology and irrigation patterns

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## Abstract

A species in the *Bactrocera dorsalis* (Hendel) complex was detected in Kenya during 2003 and classified as *Bactrocera invadens* Drew, Tsuruta & White. Having spread rapidly throughout Africa, it threatens agriculture due to crop damage and loss of market access. In a recent revision of the *B. dorsalis* complex, *B. invadens* was incorporated into the species *B. dorsalis*. The potential distribution of *B. dorsalis* has been previously modelled. However, previous models were based on presence data and did not incorporate information on the seasonal phenology of *B. dorsalis*, nor on the possible influence that irrigation may have on its distribution. Methyl eugenol-baited traps were used to collect *B. dorsalis* in Africa. Seasonal phenology data, measured as fly abundance throughout the year, was related to each location's climate to infer climatic

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growth response parameters. These functions were used along with African distribution records and development studies to fit the niche model for *B. dorsalis*, using independent global distribution records outside Africa for model validation. Areas at greatest risk of invasion by *B. dorsalis* are South and Central America, Mexico, southernmost USA, parts of the Mediterranean coast, parts of Southern and Eastern Australia and New Zealand's North Island. Under irrigation, most of Africa and Australia appear climatically suitable.

**Keywords:** CLIMEX, *Bactrocera invadens*, *Bactrocera papayae*, *Bactrocera philippinensis*, seasonal phenology, distribution, invasion, climate, Africa

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## Introduction

Knowing where a pest species could potentially invade and knowledge of its taxonomy are related questions that are critical to effective management of biosecurity risks and pest populations. Knowing where invasive pests can, and cannot persist allows us to identify the natural and other assets at risk, and hence what biosecurity measures may be justified on economic or other grounds (Kriticos *et al.*, 2013). In addition to the direct and obvious impacts on the management of pest quarantine, taxonomic uncertainty also impacts on our ability to apply pest risk modelling tools (Bourdôt *et al.*, 2013; Kriticos *et al.*, 2014).

The *Bactrocera dorsalis* (Hendel) complex comprises more than 75 species, and is economically one of the most important pest complexes in global agriculture (Clarke *et al.*, 2005). Among them are highly polyphagous and highly invasive species (Clarke *et al.*, 2005), with *B. dorsalis* (Hendel) itself being regarded as a pest of major biosecurity concern (CABI, 2015; EPPO, 2015). There has been controversy for many years regarding some species of the *B. dorsalis* complex, in particular the status of *Bactrocera papayae* Drew & Hancock, *Bactrocera philippinensis* Drew & Hancock, *Bactrocera invadens* Drew, Tsuruta & White and *B. dorsalis*, with various authors suggesting that these species should be considered as one (Tan *et al.*, 2011; Krosch *et al.*, 2013; San Jose *et al.*, 2013). In 2014, *B. papayae, B. philippinensis* and *B. invadens* were finally incorporated into *B. dorsalis* (Schutze *et al.*, 2015*a*, *b*).

In 2003, *B. dorsalis* was recorded for the first time in Kenya and at that stage it was described as a new species, *Bactrocera invadens* (Lux *et al.*, 2003; Drew *et al.*, 2005). The timing and pathway of the invasion of *B. dorsalis* into Africa remains unclear (Khamis *et al.*, 2009; Vayssières *et al.*, 2009*a*, 2011), but it possibly invaded Africa from the Indian subcontinent and was only discovered in Sri Lanka after its detection in Africa (Drew *et al.*, 2005; Schutze *et al.*, 2015*b*). After its detection in Kenya, it spread rapidly throughout Africa and by 2005, it had been detected in Senegal, Ghana, Togo, Benin, Nigeria, Cameroon, Sudan, Uganda and Tanzania (Drew *et al.*, 2005).

*Bactrocera dorsalis* is currently found in approximately 40 countries in Africa, including the islands of Madagascar, Cape Verde, Comoros and Mayotte, having spread as far north as Southern Mauritania, Southern Mali, Southern Niger, Southern Chad and Central Sudan, and as far south as Northern Namibia, Northern Botswana, Northern Zimbabwe and Mozambique (De Meyer *et al.*, 2012, with additional data from the fruit fly database held at the Royal Museum for Central Africa; Mguni, 2013; CABI, 2015; EPPO, 2015). In addition, it was recently declared present in the Vhembe district in the Limpopo province of South Africa (IPPC, 2013*b*; Manrakhan *et al.*, 2015), and it has been detected in Swaziland (IPPC, 2013*a*; CABI, 2015).

*Bactrocera dorsalis* is of great economic importance to the fruit industry in Africa (Mwatawala *et al.*, 2004, 2006*a*). Damage is caused when female flies oviposit under the skin of fruit; subsequently the larvae feed inside the fruit, leading to decay and extensive crop losses (Ekesi & Billah, 2007; James & Schiffers, 2007; Vayssières *et al.*, 2008). The reported occurrence of *B. dorsalis* in parts of Africa has also resulted in major economic losses due to loss of market access (Ekesi *et al.*, 2011).

It is likely that *B. dorsalis* will continue to expand its range in Africa given the fragmented agricultural landscape of the continent and the polyphagous and invasive nature of this species. It has been recorded in association with almost 80 host plant species (De Meyer *et al.*, 2012), with mango, *Mangifera indica* L., guava, *Psidium guajava* L., loquat, *Eriobotrya japonica* (Thunb.) Lindley, banana, *Musa* spp. L. and *Citrus* spp. L. being the major cultivated hosts in Africa (Ekesi *et al.*, 2006; Mwatawala *et al.*, 2006*b*, 2009; Rwomushana *et al.*, 2008*a*; Goergen *et al.*, 2011). However, Cugala *et al.* (2014) demonstrated that Cavendish dwarf bananas are not susceptible during the mature green stage at which they are harvested and only becomes susceptible during the later stages of ripening, indicating that bananas may not be one of the most favourable hosts. Being a strong flier (Vayssières *et al.*, 2009*b*) with a high fecundity (Ekesi *et al.*, 2006, 2009), it is highly competitive and has been reported to outcompete the native fruit fly *Ceratitis cosyra* (Walker) on mangoes in Kenya and elsewhere in Africa (Hala *et al.*, 2006; Ndiaye *et al.*, 2008; Ekesi *et al.*, 2009; Rwomushana *et al.*, 2009; Salum *et al.*, 2014). In Africa, it is generally considered a lowland pest, decreasing in abundance with an increase in altitude (Ekesi *et al.*, 2006; Mwatawala *et al.*, 2006*a*, *b*; Geurts *et al.*, 2012). In equatorial regions such as Tanzania and Kenya, it has been found to occur at altitudes of above 1600 m above sea level (Ekesi *et al.*, 2006; Geurts *et al.*, 2012).

The potential geographical distribution of *B. dorsalis* has previously been modelled using two correlative species distribution models (GARP and MaxEnt) trained with known occurrence records in Africa and Asia (De Meyer *et al.*, 2010). Results from the models suggest that *B. dorsalis* thrives under hot and humid conditions and it appears well suited to an equatorial climate. Although most of the known occurrences in Africa fell within the modelled potential range in the GARP model (De Meyer *et al.*, 2010), the modelled potential range did not include the northern boundaries of the species' actual distribution in Sahelian areas of countries such as Mali, Mauritania, Niger, Senegal and Sudan. The MaxEnt model showed a much narrower area of suitability, excluding many of the known occurrence records. For instance, large parts of Kenya and Tanzania, where the pest is present, were modelled as being climatically unsuitable for *B. dorsalis*. These models were based on distribution data for what was then known as *B. invadens*, including only a subset of the *B. dorsalis* records in its native region, namely certain records in Sri Lanka, Southern India and Bhutan, and being tested against the records from Africa. The models' shortcomings were attributed to a lack of known distributional records of the pest in the above-mentioned region and a lack of continuous trapping data to indicate fly abundance in the areas in Africa where the pest does occur (De Meyer *et al*., 2010).

Hill & Terblanche (2014) used Ecological Niche Factor Analysis (ENFA) to address similar questions to the study reported here. Curiously, the model based on the combined distribution of three of the previously separated species in the *B. dorsalis* complex, namely *B. dorsalis*, *B. philippinensis* and *B. papayae* estimated a suitable climatic niche extending into implausibly cold and xeric continental climates in Northern and Western Asia, respectively. Hill & Terblanche (2014) also composed a single model for a combination of *B. dorsalis*, *B. invadens*, *B. philippinensis* and *B. papayae*. Their model for the four previously separated species combined shows some similarities to the GARP model of De Meyer *et al*. (2010), but again underestimating the northern and southern limits of *B. dorsalis*, considering the current distribution within Africa. Unsurprisingly, a better fit to the current distribution of *B. dorsalis* in Africa was obtained when it was modelled using only distribution records of what was previously known as *B. invadens*. However, in both models by Hill & Terblanche (2014), Southern Zambia and Zimbabwe are modelled as unsuitable, whereas *B. dorsalis* does occur in these regions, indicating that the southern boundary of its distribution may be underestimated by these models.

These inconsistencies in the correlative modelling results reinforce the difficulties such models face when dealing with novel climate situations (Webber *et al*., 2011). They do not lend themselves to including information on relative abundance and seasonal phenology of the species when estimating species distributions. They rely exclusively on presence data, and are designed to work with temporally static covariates such as the Bioclim variables (Kriticos & Randall, 2001; Venette *et al*., 2010). Their output is similarly static, so it is not possible to compare phenological observations with the model results. Because they rely on the Bioclim variables, even the diagnostic response curves provided in these models are difficult for an ecologist or biologist familiar with the species being modelled to interpret meaningfully. In contrast, CLIMEX (Hearne Scientific Software Pty Ltd., Australia) (Sutherst & Maywald, 1985; Sutherst *et al*., 2007) is a semi-mechanistic modelling package that was developed primarily to estimate the potential distribution of invasive species, and to explore the climatic factors that influence population growth or decline. CLIMEX models can be fitted using inductive or deductive methods. Inductive methods can be used to fit biologically relevant climatic stress functions to define the species range limits, adjusting parameter values until the model results agree with species distribution or phenological data. Deductive methods can be used to define parameter values based on direct experimental observations of species responses to experimentally determined climatic factors or to phenological observations.

Prior to undertaking this study, CLIMEX models were developed for *B. dorsalis* by Stephens *et al*. (2007) and EPPO (2010) (prepared by the authors Sarah Brunel and Darren Kriticos). The model of EPPO (2010) was based on the model of Stephens *et al*. (2007). There was a strong overlap between the modelled niches of the two models (Stephens *et al*., 2007; EPPO, 2010). Each model accorded well with the known distribution of the populations being modelled. In both models, extensive areas were modelled as suitable, but had no corresponding location records. This result is to be expected for a species which is actively expanding its range. These areas of apparent model commission error were judged to be plausibly suitable.

The known distribution of *B. dorsalis* in Africa spans a wide range of climatic conditions, from central tropical Africa, to the arid regions bordering the Sahara desert at the northern boundary of its distribution and the warm temperate climates in the South forming its poleward and altitudinal boundaries. Seasonal phenology data generated across the different climatic regions in Africa in which it is known to occur, allows the CLIMEX growth indices (GI) to be fitted with more confidence, improving our ability to estimate the climatic niche of the species. In this paper, we collected year-round abundance data for *B. dorsalis* in Africa and combined this information with distribution data from the region to build a CLIMEX Compare Locations model. The CLIMEX model was then applied to all areas outside Africa, including both native and invasive ranges, where *B. dorsalis* is known to occur, to compare model fit with the independent distribution data in those regions. The validated model was then used to create a global climatic risk map.

## Materials and methods

### *Trapping data*

Twenty-three sampling sites across Benin, Ghana, Kenya, Niger, Senegal, Sudan, Tanzania and Zambia were used to measure the distribution and seasonal phenology of *B. dorsalis* (fig. 1). Sites were selected to span marginally suitable climatic regions based on Köppen-Geiger climate classes (Kriticos *et al*., 2012) and according to the availability of monitors to service the traps. Three yellow bucket traps (Chempac [Pty] Ltd., Paarl, South Africa), with the attractant methyl eugenol (Ran Chem Group Ltd., Shanghai, China) and the toxicant Dichlorvos (Acorn Products [Pty] Ltd., Roodepoort, South Africa) were deployed at each location. Where possible, traps were placed mainly in mango trees, in either home gardens or orchards, depending on the availability at the sites. Where mango trees were not available, traps were placed in citrus trees (at some sites in Kenya and Tanzania). In Makutupora village of Dodoma, Tanzania, one trap was placed in tropical almond, *Terminalia catappa* L., and one trap in lucky nut, *Thevetia peruviana* (Pers.) K. Schum. The fruit ripening periods of the hosts in which the traps were placed were recorded to be able to compare this with the phenology of the fly, to help interpret the CLIMEX output. Traps were placed at least 400 m apart (two instances), but in most cases the distance between traps was more than 1.5 km. Sampling was continued over a 2-year period, with traps being deployed for a period of 1 week only during each month, with the exception of Zambia, where sampling was only undertaken for 9 months. Only 1 year's data could be used for Wad Madani (Sudan), as *Bactrocera zonata* (Saunders) had entered the area (Salah *et al*., 2012), with monitors being unaware of this, and species differentiation took place only during the second

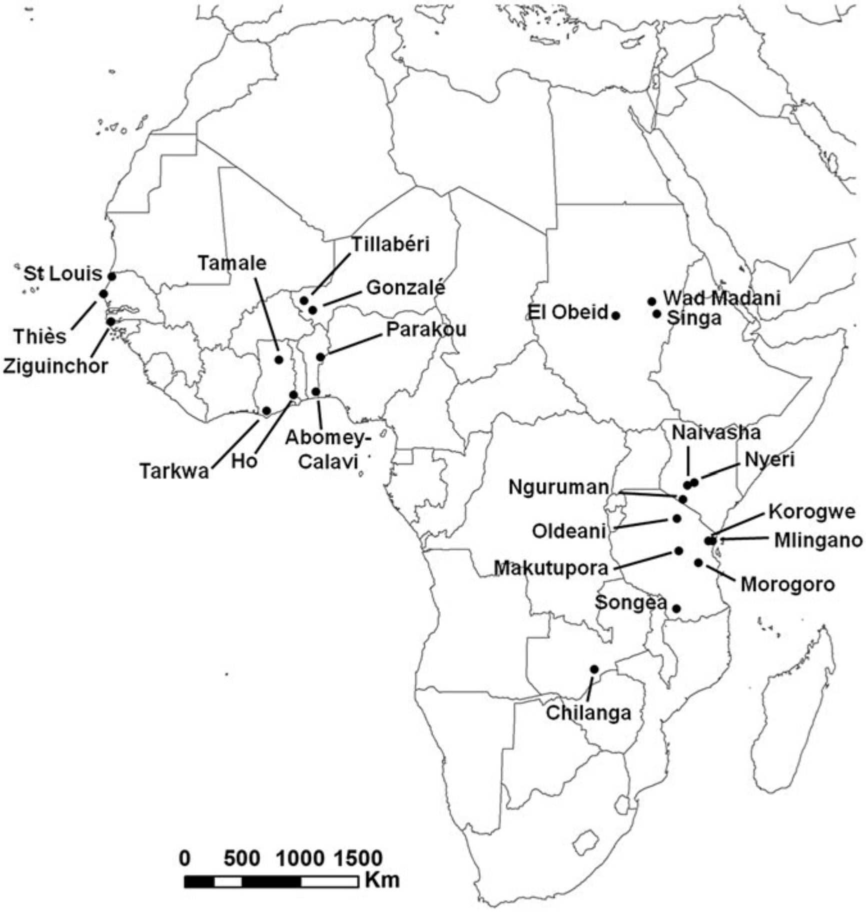

Fig. 1. Sampling sites used to monitor the distribution and seasonal phenology of *Bactrocera dorsalis* across different climates in Africa.

year of monitoring. Fresh lures and toxicants were used for every week that sampling was performed.

At each site, seasonal abundance was estimated by calculating the average number of flies caught per trap for each month. Thus, the fly counts from the three traps per site were averaged for each month, and the data for 2 years (e.g., August 2011 and August 2012) were then again averaged, resulting in 12 monthly abundance values for each site.

### *Distribution data*

Distribution data for *B. dorsalis* in Africa was obtained from the fruit fly database held at the Royal Museum for Central Africa, Mguni (2013) and Manrakhan *et al.* (2015). Distribution data from areas outside Africa were obtained from Stephens *et al.* (2007) and Hill & Terblanche (2014).

### *CLIMEX*

The influence of climate on the distribution and abundance of poikilotherms has been well documented (Andrewartha & Birch, 1954, 1984; Woodward, 1987). Much of this understanding has been incorporated into CLIMEX. CLIMEX uses the Compare Locations model to mimic the mechanisms that influence a species' population growth and survival responses to climate, in order to estimate its potential geographical distribution and seasonal abundance (Sutherst *et al.*, 2007). CLIMEX assumes that a population may experience two types of season each year, those that are favourable for growth and those that are stressful, during which the population will decline (Sutherst & Maywald, 1985; Sutherst *et al.*, 2007). The programme integrates a population's weekly responses to climate and uses these to calculate a number of weekly and annual indices, including annual and weekly growth indices ($GI_A$ and $GI_W$, respectively), stress indices (SI) and the ecoclimatic index (EI), which indicates the overall climatic favourability (Sutherst *et al.*, 2007).

CLIMEX includes the option of fitting stress functions for cold, dry, hot, wet, cold–dry, cold–wet, hot–dry and hot–wet SI. In addition to the temperature and moisture stresses, the potential distribution of a species may also be constrained by a minimum length of the growing season measured in degree-days. The annual growth index ($GI_A$) represents the potential for population growth and development and combines the organism's response to temperature, soil moisture and, where relevant, day-lengths and diapause (Sutherst *et al.*, 2007). CLIMEX combines the GI and SI into an overall EI, ranging from 0 to 100 (Sutherst *et al.*, 2007). Assigning classes of suitability to EI values between 0 and 100 is usually an arbitrary process intended to reduce the perceived level of

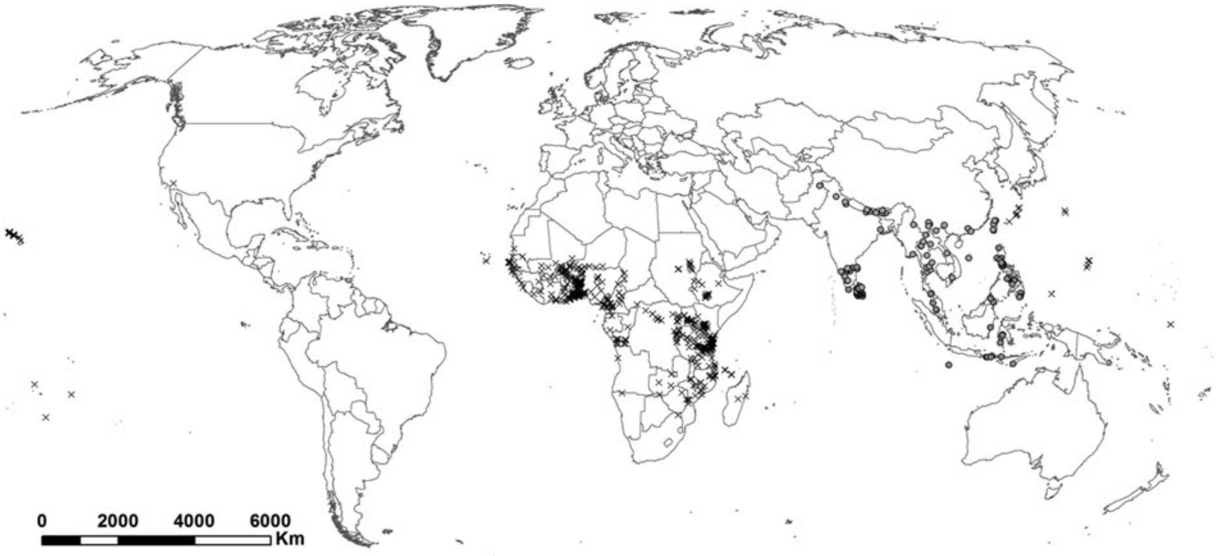

Fig. 2. The current distribution of *Bactrocera dorsalis* (in South Africa, only one location, representative of the Vhembe district, is shown). Native ranges: grey circles; invasive ranges (including the trap sites used for sampling): crosses.

Table 1. CLIMEX parameters used to model the distribution of *Bactrocera dorsalis*, based on its distribution and seasonal phenology in Africa. Parameters for CLIMEX models by Stephens *et al.* (2007) and EPPO (2010) are also given as a means of comparison.

| Index | Parameter | Value[1] | | |
|---|---|---|---|---|
| | | Stephens *et al.* (2007) | EPPO (2010) | Current model |
| Temperature | DV0 = lower threshold | 13°C | 9°C | 9°C |
| | DV1 = lower optimum temperature | 25°C | 30°C | 25°C |
| | DV2 = upper optimum temperature | 33°C | 35°C | 33°C |
| | DV3 = upper threshold | 36°C | 39°C | 42°C |
| Moisture | SM0 = lower soil moisture threshold | 0.1 | 0.1 | 0.1 |
| | SM1 = lower optimum soil moisture | 0.25 | 0.25 | 0.25 |
| | SM2 = upper optimum soil moisture | 1 | 1 | 1.8 |
| | SM3 = upper soil moisture threshold | 1.5 | 1.5 | 2 |
| Cold stress | TTCS = cold stress temperature threshold | 2.5° C | 8° C | 2.5° C |
| | THCS = stress accumulation rate | −0.012 week$^{-1}$ | −0.012 week$^{-1}$ | −0.012 week$^{-1}$ |
| | DTCS = degree–day threshold (stress accumulates if the number of degree–days above DVCS is below this value) | 8° C days | Not used | 12° C days |
| | DHCS = stress accumulation rate | −0.002 week$^{-1}$ | Not used | −0.002 week$^{-1}$ |
| | DVCS = developmental temperature threshold | 10° C | Not applicable | 9° C |
| Dry stress | SMDS = soil moisture dry stress threshold | 0.1 | 0.1 | 0.1 |
| | HDS = stress accumulation rate | −0.024 week$^{-1}$ | −0.03 week$^{-1}$ | −0.03 week$^{-1}$ |
| Heat stress | TTHS = heat stress temperature threshold | 36° C | 39° C | 42° C |
| | THHS = stress accumulation rate | 0.005 week$^{-1}$ | 0.001 week$^{-1}$ | 0.005 week$^{-1}$ |
| Wet stress | SMWS = wet stress threshold | 1.5 | 1.6 | Not used |
| | HWS = stress accumulation rate | 0.007 week$^{-1}$ | 0.001 week$^{-1}$ | Not used |
| Annual heat sum | PDD = number of degree-days above DV0 needed to complete one generation | 470° C days | 450° C days | 380° C days |

[1] Values without units are dimensionless indices of a 100 mm single bucket soil moisture model (0 = oven dry, 1 = field capacity).

model precision compared with that implied by a percentile score.

CLIMEX provides the user with two distinct data product types: (i) maps of annual summary variables, such as the EI, the $GI_A$ or the SI; and (ii) weekly time-series graphs of state variables such as the $GI_W$ (Sutherst & Maywald, 1985). The CLIMEX model was constructed by manually, iteratively fitting the stress parameters until the geographical distribution simulated by CLIMEX ($EI \geq 1$) coincided with the African distribution (fig. 2), and seasonal phenology as gauged by the trapping data accorded with graphs of $GI_W$ (table 1). Relevant biological information (e.g., developmental thresholds and the species' reaction to different levels of relative humidity) informed the parameter value selection to ensure that they were biologically plausible. Parameters for the temperature and soil moisture GI were mostly informed by reported

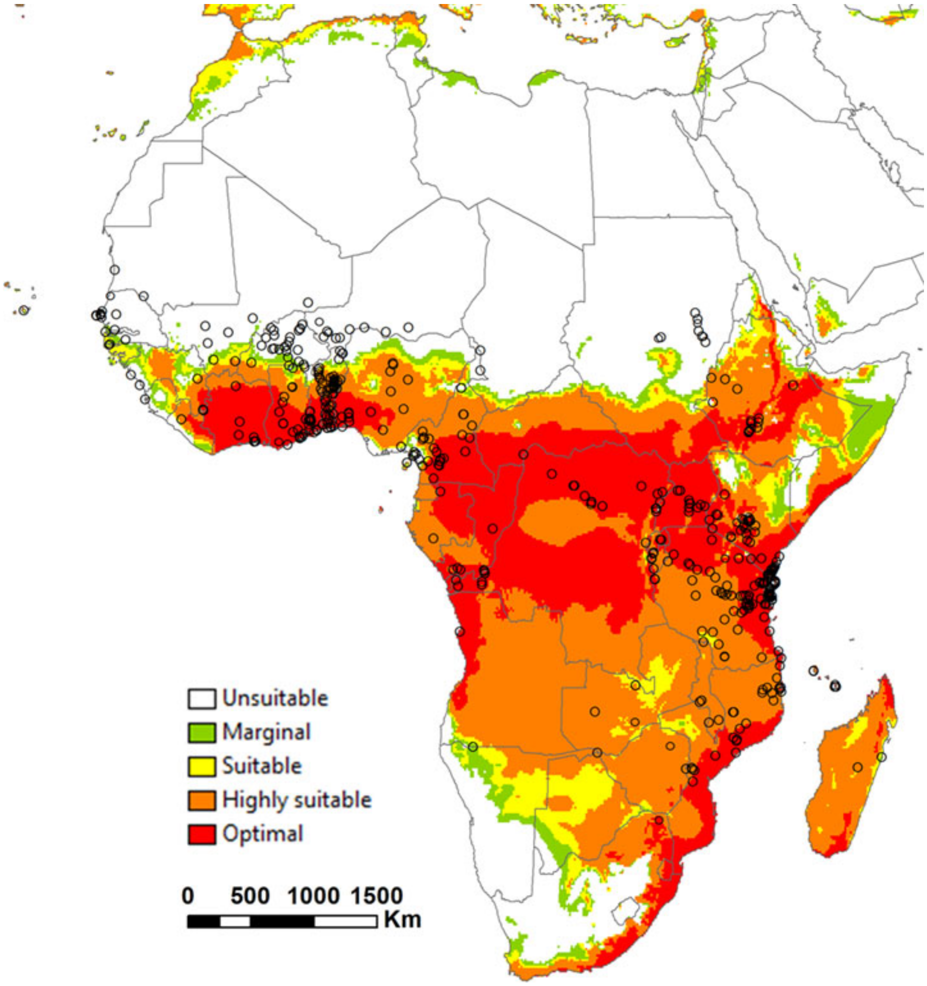

Fig. 3. The projected climate suitability for *Bactrocera dorsalis* in Africa, as modelled by Stephens *et al.* (2007) using the CLIMEX EI and the CM10_1975H_V1.2 dataset. Open circles indicate all occurrence records of *B. dorsalis*, including the trap sites used for sampling. Unsuitable: EI = 0; marginal: EI = 1–4; suitable: EI = 5–9; highly suitable: EI = 10–29; optimal: EI = 30–100.

experimental observations, theoretical knowledge and the phenological observations, aiming to get the start and finish dates, and peak climate suitability at each site to agree with the corresponding patterns of abundance.

The 10′ CliMond climate dataset was used within CLIMEX to represent current climate (Kriticos *et al.*, 2012). The CM10_1975H_V1.2 dataset of historical long-term monthly climate averages for minimum and maximum temperatures, precipitation and relativity humidity at 09h00 and 15h00 is centred on 1975.

### *Parameter fitting*

The parameter set of the CLIMEX model of *B. dorsalis* composed by Stephens *et al.* (2007) was taken as a starting point while building the new model. The model of Stephens *et al.* (2007) was run with the CM10_1975H_V1.2 dataset, which differs from the original TYN SC2.0 dataset used by Stephens *et al.* (2007) to fit the *B. dorsalis* model. Errors in the gridded precipitation data in TYN SC2.0 and the temperature layers in the Worldclim dataset drove the development of the CliMond dataset (Kriticos *et al.*, 2012). Despite idiosyncratic differences between the CM10_1975H_V1.2 and TYN SC2.0 climatologies (Kriticos *et al.*, 2012), the new dataset gave a similar output to that published in Stephens *et al.* (2007), fitting well with the distribution data of *B. dorsalis* (fig. 2). The *B. dorsalis* distribution data for Africa were mapped along with the climatically suitable range modelled by Stephens *et al.* (2007), where EI > 0 (fig. 3), to investigate whether or not the model of Stephens *et al.* (2007), which was constructed while *B. invadens*, *B. papayae* and *B. philippinensis* were still considered separate species and distribution data for these species were not included, could be used as a departure point for development of a new model for the potential distribution of *B. dorsalis*. Distribution points for *B. dorsalis* in the northern boundaries in Africa fell out of the modelled range for *B. dorsalis*. While climate is the primary range-limiting factor for poikilotherms (Andrewartha & Birch, 1954; Woodward, 1987), climate-modifying factors such as irrigation can also play an important role in extending a species range beyond the limits afforded by climate. Therefore, we hypothesized that the persistence of *B. dorsalis* in these xeric regions may be predicated on irrigation practices. Hence, we explored Google Earth, looking for spatial patterns that indicated the likely presence of irrigation, and also whether including irrigation provided a better model fit. Further adjustments were made to the *B. dorsalis* model of Stephens *et al*. (2007) according to the published information on the temperature thresholds for *B. dorsalis*, as well as phenological observations made through year-round trapping in Africa (table 1). The parameter set by EPPO (2010) is also given in table 1 as a means of comparison between previous CLIMEX models and the current model.

### *Temperature index*

The minimum temperature for development (DV0) was set to 9° C, which was in line with results from Rwomushana *et al.* (2008*b*), who reported lower developmental thresholds of 8.8, 9.4 and 8.7° C for eggs, larvae and pupae, respectively, for *B. dorsalis* in Africa. The lower optimum temperature (DV1) was set to 25° C, with the optimum temperature (DV2) set to 33° C, being the same as in the *B. dorsalis* model of Stephens *et al*. (2007). The maximum temperature for development (DV3) was set to 42° C to model Wad Madani and Singa, Sudan, as suitable during the hot summer months of April and May, when maximum monthly average temperatures rise above 40° C and large numbers of *B. dorsalis* were trapped. With the lower DV3 values of Stephens *et al.* (2007) and EPPO (2010) (36 and 39° C, respectively), the Temperature index during these months was zero, which did not allow a positive $GI_W$, even under an irrigation scenario, hence not corresponding with the seasonal phenology data. The number of degree-days per generation (PDD) was set to 380, which was in line with the value of 376 determined by Rwomushana *et al.* (2008*b*) for *B. dorsalis* in Africa.

### *Moisture index*

The lower moisture threshold (SM0) was set to 0.1 to indicate the permanent wilting point, which is normally about 10% of soil moisture. The lower optimal soil moisture threshold was set to 0.25 (Stephens *et al*., 2007). The upper optimal soil moisture threshold (SM2) and limiting high soil moisture threshold (SM3) was set to 1.8 and 2, respectively. This improved the modelled $GI_W$ in Ziguinchor, Senegal, during August when modelled soil moisture levels reached a maximum value of 1.97, and better fitted observed patterns of high abundance in the trapping data, while with the lower SM2 and SM3 values of the *B. dorsalis* models of Stephens *et al.* (2007) and EPPO (2010), the $GI_W$ would have been zero during this period.

### *Cold stress*

In Africa, the areas where *B. dorsalis* does occur do not experience extreme levels of cold. Therefore, the cold stress model of Stephens *et al.* (2007) was used. Since the DV0 value in the current model was set to 9° C, as opposed to 13° C in the model of Stephens *et al.* (2007), the degree-day threshold (DTCS) value had to be adjusted from 8 to 12° C days to produce a similar cold stress scenario.

### *Dry stress*

A dry stress scenario similar to that in Stephens *et al.* (2007) was used with the soil moisture dry stress threshold (SMDS) set to 0.1, and increasing the stress accumulation rate (HDS) from −0.024 to −0.03 week$^{-1}$ (EPPO, 2010). This resulted in the drier regions of the North African boundary being modelled as unsuitable (e.g., Senegal, Sudan and Niger, where persistence of *B. dorsalis* is more logically a result of irrigation).

### *Heat stress*

The heat stress scenario was similar to the scenario used by Stephens *et al.* (2007). However, the heat stress temperature threshold (TTHS) had to be increased from 36 to 42° C to accommodate the higher DV3 value in the current model. The heat accumulation rate (THHS) was kept the same at 0.005 week$^{-1}$.

### *Wet stress*

Wet stress was not included in the model, as it had minimal impact on the modelled potential distribution and *B. dorsalis* in Africa reportedly prefers high levels of rainfall and relative humidity (Wih, 2008; Vayssières *et al*., 2009*a*, *b*; De Meyer *et al*., 2010).

### *Irrigation*

The only monitoring sites that were irrigated were those in Senegal, Niger, Sudan and Nguruman in Kenya. The following irrigation scenarios were used according to the timing and frequency of irrigation at the different sites: 2.5 mm irrigation applied as a top-up to natural rainfall during the months of March to July for the Senegal and Niger sites, as well as for El Obeid in Sudan. For Singa and Wad Madani (Sudan), the same scenario was used, but 1.5 mm top-up irrigation was added for the rest of the year. For Nguruman, 2.5 mm top-up irrigation all year round was used. These different scenarios for the different sites were used, as different irrigation practices were followed in the different regions and it provided the best fit with the data. The $GI_W$ values were extracted for all sites for comparison with the recorded seasonal phenology data. However, a 2.5 mm year-round top-up irrigation scenario was also applied to the world to produce a risk map contingent on irrigation being practiced in the 10′ cell according to the global irrigation map (Siebert *et al*., 2005), producing a composite risk map. In areas where more than zero hectares were under irrigation according to Siebert *et al.* (2005), the EI of the irrigation scenario was mapped, while in areas where zero irrigation is applied, the EI of the non-irrigation scenario was mapped.

### *Seasonal phenology data*

For each of the trapping sites, the seasonal phenology was compared graphically with the $GI_W$ values from the model output, and where necessary, the values for the moisture and temperature GI were adjusted to gain concordance between the threshold values (SM0 and DV0) and the seasonal onset of trap catches, the optimal ranges (SM1, SM2, DV1 and DV2) and the period of maximum trap catches.

## Results

The potential distribution of *B. dorsalis* in Africa, in the absence of irrigation, is shown in fig. 4. As with the *B. dorsalis*

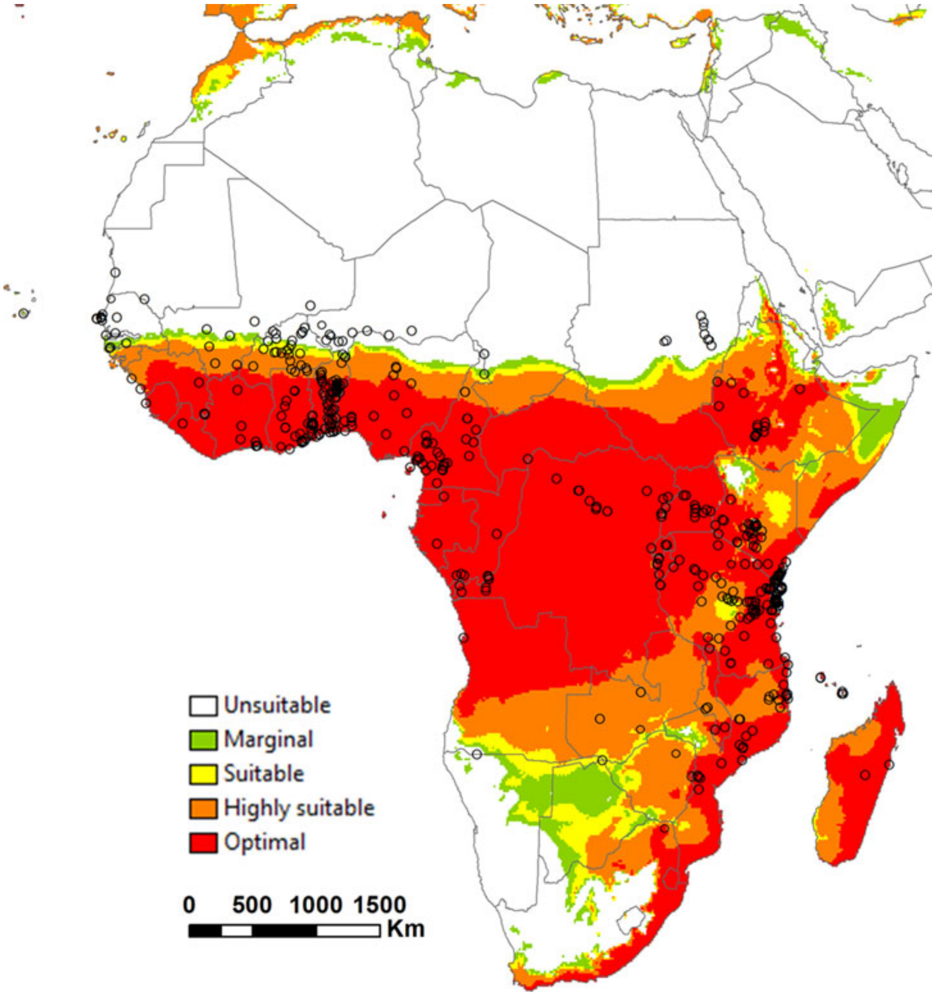

Fig. 4. The projected climate suitability for *Bactrocera dorsalis* in Africa in the absence of irrigation using the CLIMEX EI. Open circles indicate all occurrence records of *B. dorsalis*, including the trap sites used for sampling. Unsuitable: EI = 0; marginal: EI = 1–4; suitable: EI = 5–9; highly suitable: EI = 10–29; optimal: EI = 30–100.

model of Stephens *et al*. (2007), the northern boundaries of the species' distribution do not fall within the modelled suitable range. This is due to dry stress (fig. 5a), with these areas falling into the arid desert (BWh) and arid steppe (BSh) climates of the Köppen-Geiger climate classification system (Kriticos *et al*., 2012). In non-irrigated areas, the seasonal phenology data generally fitted well with the $GI_W$ from the model (see figs 6a–c, for examples). In some areas the $GI_W$ stayed high for a longer period than the peak in the fly population. An example of this is in Parakou, Benin, where the $GI_W$ stayed high until November, but fly numbers peaked during May and declined towards October (fig. 6d). In most sites where irrigation was applied, the fit between $GI_W$ and seasonal phenology of the flies was improved compared with a natural rainfall scenario (see, e.g. figs 6e–g). However, at some irrigated sites, e.g., Thiès and St Louis, Senegal, a better fit was obtained using the natural rainfall scenario (figs 6h, i). For the remaining sampling sites, the graphs of seasonal phenology data and $GI_W$ are shown as Supplementary material (Supplementary Figure S1).

The potential global distribution in the absence of irrigation is shown in fig. 7a (see fig. 2 for differentiation between native and invasive ranges for *B. dorsalis*). The main limiting factors in their distributions are dry and cold stresses (figs 5a, b). The potential global distribution when 2.5 mm irrigation is added as a top-up to natural rainfall is shown in fig. 7b. All the data points in the northern boundary of the distribution of *B. dorsalis* in Africa accord with the modelled suitable range of the species. Fig. 7c gives a composite risk map, based on areas across the globe considered to be under irrigation according to Siebert *et al*. (2005). Here, some of the occurrence points in the northern boundary of the distribution of *B. dorsalis* in Africa fall out of the modelled range. In all three scenarios (figs 7a–c), all data points for *B. dorsalis* outside Africa also fall into the climatically suitable zone, with the exception of one location point in California, and one location point in Bhutan, where modelled cold stress prevents persistence (fig. 5b). However, there are a few sites in China in the Hubei, Jiangsu, Chongqing, Guizhou and Hunan provinces, from which *B. dorsalis* has been recorded (Wu *et al*., 2011; Shi

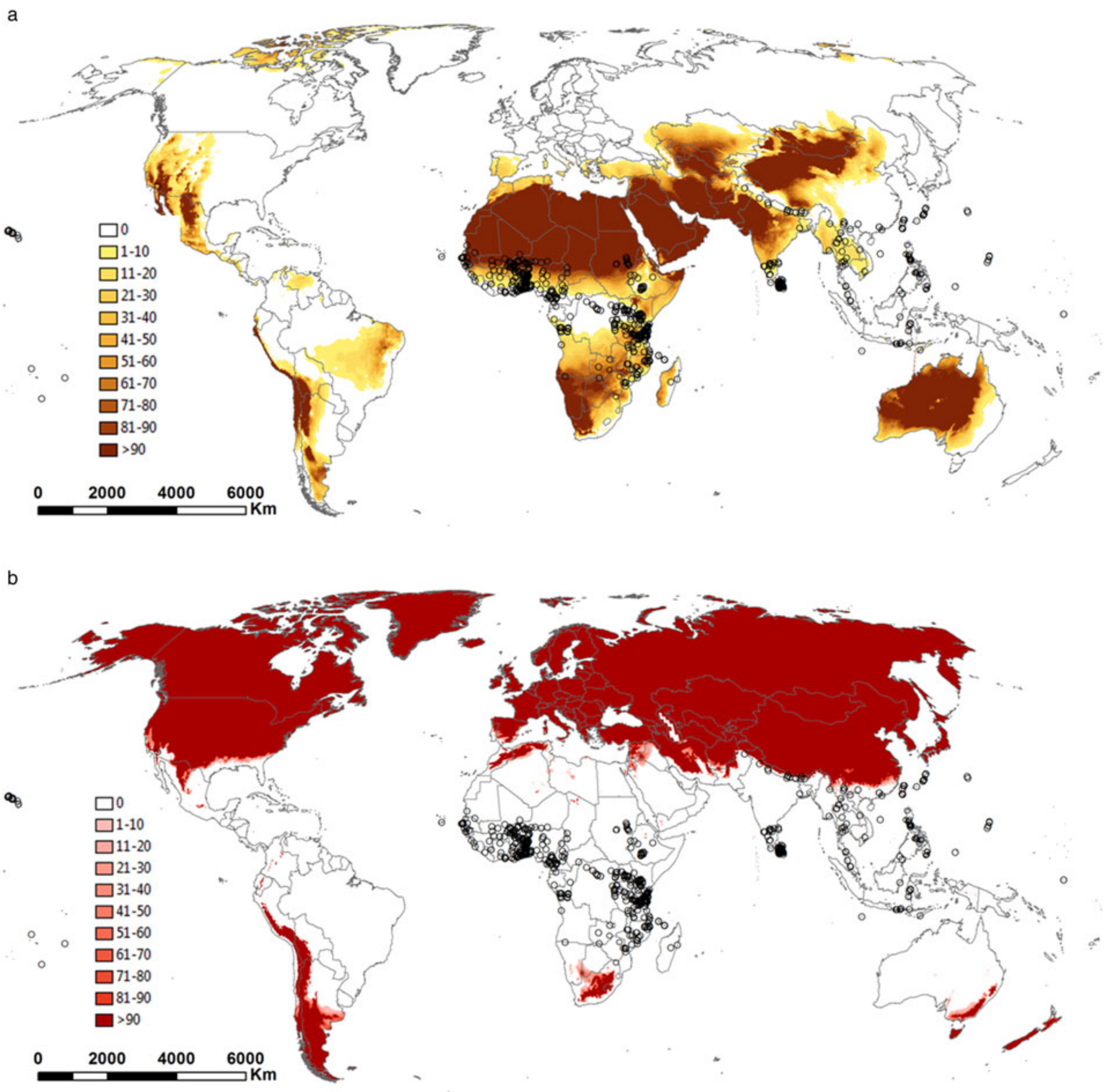

Fig. 5. Annual (a) dry stress (DS) and (b) cold stress (CS) indices for *Bactrocera dorsalis*. Open circles indicate all occurrence records of *B. dorsalis*, including the trap sites used for sampling.

*et al*., 2012; Wan *et al*., 2012) and which do not fall into this climatically suitable zone. These records were not included in the model validation and omitted from the figures, as the georeferencing of some of the records in these datasets was estimated, as opposed to being exact recordings, while others were erroneous. In addition, the majority of the records in these provinces lie along riverbeds, where (i) the climate may possibly not be represented by the courser resolution of the climatic dataset; and (ii) the records possibly represent ephemeral populations, suitable for *B. dorsalis* only during favourable seasons. The natural rainfall and composite risk maps (figs 7a, c) indicate the tropical climates (Af, Am and Aw) to be most suitable, while with an all year-round irrigation scenario across the globe (fig. 7b), high suitability is indicated in most areas where cold stress is not experienced.

## Discussion

It is clear that *B. dorsalis* is adapted to a wide range of climates. As long as irrigation is applied to alleviate the detrimental effects of dry stress, the main limiting factor appears to be cold stress, which makes a large part of the northern hemisphere unsuitable. Host availability also appears to play

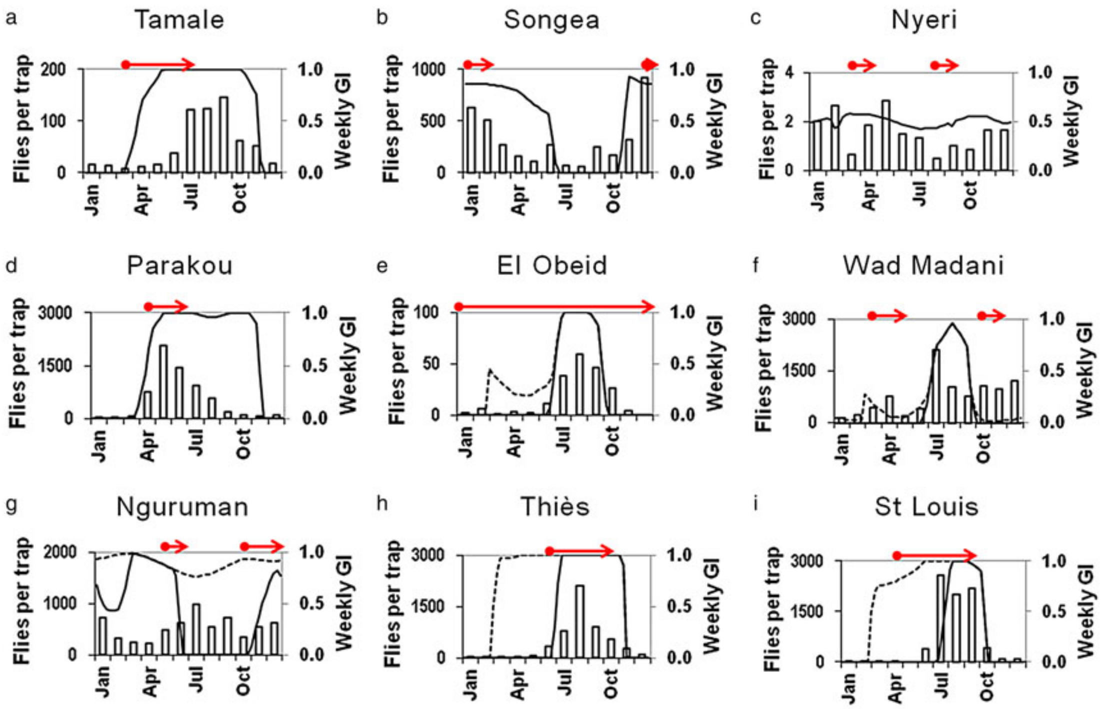

Fig. 6. Seasonal phenology, as the average number of *Bactrocera dorsalis* caught per trap per month over the 2-year sampling period, and CLIMEX weekly growth indices ($GI_W$), as projected by the CLIMEX model. White columns: flies per trap; solid black line: $GI_W$ without irrigation; dotted black line: $GI_W$ with top-up irrigation (2.5 mm year-round for Nguruman; 2.5 mm from March to July for El Obeid, Thiès and St Louis; 2.5 mm from March to July, as well as 1.5 mm for the rest of the year for Wad Madani); red arrows: period during which main fruit hosts were in a stage of ripeness susceptible to damage by *B. dorsalis* (other hosts may also have been present, without the susceptible period being recorded).

an important role in seasonal phenology. This possibly explains the reason why anomalies were observed between the $GI_W$ and fly counts in Parakou, Benin, and other sites, where the $GI_W$ was high for extended periods, which was not reflected by the pattern of fly counts. In Parakou, for instance, the period during which mangoes persisted on the trees in a stage of ripeness that makes it susceptible to fruit fly damage was from April to June (also see Vayssières *et al.*, 2008), which may explain why the numbers started to decline in the later stages of a climatically suitable period stretching from April to November. Host availability can also explain the better fit that was obtained in some of the irrigated sites between seasonal phenology and $GI_W$ of a natural rainfall scenario versus the $GI_W$ of an irrigation scenario. For instance, in Thiès, Senegal, the period with susceptible mangoes on the trees was from June to October, which matched the phenology of the fly. Irrigation applied during March–May did not influence the phenology of the fly, due to a lack of hosts, and the high $GI_W$ during this period will not match the phenology of the fly populations.

The known occurrence records for *B. dorsalis* in Africa that fall out of the modelled range in the composite risk map may be a result of an incomplete dataset, with inadequate information on which areas are irrigated globally and not including all areas bordering the Sahara. It may also be that some of the occurrence records in this region represent reported occurrences of the species during favourable seasons only, and do not indicate year-round persistence. However, in El Obeid, Sudan, which falls out of the modelled suitable range in the composite risk map, flies were active almost all year round, indicating that this region is climatically suitable and that the dataset by Siebert *et al.* (2005) used for the composite risk map, which does not show this site to be irrigated, is incomplete, at least for this region.

In the current model, only two *B. dorsalis* occurrence records that were used for model validation fell out of the modelled climatically suitable range (in southern California and Bhutan). The distribution data for *B. dorsalis* presented in Stephens *et al.* (2007) indicated a presence site in California. However, this site is possibly miscoded geographically, as it falls in a desert area, which would be unsuitable for fruit flies. In addition, there is controversy surrounding the status of *B. dorsalis* in California. EPPO (2015) reports the species to be eradicated from California. However, Papadopoulos *et al.* (2013) presented evidence that *B. dorsalis* may well be established in California, mapping recurrent detections of *B. dorsalis* over the last five decades in three regions in California (the Bay Area, Los Angeles Basin and San Diego). Whilst both the California Department of Food and Agriculture (CDFA) and the US Department of Agriculture (USDA) declared complete success for all eradication programmes against fruit flies in California (Papadopoulos *et al.*, 2013), USDA considers large areas of California as being climatically suitable for population growth (Margosian *et al.*, 2007). Papadopoulos *et al.* (2013) reported that both USDA and CDFA consider California to be suitable for establishment by *B. dorsalis*, though a careful

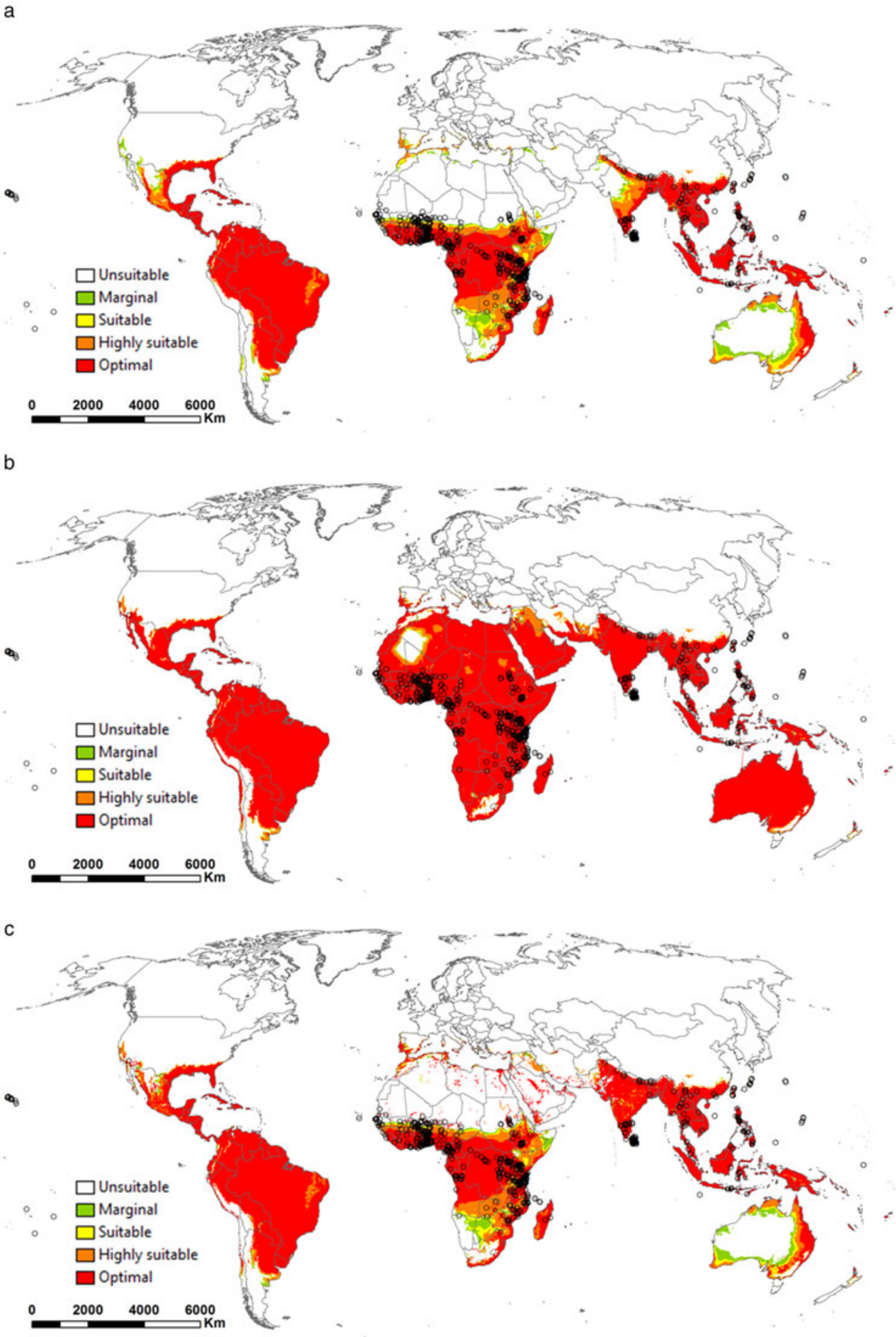

Fig. 7. The projected global climate suitability for *Bactrocera dorsalis*, (a) without irrigation, (b) with 2.5 mm top-up irrigation all year round and (c) with a composite risk irrigation scenario (where areas are not under irrigation, the EI of the natural rainfall scenario is mapped, while with areas under irrigation the EI of the irrigation scenario is mapped), using the CLIMEX EI. Open circles indicate all occurrence records of *B. dorsalis*, including the trap sites used for sampling. Unsuitable: EI = 0; marginal: EI = 1–4; suitable: EI = 5–9; highly suitable: EI = 10–29; optimal: EI = 30–100.

reading of Margosian *et al*. (2007) revealed that the modelling estimated the potential to complete generations, but did not address the potential for population persistence during inclement seasons. Therefore, it remains unclear whether or not the climate in California is suitable to sustain year-long populations of *B. dorsalis*. However, the epicentres of all three

Californian regions with recurrent *B. dorsalis* detections, presented by Papadopoulos *et al.* (2013), do fall into the modelled climatically suitable range of all three scenarios presented here. The record in Bhutan occurs in an area with large topographic relief, where the reported location fell in high elevation sites that were modelled as being excessively cold. Whilst the model may be wrong, it is plausible that this record may represent specimens trapped during a favourable season, or more likely that the gridded climate at this point may not be indicative of the area actually occupied by the flies (Kriticos & Leriche, 2009). The distribution records in central and Northern China that were not included in the model validation process and that fell out of the climatically suitable range in the current model also fell out of the climatically suitable range in the final models by Hill & Terblanche (2014), despite these authors including these records when constructing their models. These areas were also predicted to be climatically unsuitable by the MaxEnt model of De Meyer *et al.* (2010) and the CLIMEX models of Stephens *et al.* (2007) and EPPO (2010). However, the GARP model of De Meyer *et al.* (2010) indicated these areas to be climatically suitable. It is therefore unclear if the current model is underestimating the suitable range in the species' northern boundary in China. However, these areas did have a positive $GI_A$, which supports the hypothesis that these records may represent ephemeral populations.

The potential distribution as modelled using the natural rainfall and composite risk scenarios showed similarities to the overall potential distribution for *B. dorsalis* modelled using GARP (De Meyer *et al.*, 2010) and CLIMEX (Stephens *et al.*, 2007; EPPO, 2010), especially in the tropical regions where high suitability is modelled in all these models. The main difference lies in the North African boundary of distribution, where the increase of the upper temperature threshold in the current model allowed larger parts of the warmer desert areas to be suitable. In the final models by Hill & Terblanche (2014), suitability was only indicated in terms of presence and absence, and differentiation was not made between the different levels of suitability. The modelled ranges also showed similarities with the current model. However, their models showed a much more restricted potential distribution in the southern boundaries of distribution in Africa, which does not correspond with the actual distribution.

The important effect of irrigation in the distribution of *B. dorsalis*, has been demonstrated. Since dry stress is an important limiting factor, applying irrigation naïvely (ignoring whether it is practiced or whether the infrastructure is available) extends the possible range of the species dramatically, making almost the entire African and Australian continents suitable (fig. 7b). This demonstrates that, as long as irrigation is applied, which is a requirement for hosts to be grown in these areas, almost all warm, dry climates could be at risk. Such risks should be borne in mind when considering large-scale irrigation projects such as extending agriculture into Northwestern Australia. Our findings regarding the sensitivity of some species distributions to the effects of irrigation resonate with those of Vera *et al.* (2002) who modelled the potential range of the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann, and underlines the need for cautious interpretation of the meaning of species distribution data points when using them for bioclimatic modelling. While using CLIMEX, the modeller is confronted with such issues when the parameters required to fit distribution data do not accord with biologically reasonable values. With dry and cold stresses being the main limiting factors, almost all areas where irrigation is applied and where cold stress is not experienced, will be suitable for persistence of the species, highlighting the great risk posed by this pest.

The areas of greatest climatic suitability for *B. dorsalis* are large parts of Africa, South America, Central America, Mexico, the southernmost part of the USA, patches in the coastal regions of the Mediterranean, the southern and south-eastern countries in Asia, as well as parts of Southern and Eastern Australia and the North Island of New Zealand.

## Supplementary Material

The supplementary material for this article can be found at www.journals.cambridge.org/BER

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