Published version:
Bulletin of Entomological Research (2010), 100:35-48 Cambridge University Press

doi:10.1017/S0007485309006713

Ecological Niche and Potential Geographic Distribution of the Invasive Fruit Fly *Bactrocera invadens* (Diptera, Tephritidae)

M. De Meyer[a], M.P. Robertson[b], M.W. Mansell[b,c], S. Ekesi[d], K. Tsuruta[e], W. Mwaiko[f], J-F Vayssières[g], A.T. Peterson[h]

[a]Royal Museum for Central Africa, Entomology Section, Tervuren, B-3080 Tervuren, Belgium

[b]Department of Zoology and Entomology, University of Pretoria, Pretoria, 0001, South Africa

[c]United States Department of Agriculture, APHIS, Pretoria, 0001, South Africa

[d]International Centre of Insect Physiology and Ecology, PO Box 30772-00100, GPO, Nairobi, Kenya.

[e]Moji Plant Protection Station, MAFF, Nishikaigan, Moji-ku, Kitakyushu, 801-0841, Japan

[f]Ministry of Agriculture and Food Security, Plant Health Services, P.O.Box 9071, Dar es Salaam, Tanzania

[g]CIRAD, UPR Production Fruitière, Montpellier, F-34398 France ; IITA, Cotonou, Bénin.

[h]Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas 66045 USA

*Corresponding author: Marc De Meyer

Running title: Potential geographic distribution of *B. invadens*

ABSTRACT

Two correlative approaches to the challenge of ecological niche modeling (genetic algorithm, maximum entropy) were used to estimate the potential global distribution of the invasive fruit fly, *Bactrocera invadens*, based on associations between known occurrence records and a set of environmental predictor variables. The two models yielded similar estimates, largely corresponding to Equatorial climate classes with high levels of precipitation. The maximum entropy approach was somewhat more conservative in its evaluation of suitability, depending on thresholds for presence/absence that are selected, largely excluding areas with distinct dry seasons; the genetic algorithm models, in contrast, indicate that climate class as partly suitable. Predictive tests based on independent distributional data indicate that model predictions are quite robust. Field observations in Benin and Tanzania confirm relationships between seasonal occurrences of this species and humidity and temperature.

Keywords

Fruit flies, *Bactrocera invadens*, ecological niche models, potential distribution, GARP, Maxent

doi:10.1016/j.ympev.2009.11.014

INTRODUCTION

Fruit flies (Diptera: Tephritidae) are globally distributed, picture-winged flies of variable size. With >4000 species described, the family ranks among the most diverse groups of true flies (White & Elson-Harris, 1992; Thompson, 1999). Most are phytophagous, with larvae developing in the seed-bearing organs of plants. Although commonly named 'fruit flies,' larval development can take place in other parts of host plants besides fruits, including flowers and stems. About 35% of fruit fly species attack soft fruits, including many commercially important ones (White & Elson-Harris, 1992).

Several tephritids are critically important as fruit crop pests (Thompson, 1999). Economic impacts can be enormous, and control or eradication requires substantial budgets. For example, Dowell & Wange (1986) stated that establishment of major fruit fly threats to the Californian fruit industry would cause crop losses of US $910M yearly, and an eradication program would cost US $290M. Annual losses in the eastern Mediterranean (Israel, Palestinian Territories, Jordan) linked to fruit fly infestations are estimated at US $192M (Enkerlin & Mumford, 1997). Indirect losses resulting from quarantine restrictions imposed by importing countries to prevent entry and establishment of unwanted fruit fly species can also be enormous. Most economically important fruit fly pests belong to four genera: *Anastrepha* Schiner (New World Tropics), *Bactrocera* Macquart, *Ceratitis* MacLeay, and *Dacus* Fabricius (Old World Tropics).

In recent decades, several *Bactrocera* species have been introduced accidentally in other parts of the world with established fruit industries in spite of quarantine procedures, often with major economic consequences. For example, the papaya fruit fly (*B. papayae* Drew & Hancock), introduced in Australia in 1995, led to a major

doi:10.1016/j.ympev.2009.11.014

blockade of papaya exports from northern Queensland and major losses to local growers in 1995-1998. Only through an eradication program, costing US $32.5M, could the pest be eradicated and commercial trade restored (Cantrell *et al.*, 2002). The carambola fruit fly (*B. carambolae* Drew & Hancock), introduced into Suriname, has lead to drastic export reductions in the region, threatening the US $1M annual export from Guyana to neighboring Caribbean countries (USDA/APHIS, 2000).

Bactrocera invadens, a species native to Asia, was recorded for the first time on the African mainland in 2003 (Lux *et al.*, 2003), and has already become a pest species of major concern to fruit growers. Here, we develop correlative ecological niche models (ENMs) for this species, which can be projected geographically to estimate the global distributional potential of the species (Peterson, 2003). ENMs are based on digital geospatial data layers and how they correlate with known occurrences of the species in its region of origin. We develop ENM predictions of invasive potential, and test them quantitatively in Africa to measure the predictive power of the methodology for anticipating the species' global potential distribution.

Invasion history and economic impact of *Batrocera invadens*

In 2003, an unknown *Bactrocera* species was found in Kenya (Lux *et al.*, 2003). Taxonomic expertise showed that it was a member of the *B. dorsalis* complex, an Asian complex including several pest species (Drew & Hancock, 1994). Identical specimens from earlier surveys in Sri Lanka were initially classified as aberrant forms of *B. dorsalis* (Hendel), but eventually were re-identified as *B. invadens* (Drew *et al.*, 2005).

Immediately subsequent to its discovery in Kenya, the species was recorded in several countries on the African mainland (Mwatawala *et al.*, 2004, Drew *et al.*, 2005). It is

doi:10.1016/j.ympev.2009.11.014

now known to occur in tropical Africa from Senegal to Mozambique, as well as in the Comoro Islands in the Indian Ocean (De Meyer *et al*., 2007). The native range, known so far, ranges from Sri Lanka to southern India (Drew *et al.*¸2005; Sithanantham *et al*., 2006) with some isolated records from Bhutan (Drew *et al.*, 2007). It is not clear whether Bhutan should be considered as part of the native range. *T*he *B. dorsalis* species complex comprises several morphologically very similar taxa (Drew *et al.*, 2008). Other representatives of this complex occur in the same region (*e.g.*, *B. dorsalis* and *B. kandiensis*; Drew & Hancock 1994). The native range of *B. invadens* is likely larger than currently assumed, since specimens may be misidentified as other representatives of the complex (see, for example, records for *B. dorsalis* distribution by Stephens *et al.*, 2007). Therefore, the Bhutan records are considered here as part of the native range.

This invasive species has major economic impacts, ranking among the most devastating pests of local horticultural products, particularly mango (Pouilles-Duplaix, 2007). Research in West (Vayssières *et al*., 2005) and East Africa (Ekesi *et al*., 2006; Mwatawala *et al*., 2006a,b; Rwomushana *et al*., 2008) has demonstrated that it can become dominant in mango monocultures. In Benin, >60% losses due to fruit flies were recorded on main mango cultivars of economic interest in the second half of the mango season (Vayssières, 2007a), and phytosanitary pressure lead to uprooting mango plantations in one area (Borgou) in this country (Vayssières, 2007b). Native pest species such as the mango fruit fly [*Ceratitis cosyra* (Walker)] appear to be outcompeted by this invasive species, although pre-invasion data are largely lacking. In addition, *B. invadens* is polyphagous in nature, and has been reported from 44 different hosts belonging to 23 plant families (De Meyer *et al*., 2007).

doi:10.1016/j.ympev.2009.11.014

The timing and exact pathway of invasion by *B. invadens* into Africa are not known. An intensive 1999-2004 sampling program (Copeland *et al*., 2006) examined ~4000 fruit samples (~980,000 pieces of fruit) from 882 plant taxa and 116 plant families from coastal and western Kenya, and from the Central Highlands. However, not until March 2003 was *B. invadens* collected in the coastal region (Lux *et al.*, 2003). Fruit flies were sampled intensively in commercial mango orchards across coastal Guinea in West Africa in 1992-1996 (Vayssières & Kalabane, 2000) and Mali in 2000 (Vayssières *et al.*, 2004), but did not detect *B. invadens*; the first *B. invadens* specimens in that part of the African mainland were not detected until June 2004 (Drew *et al*., 2005). This species' presence in these countries before 2000 is, therefore, unlikely. Unfortunately, no similar studies were conducted at that time elsewhere in Africa where the fly currently occurs. That the first specimens were from the East African coast may indicate that the species' port of entry was the East African coast, although clear proof is lacking. A brief outbreak of a methyl eugenol-responding species in Mauritius in 1996, attributed to *B. dorsalis* (White *et al*., 2001), may actually have been *B. invadens*. The available non-teneral sample was recently re-examined, but results were inconclusive (White, 2006). In Asia, the earliest specimens date to 1993 in Sri Lanka (Drew *et al*., 2005), 2000 for Bhutan (Drew *et al*., 2007), and 2005 for India (Sithanantham *et al*., 2006). However, given likely confusion with *B. dorsalis*, careful revision of all *Bactrocera* material from that region is needed.

MATERIAL AND METHODS

Occurrence data

doi:10.1016/j.ympev.2009.11.014

Native-range distributional data for *B. invadens* were derived from surveys in Sri Lanka during 1993-1996 (Tsuruta, unpubl. data) and from the literature (Sithanantham *et al.* 2006). Records from Bhutan were drawn from Drew *et al.* (2007). Sources for non-native (i.e., non-Asian) distributional data are summarized in Table 1, resulting from independent surveys conducted by the authors in different parts of Africa, supplemented by published records (Drew *et al.*, 2005; White 2006). All records are based upon specimens clearly identified as *B. invadens* and differentiated from other taxa within the *B. dorsalis* complex. All, bar the records from southern India, were based on specimens for which identification was confirmed by taxonomic experts. After removal of duplicate records, 34 native and 192 non-native records could be referenced to reasonably precise (i.e., to within 10 km) sites. This list is exhaustive, in the sense that it comprises all distributional data currently published, as well as extensive unpublished data made available for this study. The non-native data enable quantitative tests of the predictive ability of the ecological niche models regarding the geographic potential of the species.

For georeferencing, when possible, we used coordinates from specimen labels. When such information was lacking, however, we extracted coordinates from electronic gazetteers, like GeoNet (http://earth-info.nga.mil/gns/html/index.html), or from specialized locality databases available in some institutions for their collections. Records were plotted on maps and inspected visually to detect obvious errors; peripheral records were investigated individually.

Only occurrence data originating from the species' native distribution were used to generate ENMs. Since no evidence indicates recent range expansion by *B. invadens* in Asia, and given that model predictions with and without the Bhutanese records

doi:10.1016/j.ympev.2009.11.014

differed only slightly, we present here only results from models based on distributional data including the Bhutanese records (see above).

Environmental data

Raster geospatial data sets used to characterize environments across the native distributional area and worldwide consisted of 'bioclimatic' variables interpolated at 1 km spatial resolution (Hijmans *et al.*, 2005). Particular variables used included annual mean temperature, mean diurnal range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, and precipitation of the wettest and driest months. These particular climate dimensions were chosen to represent environmental dimensions relevant to distributions and survival of small arthropods, in particular fruit flies (Fletcher, 1989; Vargas *et al.*, 1987; Vera *et al.*, 2002). No vegetation or land cover data layers were used owing to the heterogenous nature of habitats, including man-made horticultural environments, that can potentially be occupied by these species. Although host range can provide useful information with regard to species recognition in *Bactrocera* (Drew, 2004; Drew *et al.*, 2008), this information remains incomplete for *B. invadens*, particularly as regards the native range. In addition, as the majority of point localities used in this study are derived from para-pheromone trapping surveys they do not comprise host data.

Ecological niche modeling (ENM)

Our approach is based on the idea of modeling species' ecological niches, which are considered to constitute long-term stable constraints on species' potential geographic distributions (Martínez-Meyer *et al.*, 2004; Peterson, 2003; Peterson *et al.*, 1999; Raxworthy *et al.*, 2003; Wiens & Graham, 2005). Niche shifts have recently been

doi:10.1016/j.ympev.2009.11.014

reported for some species (Broennimann *et al*., 2007; Fitzpatrick *et al*., 2007; Steiner *et al*., 2008), but niche shifts over short evolutionary time frames remain controversial (Peterson & Nakazawa, 2008). Ecological niches are herein defined as the set of conditions under which a species is able to maintain populations without immigration (Grinnell, 1917; Grinnell, 1924). Several avenues of research have demonstrated accurate predictions of invasive species' potential distributions (Peterson, 2003; Peterson & Vieglais, 2001; Welk *et al.*, 2002; Morrison *et al.*, 2004; Thuiller *et al.*, 2005; De Meyer *et al.*, 2008). Our approach consisted of four steps: (1) model ecological niche requirements based on known native-range occurrences of the species; (2) test the accuracy of the native range predictions by splitting the dataset into a training and testing set; (3) test the accuracy of non-native range predictions (trained using all native records) using all available African distributional records; and (3) project the niche model globally to identify areas putatively susceptible to invasion. The global projection was based on a niche model trained using all the native range records. Other studies have used the software package CLIMEX to describe potential distributions of invasive fruit fly species (e.g., Yonow & Sutherst 1998; Sutherst *et al*., 2000; Vera *et al*., 2002; Stephens *et al*., 2007). CLIMEX differs from correlative ENM techniques in that it simulates mechanisms considered to limit geographical distributions of species in relation climate (Sutherst 2003; Stephens *et al*., 2007).

We used two correlative ENM techniques to estimate the potential distribution of this species—a genetic algorithm (GARP; Stockwell & Peters 1999) and a maximum entropy method (Maxent; Phillips *et al*. 2006), both on default settings. These two techniques provided contrasting results in recent comparisons of niche modeling

doi:10.1016/j.ympev.2009.11.014

techniques (Elith *et al.*, 2006; Peterson *et al.*, 2007; Peterson *et al.*, 2008). GARP is an evolutionary-computing approach to discovery of nonrandom associations between occurrences and raster GIS data layers that describe potentially relevant aspects of ecological landscapes. As GARP has been used widely (Peterson 2001; Anderson *et al.*, 2002; Stockwell & Peterson 2002; Anderson *et al.*, 2003; Peterson 2005), we do not present detailed descriptions of the methodology herein. In general, all analyses were run on default settings, and the best-subsets procedure (Pearson *et al.*, 2007) was used to choose a subset of models for further consideration, which were then summed to produce a single grid summarizing model agreement in predicting presence versus absence. This grid was converted to a binary prediction of presence versus absence by choosing the lowest threshold at which the species was known to occur (Rice *et al.*, 2003). The result was a set of binary grids summarizing the geographic extents of the environmental niche calculated by GARP for the species.

Maxent estimates the ecological niche of a species by determining the distribution of maximum entropy, subject to the constraint that the expected value of each environmental variable (or functions of these) under this estimated distribution matches its empirical average (Phillips *et al.*, 2006). Maxent makes use of presence records and a set of background values (pseudoabsences) drawn from the entire study region. We used default parameters in Maxent (version 1.3.0) to produce models: feature selection automatic, regularization multiplier at unity, maximum iterations 500, convergence threshold 10^{-5}, and random test percentage at zero. The result is a set of probabilities that sum to unity across the entire study area; to make values more manageable, these suitability indices are usually presented as logistic transformations

doi:10.1016/j.ympev.2009.11.014

of cumulative probabilities (Phillips *et al.*, 2006), with values ranging 0-100 (low to high suitability).

Spatial predictions of presence and absence can include two types of error: omission (predicted absence in areas of actual presence) and commission (predicted presence in areas of actual absence; Fielding & Bell, 1997). Because GARP is a random-walk procedure, it does not produce unique solutions; consequently, we followed best-practices approaches to identifying optimal subsets of resulting replicate models (Anderson *et al.*, 2003). In particular, we developed 100 replicate models; of these models, we retained the 20 with lowest extrinsic omission error rates, and then retained the 10 models with intermediate extrinsic commission error (i.e., we discarded the 10 models with area predicted present showing greatest deviations from the overall median area predicted present across all low-omission models). This 'best subset' of models was summed pixel by pixel to produce final predictions of potential distributions in the form of grids with values ranging from 0 (all models agree in predicting absence) to 10 (all models agree in predicting presence). Since the two modeling techniques produce different sorts of output with very different frequency distributions, correct choice of thresholds becomes critical in interpreting the resulting maps (Peterson *et al.*, 2007). As such, we used the lowest training presence threshold approach (LTPT) of Pearson *et al.* (2007): specifically, we inspected the native-range occurrence information relative to the raw outputs from GARP and Maxent. We determined the lowest predictive level at which any training presence point was predicted, and used that level as a minimum criterion for prediction of presence (*versus* absence) in non-native regions.

doi:10.1016/j.ympev.2009.11.014

Model testing

To evaluate the model predictions, we offer two sets of tests. First, we developed initial models across the native range region based on a subset of available data, in which 10 randomly chosen points were set aside (for testing) prior to model development; this procedure was repeated twice, with different random subsamples. Statistical significance of these predictions was assessed using the cumulative binomial probability approach described below. Second we assessed the predictive ability in Africa (using African records) for a model that was calibrated using all records from the native region. Given the rather crude resolution of this initial exploration, we assumed that different invaded-range occurrences were independent, neglecting possible effects of spatial autocorrelation. Because our goal was predicting global invasive potential, we tested model predictivity with the null hypothesis that the observed coincidence between prediction and test points was no better than chance expectations.

The most common mode of evaluating niche models in recent literature is via the area under the curve in a receiver operating characteristic (ROC) analysis (e.g., Elith *et al.* 2006). ROC analysis, however, is not appropriate to the present situation for two reasons: (1) ROCs require absence data, which are not available in the present case; and (2) ROCs weight type 1 and type 2 errors equally, but the focus on invasive potential would weight omission error more heavily than commission error (Soberón and Peterson, 2005; Peterson *et al.*, 2008). However, we use an adaptation of the ROC curve approach as a means of assessing predictive ability visually, plotting omission on an inverse scale (= “sensitivity”) against proportion of area predicted present (an estimator of 1 – specificity; Phillips *et al.*, 2006, Peterson *et al.*, 2008).

doi:10.1016/j.ympev.2009.11.014

Models were tested using binomial tests that incorporate dimensions of correct prediction of both presences (based on success in predicting independent test data) and absences (based on proportion of the area predicted present, which is taken as the probability of a success). Given that *B. invadens* has as yet only invaded Africa broadly, the universe of testing was taken as Africa (including Madagascar and the Comoro Islands) south of 18°N. Models were tested at the LTPT threshold described above.

RESULTS

Fig. 1 shows the known distributional information for *B. invadens* from its native range (Asia) and non-native distributional areas (Africa and the Indian Ocean). The projections of the two ENMs for the native range (Fig. 2) were similar: both indicate Sri Lanka and southern India as highly suitable. GARP predicted higher suitability in coastal regions (particularly the east coast) and the Ganges Delta in Bangladesh, while Maxent indicated suitability more restricted to isolated pockets in these parts when high threshold values are taken into account only. When lower thresholds were included in Maxent, the predicted areas were more similar between the two methods (Fig. 2)—we note that the LTPT for Maxent was 0.027 out of 100, whereas for GARP it was 8 out of 10. Testing model predictions by the two algorithms based on two separate random subsets, predictions from both models were significantly ($P < 0.05$) better than random expectations. For example, in one of the random subsamplings, the GARP model predicted 11.5% of the area present, but managed to predict 9 of 10 independent test points correctly; similarly, the Maxent model predicted 14.7% of the area present, but predicted all 10 test points correctly--the associated binomial probabilities were both lower than 10^{-9}. The training and

doi:10.1016/j.ympev.2009.11.014

testing sets may not be completely independent, as the native-range occurrence records are clustered in a small region; however, model predictions were also tested with records from the invaded range in Africa (see below).

Projecting niche models to Africa and Madagascar (Fig. 3) again yielded similar predictions between the two methods, with Maxent again appearing more conservative. Both models predicted high suitability in the Equatorial rain forest belt and the East African coastal regions. The GARP model predicted higher suitability in areas farther removed from the coast, particularly in Ivory Coast in the west, and Tanzania and Mozambique in the east. Also, the latitudinal limits identified by GARP predictions were broader, especially southwards, with high suitability being predicted for much of the Angolan and Mozambican coastlines; these differences were less dramatic once lower thresholds were considered in Maxent. The same tendencies are observed in global projections (Fig. 4): GARP predicted somewhat broader potential distributional areas in tropical South America and Southeast Asia (particularly Thailand, Cambodia, and Vietnam). The only areas where Maxent indicated broader potential distributional areas than GARP are in parts of Borneo, Papua New Guinea, and the western Amazon.

We used the non-native populations of *B. invadens* in Africa as a means of testing model predictivity regarding suitable areas for the species globally. Omission error was minimal—3 of 192 invaded-range test points were excluded from model predictions in each case. In both cases, model predictions were considerably better than expectations under random (null) models (binomial tests, both $P < 10^{-14}$), indicating that both approaches offer significant predictivity regarding the global potential distribution of the species. Inspecting ROC plots for the two model predictions based on independent testing data on a landscape distant from that where the models were trained, it is clear that the two models are similar in performance. Maxent appears to perform better at middle-level omission values, while GARP appears to perform better at lower omission values (Fig. 5).

DISCUSSION

Models in ecological dimensions

The two niche modeling algorithms employed in this study present a similar overall picture, although Maxent is somewhat more conservative. Comparing with the updated Köppen-Geiger Climate classification (Kottek *et al*., 2006), most suitable areas identified by our models fall within the Equatorial climate categories (minimum temperatures $\geq$18°C), especially Af (Equatorial rainforest, fully humid) and Am (Equatorial monsoon). The GARP model also assigns high suitability to a large part of the Aw (Equatorial savannah with dry winter) climate class.

This result suggests that *B. invadens* prefers hot and humid environments. Annual precipitation must be high, although it does not have to be continuous. Equatorial monsoon type climate (Am) is defined as a climate with a short dry season, but with still sufficient moisture to keep the soil humid throughout the year. Equatorial savannah climate type has a distinct dry period with driest-month precipitation of <60 mm. Continuous presence of *B. invadens* in Af amd Am climates is not as-yet supported by field data, for lack of field studies, but presence in Aw climates is now amply demonstrated. Mwatawala *et al.* (2006b) trapped *B. invadens* in orchards in the Morogoro region of central Tanzania continuously for 61 weeks in 2004-2005. Morogoro is situated in the transition zone between bimodal and unimodal rainfall belts in Tanzania with a distinct dry season: *B. invadens* is present year-round, although populations increase dramatically during the rainy season. Similar

doi:10.1016/j.ympev.2009.11.014

observations were made in Benin, in areas also demonstrating fly activity during a clear dry season (Vayssières, 2004; Vayssières *et al*., 2005).

Stephens *et al*. (2007) developed a model for the closely related *B. dorsalis* using a different approach (CLIMEX). The optimal climate suitability for Africa identified in that study corresponds reasonably well with optimal conditions for *B. invadens*, although some marked differences are evident. The CLIMEX model for *B. dorsalis* predicts optimal suitability further south along the South African coast (representing a warm temperate climate type, fully humid, with hot summers), while parts of the interior of Tanzania and northern Mozambique and parts of Nigeria were rated as less suitable. Non-native populations of *B. dorsalis* in Hawaii, have been rated to prefer humid areas (Vargas *et al*., 1989, 1990); hence, the climatic optimal conditions for the two species likely overlap broadly. Studies on niche partitioning in areas where both taxa occur are, however, lacking.

Model predictivity

Despite the fact that the great majority of known occurrences fall within predicted areas, some isolated occurrences of *B. invadens* in other ecological situations are known. Observations show that the species can occur in lowland moist and dry savannah in western Africa, the Sudan, and Zambia, which present climates with longer dry periods and hot conditions during part of the year. Some of these occurrences may correspond to anthropogenic microclimates (see, e.g., Coetzee, 2004). For example, the *B. invadens* collecting sites in the Sudan (Fig. 1) are irrigation schemes along the Blue Nile River: although situated in low-rainfall savannah habitat, these irrigated areas are typically very humid and partly under

doi:10.1016/j.ympev.2009.11.014

cultivation, with suitable host plants such as mango, citrus, guava, and banana. However, such is not the case for the other sites in Zambia and West Africa.

These discrepancies can be caused by two factors: incomplete sampling in the native region or actual niche differentiation in the non-native populations. It is plausible that the currently available native-range occurrence data are incomplete (*cf.* above). *Bactrocera invadens* might then have a much broader ecological niche in its native range. We should also take into consideration that these particular habitat types (lowland wet and dry savannah) are not present in the native distributional area, so the modeling algorithms have been presented with incomplete data on the species' distributional potential in such habitats: regions with similar climate conditions are found in central and northern India, but *B. invadens* records are not available from these regions. A more thorough inventory for the species in its native region, or at least detailed inspection and re-evaluation of *Bactrocera* records from the region, might present additional information that could improve the models. Currently, however, such information is not available.

In case of niche differentiation in invaded regions, two elements are known to cause exotic species to expand beyond their predicted climate envelope. It may result from adaptive changes in the fundamental niche of the species or changes in the realized niche (i.e. fundamental niche constrained by biotic interactions) (Broennimann *et al.*, 2007). Given the short time span between detection of the invasion and the observation of presence beyond the predicted range, the likelihood that evolutionary change has occurred that might have affected the fundamental niche of the species seems unlikely. More likely, release from biotic constraints like enemy release, (Colautti *et al.*, 2004) has an effect on the realized niche of *B. invadens*. As such, caution should be taken with regard to the boundaries of the models presented here,

doi:10.1016/j.ympev.2009.11.014

since these isolated records indicate some potential for the taxon to occur outside them. The fly's abundance in these areas is unclear for lack of continuous trapping data.

Potential threat of *B. invadens* outside its native range

Given the apparent rapid spread of *B. invadens* across Africa, and its impact on local horticulture, the risk of this species being introduced, establishing and invading other regions of the world should be considered. Our models indicate regions of the world that are climatically suitable for the species, but they do not indicate regions that *will* necessarily become invaded by the species. For a species to invade in a new region, it must overcome a series of challenges (Richardson and van Wilgen, 2004; De Meyer *et al.*, 2008). Richardson and van Wilgen (2004) listed six barriers that a species has to overcome to become invasive in a new region. Our analyses are only able to assess one of them: the likelihood of the species surviving in the new region. Regions highly suitable for the species as indicated by the models are more likely to be invaded than regions that have a low suitability. In Africa, for example, most of West Africa, Central Africa, and Madagascar, and parts of East Africa, are indicated as highly suitable by the models. Large regions of the Neotropics are also indicated as being suitable, as is most of Southeast Asia. A comprehensive assessment of invasion risk for this species for various parts of the world will require that other barriers be assessed (Thuiller *et al.*, 2005), which will require better knowledge of the species' basic biology and natural history.

As we have not explored all of the invasion challenges that non-native species face, our maps should not be interpreted as maps of invasion risk or likelihood of establishment. However, a region presenting suitable climatic conditions for the

doi:10.1016/j.ympev.2009.11.014

species is likely more vulnerable than one presenting unsuitable conditions. Regions highlighted as highly suitable by the models include areas already invaded by the species, giving some confidence in the models. Although the species has invaded several parts of Africa, we cannot be certain about risk of individuals being introduced to other regions (e.g., Neotropics or Southeast Asia), and whether propagule pressure will be sufficient to enable the species to establish there. Insights into propagule pressure can be obtained by examining the volume of trade between regions where the fly currently occurs and those regions that have suitable climate conditions (Thuiller *et al.*, 2005).

Another important consideration is whether individuals introduced to these areas can survive the local conditions long enough to breed successfully. An important element in this respect will be interspecific competition with native fruit flies. Most regions identified as being at risk already have established fruit fly faunas, comprising native species and sometimes previously introduced exotics: polyphagous species, infesting diverse fruits that also act as hosts for *B. invadens*, are already present. Duyck *et al.* (2004) stated that where polyphagous tephritid species have been introduced in areas already occupied by a polyphagous tephritid, interspecific competition has generally resulted in a decrease in numbers and niche shifts of the previously established species, without leading to complete exclusion. Duyck *et al.* (2004, 2007) assumed that life-history strategy could be a determining factor in this competition.

In Africa, most native polyphagous pests, such as *Ceratitis capitata*, express *r*-selected traits. Invasive *Bactrocera* species, on the other hand, display more *K*-selected traits. From the case studies presented by Duyck *et al.* (2004, 2007), *K*-selected species appear to be better invaders. In the case of *B. invadens* on the African mainland, some details seem to confirm this hypothesis. Data from Nguruman Rift

doi:10.1016/j.ympev.2009.11.014

Valley Province in Kenya show that the principal pest detected in monitoring traps in mango orchards, was *C. cosyra* prior to 2003, but has gradually been replaced by *B. invadens* since then (S. Ekesi, unpubl. data). Although pre-invasion data are lacking, Mwatawala *et al*. (2006a, b) showed that, in Tanzania, *B. invadens* is the major pest species in hosts such as mangoes, which were initially predominantly infested by native *Ceratitis* species such as *C. cosyra*. The latter seems to be displaced in large part by the former. However, abiotic factors may also determine different use of host resources. Vayssières *et al*. (2005), for example, showed that *C. cosyra* is still dominant during the dry season, but *B. invadens* dominates during the rainy season, probably reflecting its preference for humid environments. Whether the presence of *C. cosyra* in the dry season is the result of a shift due to interspecific pressure from the invasive species is, however, not clear for lack of comparative data predating the invasion. A better understanding of both the various biotic and abiotic factors, and of the particular interspecific competition mechanisms is needed for a more complete predictive model for invasive fruit flies such as *B. invadens*.

ACKNOWLEDGMENTS

This work was financed in part by the International Atomic Energy Agency (contract 12710). Thanks to various collaborators throughout Africa who provided distributional data from different regions in the continent.

REFERENCES

doi:10.1016/j.ympev.2009.11.014

Anderson, R.P., Gomez-Laverde, M. & Peterson, A.T. (2002) Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography*, **11**, 131–141.

Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling* **162**, 211-232.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters* **10**, 701-709.

Cantrell, B., Chadwick, B. & Cahill, A. (2002) *Fruit Fly Fighters – Eradication of the Papaya Fruit Fly*. Csiro, Collingwood, Australia 200pp.

Coetzee, M. (2004) Distribution of the African malaria vectors of the *Anopheles gambiae* complex. *American Journal of Tropical Medicine and Hygiene* **70**, 103-104.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* **7**, 721-733.

Copeland, R.C., Wharton, R.A., Luke, Q., De Meyer, M., Lux, S., Zenz, N., Machera, P. & Okumu, M. (2006) Geographic distribution, host fruit, and parasitoids of African fruit fly pests *Ceratitis anonae*, *Ceratitis cosyra*, *Ceratitis fasciventris*, and *Ceratitis rosa* (Diptera: Tephritidae) in Kenya. *Annals of the Entomological Society of America* **99**, 262-178.

De Meyer, M., Mohamed S. & White I.M. (2007) Invasive fruit fly pests in Africa. http://www.africamuseum.be/fruitfly/AfroAsia.htm. accessed on February 5th, 2008.

De Meyer, M., Robertson, M.P., Peterson, A.T. & Mansell, M.W. (2008) Ecological niches and potential geographical distributions of Mediterranean fruit fly (*Ceratitis capitata*) and Natal fruit fly (*Ceratitis rosa*). *Journal of Biogeography* **35**, 270-281.

Dowell, R.V.& Wange, L.K. (1986) Process analysis and failure avoidance in fruit fly programs pp. 43-65 in Mangel, M., Carey J.R. & Plant, R.E. (Eds) *Pest Control*. NATO ASI Series, Springer-Verlag, New York.

Drew, R.A.I. (2004) Biogeography and speciation in the Dacini (Diptera: Tephritidae: Dacinae). *Bishop Museum Bulletin in Entomology* **12**, 165-178.

Drew, R.A.I. & Hancock, D.L. (1994) The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. *Bulletin of Entomological Research, supplement* **2**: 1-68.

Drew, R.A.I, Tsuruta, K. & White, I.M. (2005) A new species of pest fruit fly (Diptera:Tephritidae:Dacinae) from Sri Lanka and Africa. *African Entomology* **13**, 149-154.

Drew, R.A.I., Romig, M.C. & Dorji, C. (2007) Records of Dacine fruit flies and new species of *Dacus* (Diptera: Tephritidae) in Bhutan. *Raffles Bulletin of Zoology* **55**, 1-21.

Drew, R.A.I., Raghu, S. & Halcoop, P. (2008) Bridging the morphological and biological species concepts: studies on the *Bactrocera dorsalis* (Hendel) complex (Diptera: Tephritidae: Dacinae) in South-east Asia. *Biological Journal of the Linnean Society* **93**, 217-226.

Duyck, P.F.; David, P. & Quilici, S. (2004) A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology* **29**, 511-520.

doi:10.1016/j.ympev.2009.11.014

Duyck, P.F., David, P. & Quilici, S. (2007) Can more *K*-selected species be better invaders ? A case study of fruit flies in La Réunion. *Diversity and Distributions* **13**, 535-543.

Ekesi, S., Nderitu, P.W. & Rwomushana, I. (2006) Field infestation, life history and demographic parameters of the fruit fly *Bactrocera invadens* (Diptera: Tephritidae) in Africa. *Bulletin of Entomological Research* **96**, 379-386.

Elith, J., Graham, C.H., Anderson, R.P. Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R. Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.McC., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129-151.

Enkerlin, W. & Mumford, J.D. (1997) Economic evaluation of three alternative methods for control of the Mediterranean fruit fly (Diptera: Tephritidae) in Israel, Palestinian Territories, and Jordan. *Journal of Economic Entomology* **90**, 1066-1072.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**, 38-49.

Fitzpatrick, M.C.; Weltzin, J.F.; Sanders, N.J. & Dunn, R. (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Global Ecology and Biogeography* **16**, 24-33.

Fletcher, B.S. (1989) Temperature-development rate relationships of immature stages and adult of tephritid fruit flies pp. 273-289 in Robinson, A.S. & Hooper, G.

doi:10.1016/j.ympev.2009.11.014

(Eds) *Fruit flies: their biology, natural enemies and control.* Elsevier, Amsterdam.

Grinnell, J. (1917) Field tests of theories concerning distributional control. *American Naturalist* **51**, 115-128.

Grinnell, J. (1924) Geography and evolution. *Ecology* **5**, 225-229.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965-1978.

Kottek, M, Grieser, J, Beck, C, Rudolf, B. & Rubel, F. (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**, 259-263.

Lux, S.A., Copeland, R.S., White, I.M., Manrakhan, A. & Billah, M.K. (2003) A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *Insect Science and its Application* **23**, 355-360.

Martínez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography* **13**, 305-314.

Morrison, L. W., Porter, S. D., Daniels, E. & Korzukhin, M. D. (2004) Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. *Biological Invasions* **6**, 183-191.

Mwatawala, M.W., White, I.M., Maerere, A.P., Senkondo, F.J. & De Meyer, M. (2004) A new invasive *Bactrocera* species (Diptera: Tephritidae) in Tanzania. *African Entomology* **12**, 154-156.

doi:10.1016/j.ympev.2009.11.014

Mwatawala, M.W., De Meyer, M., Makundi, R.H. & Maerere, A.P. (2006a) Biodiversity of fruit flies (Diptera, Tephritidae) at orchards in different agro-ecological zones of the Morogoro region, Tanzania. *Fruits* **61**, 321-332

Mwatawala, M.W., De Meyer, M., Makundi, R.H. & Maerere, A.P. (2006b) Seasonality and host utilization of the invasive fruit fly, *Bactrocera invadens* (Dipt., Tephritidae) in central Tanzania. *Journal of Applied Entomology* **130**, 530-537.

Peterson, A.T. & Nakazawa, Y. (2008) Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri. Global Ecology and Biogeography* **17**, 135–144.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**, 102-117.

Peterson, A.T. (2001) Predicting species' geographic distributions based on ecological niche modeling. *The Condor* **103**, 599-605.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* **78**, 419-433.

Peterson, A.T. (2005) Predicting potential geographic distributions of invading species. *Current Science* **89**, 9.

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science* **285**, 1265-1267.

Peterson, A.T. & Vieglais, D.A. (2001) Predicting species invasions using ecological niche modeling. *BioScience* **51**, 363-371.

doi:10.1016/j.ympev.2009.11.014

Peterson A.T., Papeş, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* **30**, 550-560.

Peterson, A.T., Papeş, M. & Soberón, J. (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modeling* **213**, 63-72.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modeling* **190**, 231-259.

Pouilles-Duplaix, A. (2007) Edito. La lutte régionale contres les mouches des fruits et legumes en Afrique de l'Ouest. *COLEACP/CIRAD Lettre d'information* **1**, 1.

Raxworthy, C.J., Martínez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. & Peterson, A.T. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature* **426**, 837-841.

Rice, N., Martınez-Meyer, E. & Peterson, A.T. (2003) Ecological niche differentiation in the Aphelocoma jays: a phylogenetic perspective. *Biological Journal of the Linnean Society*, **80**, 369–383.

Richardson, D.M. & van Wilgen, B.M. (2004) Invasive alien plants in South Africa: how well do we understand the ecological impacts? *South African Journal of Science* **100,** 45-52.

Rwomushana, I., Ekesi, S., Gordon, I. & Ogol, C.K.P.O (2008) Host plant and host plant preference studies for *Bactrocera invadens* (Diptera: Tephritidae) in Kenya, a new invasive fruit fly species in Africa. *Annals of the Entomological Society of America* **101**, 331-340.

Sithanantham, S., Selvaraj, P. & Boopathi, T. (2006) The fruit fly *Bactrocera invadens* (Tephritidae: Diptera) new to India. *Pestology* **30**, 36-37.

doi:10.1016/j.ympev.2009.11.014

Soberón, J., & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* **2,** 1-10.

Stephens, A.E.A., Kriticos, D.J. & Leriche, A. (2007) The current and future potential geographical distribution of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Bulletin of Entomological research* **97**, 369-378.

Steiner, F.M., Schlick-Steiner, B.C., Van der Wal, J., Reuther, K.D., Christian, E., Stauffer, C., Suarez, A.V., Williams, S.E. & Crozier, R.H. (2008) Combined modeling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Diversity and Distributions* **14**, 538-545.

Stockwell, D.R.B. & Peters, D.P. (1999) The GARP modeling system: Problems and solutions to automated spatial prediction. *International Journal of Geographic Information Systems* **13**, 143-158.

Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**, 1–13.

Sutherst, R.W. (2003) Prediction of species geographical ranges. *Journal of Biogeography* **30**, 805–816.

Sutherst, R.W., Collyer, B.S. & Yonow, T. (2000) The vulnerability of Australian horticulture to the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, under climate change. *Australian Journal of Agricultural Research* **51**, 467–480.

Thompson, F.C. (Ed.) (1999) *Fruit fly expert identification system and systematic information database*. Myia, **9**, ix + 524pp.

doi:10.1016/j.ympev.2009.11.014

Thuiller, W., Richardson, D. M., Pysek, P., Midgley, G. F., Hughes, G. O. & Rouget, M. (2005) Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* **11**, 2234-2250.

USDA/APHIS (2000) Cooperative Carambola fruit fly Eradication Program. Environmental Assesment, December 2000. http://www.aphis.usda.gov/ppd/es/pdf%20files/carambola.pdf

Vargas, R.I., Chang, H.B.C., Komura, M. & Kawamoto, D. (1987) Mortality, stadial duration, and weight loss in three species of mass-reared fruit fly pupae (Diptera: Tephritidae) held with and without vermiculite at selected relative humidities. *Journal of Economic Entomology* **80**, 972-974.

Vargas, R.I., Stark, J.D & Nishida, T. (1989) Abundance, distribution and dispersion indices of the oriental fruit fly and melon fly (Diptera: Tephritidae) on Kauai, Hawaiian Islands. *Journal of Economic Entomology* **82**, 1609-1615.

Vargas, R.I., Stark, J.D. & Nishida, T. (1990) Population dynamics, habitat preference, and seasonal distribution patterns of oriental fruit fly and melon fly (Diptera: Tephritidae) in an agricultural area. *Environmental Entomology* **19**, 1820-1828.

Vayssières J.F. (2004) Rapport de mission au Sénégal du 11 au 20 Décembre 2004. COLEACP-PIP. 14 p. + annexes.

Vayssières J.F. (2007a) Edito. La lutte régionale contres les mouches des fruits et légumes en Afrique de l'Ouest. *COLEACP/CIRAD Lettre d'information* **1,** 3.

Vayssières J.F. (2007b) Edito. La lutte régionale contres les mouches des fruits et légumes en Afrique de l'Ouest. *COLEACP/CIRAD Lettre d'information* **1**, 2.

doi:10.1016/j.ympev.2009.11.014

Vayssières J.F. & Kalabane S. (2000) Inventory and fluctuations of the catches of Diptera Tephritidae associated with mangoes in Coastal Guinea. *Fruits* **55**, 259-270.

Vayssières J.F., Sanogo, F. & Noussourou, M. (2004) Inventaire des espèces de mouches des fruits (Diptera: Tephritidae) inféodées au manguier au Mali et essais de lutte raisonnée. *Fruits* **59**, 1-14.

Vayssières J.F., Goergen G., Lokossou O., Dossa P. & Akponon C. (2005) A new *Bactrocera* species in Benin among mango fruit fly (Diptera: Tephritidae) species. *Fruits* **60**, 371-377.

Vera M.T., Rodriguez R., Segura D.F., Cladera J.L. & Sutherst R.W. (2002) Potential geographical distribution of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae), with emphasis on Argentina and Australia. *Environmental Entomology* **31**, 1009-1022.

Welk, E., Schubert, K. & Hoffmann, M. H. (2002) Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. *Diversity and Distributions* **8**, 219-233.

White, I.M. (2006) Taxonomy of the Dacina (Diptera: Tephritidae) of Africa and the Middle East. *African Entomology Memoir* **2**, 1-156.

White, I.M. & Elson-Harris, M.M. (1992) *Fruit flies of economic significance: their identification and bionomics,* (London: C.A.B. International and Canberra: Australian Centre for International Agricultural Research), xii + 601pp.

White, I.M., De Meyer, M. & Stonehouse, J. (2001) A review of the native and introduced fruit flies (Diptera, Tephritidae) in the Indian Ocean Islands of Mauritius, Réunion, Rodrigues and Seychelles. Pp 15-21 in *Proceedings of the Indian Ocean Commission Regional Fruit Fly Symposium, Mauritius, 5-9th*

doi:10.1016/j.ympev.2009.11.014

June 2000, (ed. by N.S. Price and I. Seewooruthun). Indian Ocean Commission, Mauritius.

Wiens, J. J. & Graham, C. H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Systematics and Evolution* **36**, 519-539.

Yonow, T. & Sutherst, R.W. (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, in relation to climate. *Australian Journal of Agricultural Research*, **49**, 935–953.

doi:10.1016/j.ympev.2009.11.014

Table 1: Distribution records for *Bactrocera invadens* with georeferences in decimal degrees. A = non-native records; O = native records

Fig. 1: Fig. 1 Distribution records for *B. invadens*. Native records in India (Ind), Sri-Lanka (Sri) and Bhutan (Bhu). Non-native records in Africa.

Fig. 2: Predicted distribution of *Bactrocera invadens* in its native range in Asia, using genetic algorithm for rule-set prediction (GARP) and maximum entropy method (Maxent). White, predicted absence, as indicated by the LTPT thresholding; shades of grey indicate higher levels of prediction (chosen arbitrarily),,with black the highest strength for predicted presence.

Fig. 3: Predicted distribution of *Bactrocera invadens* in Africa and Madagascar, using genetic algorithm for rule-set prediction (GARP) and maximum entropy method (Maxent). White, predicted absence, as indicated by the LTPT thresholding; shades of grey indicate higher levels of prediction (chosen arbitrarily),,with black the highest strength for predicted presence.

Fig. 4: Predicted distribution of *Bactrocera invadens* globally, using genetic algorithm for rule-set prediction (GARP) and maximum entropy method (Maxent). White, predicted absence, as indicated by the LTPT thresholding; shades of grey indicate higher levels of prediction (chosen arbitrarily),,with black the highest strength for predicted presence.

Fig. 5: Comparison of accumulation of predictive ability vs. proportion of area (Africa) predicted present in genetic algorithm for rule-set prediction (GARP) and maximum entropy method (Maxent) models.

doi:10.1016/j.ympev.2009.11.014