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

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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

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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
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 _Bactrocera 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
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. The 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 (Pouillès-
Duplaix, 2007). Research in West (Vayssières et al., 2005) and East Africa (Ekési 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).
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**
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

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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 (Martinez-Meyer et al., 2004; Peterson, 2003; Peterson et al., 1999;
Raxworthy et al., 2003; Wiens & Graham, 2005). Niche shifts have recently been
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.
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.
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.
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).
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
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

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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 ≥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

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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
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.
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 \textit{B. invadens} outside its native range

Given the apparent rapid spread of \textit{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 \textit{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
\textit{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 \textit{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
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
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*.

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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.