Niche Overlap of Congeneric Invaders Supports a Single-Species Hypothesis and Provides Insight into Future Invasion Risk: Implications for Global Management of the Bactrocera dorsalis Complex

Matthew P. Hill¹, John S. Terblanche¹,²

¹ Conservation Ecology & Entomology Department, Faculty of AgriSciences, Stellenbosch University, Western Cape, South Africa, ²Centre for Invasion Biology, Conservation Ecology & Entomology Department, Faculty of AgriSciences, Stellenbosch University, Western Cape, South Africa

Abstract

Background: The invasive fruit fly, Bactrocera invadens, has expanded its range rapidly over the past 10 years. Here we aimed to determine if the recent range expansion of Bactrocera invadens into southern Africa can be better understood through niche exploration tools, ecological niche models (ENMs), and through incorporating information about Bactrocera dorsalis s.s., a putative conspecific species from Asia. We test for niche overlap of environmental variables between Bactrocera invadens and Bactrocera dorsalis s.s. as well as two other putative conspecific species, Bactrocera philippinensis and B. papayae. We examine overlap and similarity in the geographical expression of each species’ realised niche through reciprocal distribution models between Africa and Asia. We explore different geographical backgrounds, environmental variables and model complexity with multiple and single Bactrocera species hypotheses in an attempt to predict the recent range expansion of B. invadens into northern parts of South Africa.

Principal Findings: Bactrocera invadens has a high degree of niche overlap with B. dorsalis s.s. (and B. philippinensis and B. papayae). Ecological niche models built for Bactrocera dorsalis s.s. have high transferability to describe the range of B. invadens, and B. invadens is able to project to the core range of B. dorsalis s.s. The ENMs of both Bactrocera dorsalis and B. dorsalis combined with B. philippinensis and B. papayae have significantly higher predictive ability to capture the distribution points in South Africa than for B. invadens alone.

Conclusions/Significance: Consistent with other studies proposing these Bactrocera species as conspecific, niche similarity and overlap between these species is high. Considering these other Bactrocera dorsalis complex species simultaneously better describes the range expansion and invasion potential of B. invadens in South Africa. We suggest that these species should be considered the same—at least functionally—and global quarantine and management strategies applied equally to these Bactrocera species.

Introduction

Alien invasive invertebrate species represent some of the most recognized vectors of agricultural damage [1], as well as important vectors of disease [2,3]. Invasions of such pests are increasingly driven by anthropogenic movements, particularly trade. After overcoming a geographic or dispersal invasion barrier, typically facilitated by high levels of propagule pressure [reviewed in [4,5]], and presuming non-limiting biotic interactions (e.g. host availability and lack of competition), the establishment success and subsequent distribution and abundance of an invasive species is ultimately determined by the species relationship to abiotic variables such as climate [e.g. [6,7]]. These relationships can be interpreted through the concept of the niche [8] and has led to the advent of species distribution models in the form of ecological niche models (ENMs) to predict the establishment and spread of invasive species [9,10]. Typically, ENMs approximate something close to the realised niche of the species [11] through characterizing species-environment relationships across a known distribution [12]. The models can then be extrapolated or projected to new geographic space (e.g. [13–15]) to investigate potential of invasion [16], and may provide information to promote risk status and aid management decisions (e.g. [17,18]). In addition to predicting invasion potential, ENMs can also be used as exploratory tools to examine niche similarity and divergence between taxonomically uncertain species (e.g. [19]). Ecological niche models have been used to help identify niche boundaries of congeneric and cryptic species [e.g. [20,21]], and in a similar way it should be possible to use ENMs to test taxonomic boundaries of
invasive species (e.g. [22–23]), leading to recommendations for pest control or management within global trade and tourism networks.

A major challenge for applying ENMs to alien invasive species is that environmental limits may be different in native and invasive ranges resulting in asymmetrical transference of models [24]. For instance, when characterizing the realized niche of the native range, the species may be inhibited by a range of barriers, including biotic and abiotic factors, that do not exist in the invasive range [25] resulting in underestimation of the potential invasive niche. Further, alien invasive species are often not in a state of equilibrium with their environment, particularly within the novel, invaded range [16,26]. This may translate into geographic range expansions as species continue to spread to fill their potential niche [6,7], or are enabled to do so through niche shifts (e.g. [27]), which may be facilitated by evolutionary adaptation (e.g. [28]). In the absence of strong biotic interactions however, it is possible to explore modelled responses and apply ENMs in an attempt to account for unstable relationships with climate, and as yet unencountered environmental conditions (e.g. [26]). To help accurately predict the extent of an invasion using ENMs, species-environment relationships in both the native and invasive ranges may need to be characterised [11,25,29]. In consequence, characterising the realised niche across both native and invasive ranges first requires that taxonomic and functional species boundaries are effectively described. For example, species descriptions may differ between countries or continents, especially in the case of cryptic species or life-stages, so that only distribution points corresponding to a particular description are employed in modelling attempts: such sub-taxon level modelling is likely to result in predictions different from ENMs considering a broader realised niche [22,25,30].

Fruit flies (Diptera: Tephritidae) are major economic pests through the world, causing huge economic losses to production of a wide range of commercial fruits. Some of the most economically important members of this family are within the Bactrocera dorsalis complex, comprising ~75 species. Two members of this complex, Bactrocera dorsalis s.s. and Bactrocera invadens, are highly polyphagous pests of a variety of plant species, with 250 identified hosts for B. dorsalis s.s. [31] and over 45 for B. invadens [32]. Bactrocera dorsalis s.s. is thought to have originated in northern southeast Asia and has since expanded its range through subtropical Asia and the Pacific Ocean [31,33]. After detection in East Africa in 2003, Bactrocera invadens was described as a separate species from B. dorsalis [34] and those invasive populations are thought to have a Sri Lankan origin [32,34].

Besides subtle morphological characters [34], there is little evidence to functionally separate B. invadens from B. dorsalis. For example, Khamis et al. [32] examined morphometry and DNA barcoding to demonstrate that B. invadens is more closely related to B. dorsalis than other Bactrocera species in that analysis. Further, Tan et al. [35] found no difference between phenylpropanoid metabolites (sex pheromones) in B. invadens and B. dorsalis males, and concluded they are a single species. While other B. dorsalis complex members are also considered separate species, recent molecular information has revealed little or no tangible species boundaries between some representatives of this complex (e.g. [32,33]) and random mating occurs readily between the investigated pairs [36]. Recent studies have examined the invasion potential of both B. dorsalis s.s. [37] and B. invadens [38] separately, using a fitted-process based model (CLIMEX) and ENMs (Maxent and GARP) respectively. De Meyer et al. [36] proposed that “the climatic optimal conditions for the two species (B. dorsalis and B. invadens) likely overlap broadly”. Since these modelling attempts, B. invadens has undergone rapid range expansion to establish in areas thought to be marginally climatically suitable, and is now reportedly present in the Limpopo province of South Africa [39], after repeated incursions and eradication reported from 2010 [40]. This B. invadens range expansion may reflect changes in drivers such as a climatic niche shift or increased propagule pressure, or that B. dorsalis and B. invadens have been considered separately, as opposed to a single species now fulfilling its potential niche.

These four Bactrocera dorsalis complex members provide an opportunity to understand niche differentiation between cryptic or conspecific species, and gain insight into biological invasions and range expansions more generally. Here we address three key questions which we answer through combining different niche exploratory methods and ENMs. First, do Bactrocera dorsalis and Bactrocera invadens display high niche overlap, and does this provide support for a single-species hypothesis (c.f. [33,35,36])? Second, is the recent range expansion of B. invadens into southern Africa likely due to niche shift, or is the species simply filling the realised niche which would have been predictable from including information from the range of B. dorsalis (and B. philippinensis and B. papayae)? Third, given potential information gained from addressing the first two questions, can revised ENMs for Bactrocera spp. provide better predictions of global invasion potential, and in turn, recommendations for management? Through addressing these questions we therefore aim to better understand niche overlap and species boundaries among Bactrocera species, range expansions and biological invasion processes in general, and direct future research to investigate key functional and phenological traits to understand outbreak potential and persistence of these important fruit fly pests.

Materials and Methods

Distribution Data

Distribution points for B. dorsalis s.s., B. invadens, B. papayae and B. philippinensis were collated from published studies [37,38,41–46] and contributions from various workers (see acknowledgements). For some localities we were required to georeference the site using Google Earth (version 7.1.1.1888; Google Inc., 2013). Due to this we selected an appropriate scale for our predictor layers (see below) and removed duplicate presence points at the grid cell level. Overall, we obtained 438 points for Bactrocera invadens, 243 points for B. dorsalis s.s., 22 points for B. papayae and 27 points for B. philippinensis (Fig. 1a). When considered at the grid cell level, this translates to 390 cells occupied for B. invadens, 185 for B. dorsalis s.s., and 25 and 19 for B. philippinensis and B. papayae respectively. This expands on the 236 points used by De Meyer et al. [38] in their modelling attempts for B. invadens. We considered the following hypotheses of species boundaries: (i) B. invadens (ii) B. dorsalis, (iii) B. dorsalis + B. papayae + B. philippinensis (iv) B. dorsalis + B. invadens + B. papayae + B. philippinensis.

Background Selection

For ENMs that are constructed within a presence-background framework, the issue of accessible area for the species is important [47,48]. For broadly distributed invasive species (where dispersal measures are largely unknown) it may be best to select backgrounds based on bioclimatic zones representing little inhibition to accessible area beyond broad climate types. Bioclimatic methods of background selection have also been recommended for their simplicity [48] and practicality [49]. We selected two different backgrounds based on broad (n = 30 global bioclimatic zones) and narrow (n = 125 global climatic strata) bioclimatic classifications, by determining Bactrocera spp. occupancy of different zones (using
point localities). For the first background we used the Köppen-Geiger climate classifications [Köppen-Geiger classifications, following the rules defined in [50] as applied to the 5’ resolution WorldClim global climatology (www.worldclim.org; Version 1.4, release 3; [51]). The climate zone types that each dataset encompassed were selected based on presence localities. As the Köppen-Geiger classification has 30 broadly classified zones, it provides a relatively broad background for ENM construction.

Our second background was selected across a finer classification system, using different classes of bioclimatic types derived through Principal Components Analysis (PCA) and then a clustering routine to classify principal components into homogeneous strata [52]. This global environmental stratification (GEns) method has high congruence with the Köppen-Geiger method, though it provides finer resolution through a higher number of classifications (strata; n = 125) [52]. Finally, we restricted both backgrounds to appropriate geographical extents. For B. dorsalis we restricted the climate zones to Asia and for B. invadens we allowed the climate zones to fall in either Africa, or Asia, but not South East Asia. Due to the resolution of our climate layers, our backgrounds did not include small islands such as Hawaii, but the presence information for such small island locations was incorporated into the models.

**Predictor Sets**

We obtained environmental data from CliMond [50], which provides 35 bioclimatic variables describing means, seasonality and trends for temperature, precipitation, solar radiation and soil moisture. We used a grid cell resolution of 10’, which is roughly 20 x 20 km at the equator. We compiled two different predictor sets for each of the Bactrocera spp. boundary hypotheses. The first of these was an expert-driven predictor set. Previously, seven of the commonly employed bioclimatic variables were included to construct ENMs for B. invadens [38]. These variables describe trends and extremes for temperature and rainfall and were chosen on the basis of them likely reflecting limits to tephritid fly distributions. These variables were also included for other tephritid (Ceratitis spp.) fly ENMs [53]. This predictor set consisted of: Mean diurnal temperature range (bio2), Temperature seasonality (standard deviation *100) (bio3), Maximum temperature of warmest month (bio5), Minimum temperature of coldest month (bio6), Temperature annual range (bio7), Precipitation of wettest month (bio13), Precipitation of driest month (bio14), and Precipitation seasonality (coefficient of variation) (bio15). We chose these eight predictor variables as our expert predictor set.

Our second predictor set was derived by first conducting exploratory analysis of the niches for each species. We used Ecological Niche Factor Analysis (ENFA) within the adehabitat package [54] in R (version 3.0.0; 2013 [55]). Some studies have used ENFA to characterize the niche of invasive species and predict distributions (e.g. [16,56]), though elsewhere ENFA has been suggested to determine variables for inclusion in ENMs [11]. All 35 predictor layers were z-transformed and ENFA was conducted for each species and a combined dataset of all species, to examine the utilization of the available environmental variables resulting in two uncorrelated axes, marginality and specialization. Marginality refers to the difference or distance between the total range of environmental variables (accessible area) and the range actually occupied by the species (point localities) [57]. Similarly, specialization refers to the variance of the variables. We used ENFA by calculating marginality for each variable and determining a predictor set that may indicate important limits to the distribution of Bactrocera spp., at the scale of climatic variables, with marginality indicating how particular the species is compared to the variable across the whole background provided [57]. Analysis was conducted on both the Köppen-Geiger and GEns defined backgrounds across both Asia and Africa (see Figure 1a) for each species, to examine the utilization of the environmental space across these backgrounds and determine variable importance...
Table 1. Variables selected for ENFA predictor sets.

| ENFA scores - Köppen | GEnS |
|----------------------|------|
| **Specialization**   |      |
| All                  | 0.44 |
| B. dorsalis s.s.     | 0.40 |
| B. invadens          | 0.82 |
| B. papayae           | 0.80 |
| B. philippinensis     | 0.59 |
| **Marginality**       |      |
| All                  | 1.98 |
| B. dorsalis s.s.     | 1.69 |
| B. invadens          | 2.47 |
| B. papayae           | 2.24 |
| B. philippinensis     | 1.84 |

| Predictor Marginality - Köppen| GEnS |
|-----------------------------|------|
| All                         |      |
| bio02                       | −0.43|
| bio03                       | −0.39|
| bio04                       | −0.69|
| bio06                       | −0.65|
| bio07                       | 0.44 |
| bio11                       | 0.41 |
| bio12                       | 0.66 |
| bio13                       | 0.79 |
| bio14                       | 0.42 |
| bio16                       | 0.56 |
| bio17                       | 0.52 |
| bio18                       |      |
| bio21                       | −0.44|
| bio26                       | −0.38|
| bio28                       | 0.43 |
| bio29                       | 0.43 |
| bio30                       | 0.36 |
| bio32                       | 0.42 |
| bio33                       | 0.61 |
| bio34                       | 0.62 |
| bio35                       | 0.44 |

The ENFA derived parameters are determined separately for each of the species boundary hypotheses and for all four species combined. The scores calculated across the Köppen-Geiger backgrounds are on the left and the GEnS scores on the right. The total marginality score will increase above 1 when considering all predictor variables.

Niche Overlap

We investigated niche overlap and similarity between the four Bactrocera spp. in both environmental (E-space) and geographic (G-space) space. We conducted PCA to summarize our predictor sets into uncorrelated axes at each Bactrocera spp. location. For the expert predictor set we included all eight variables. For the ENFA-derived sets we took the eight variables that applied to a combined dataset of all distribution points (see Table 1). We added 1000 random points from the Köppen-Geiger backgrounds of the four species, and then plotted the first two components as a biplot, clustering each of the four species with minimum convex hulls to examine overlap within E-space.

Overlap in G-space was investigated using reciprocal distribution models (RDM; [13] Fitzpatrick et al., 2007), which are reciprocally projected ENMs calibrated on separate distribution datasets and geographic backgrounds [13–15]. Such models are then reciprocally projected between native and invasive or novel ranges to measure how well models transfer and describe both distributions. Ecological niche models were constructed with Maxent (version 3.3.2i; [58,59]), a presence-background ENM method. Using Maxent (and other ENM methods) to predict the potential niche of novel environments requires model extrapolation, and thus appropriate caution should be taken to limit potential problems that result from violating underlying assumptions on training data [23,60]. Maxent has been used widely for investigating distributions of different invasive and pest invertebrates and plants (e.g. [14–16,26]) and was also applied to B. invadens [38]. For each predictor set we sampled 10 000 random points across each background, so that either every cell was accounted for, or we had good representation for each. We only examined the two datasets that were used in the PCAs; the two B. dorsalis models were projected to the background of B. invadens and vice versa. We then combined B. dorsalis with B. papayae and B. philippinensis to test against B. invadens. To test RDM performance, we used the reciprocal species occurrences as a test dataset and examined AUC (area under the receiver operating characteristic) score. Typically, models with AUC values over 0.7 are performing well, with over 0.9 being excellent.
PC1 = 68.4% and for PC2 = 24.6%. Most informative across the 4 "species"

Proportion of variance for predictor set. Proportion of variance for PC1 = 88.8% and for PC2 = 6.4%.

Below 0.5 is considered no better than random (e.g. [14–15]). For our RDMs, default Maxent parameters were used except that only hinge features were enabled (hinge features allow for a change in the gradient of the response, provide a "smoother" model when used alone (Maxent option), and are recommended for modelling invasive species; see [23,61]) and models only constructed using the 'wider' Köppen-Geiger backgrounds. As an additional evaluation of model performance, we used the True Skill Statistic (TSS) [62] which ranges from -1 to +1, with values of 1 being perfect and ≤0 considered no better than random [62]. The TSS is threshold-dependent and was calculated using omission and commission rates set at a threshold of maximum sensitivity plus specificity. Like AUC, TSS weights sensitivity and specificity equally [62], this needs to be considered when evaluating false negative predictions (omission errors), and consequences of, for invasive species [18]. We aimed to reduce false negative predictions prior, by exploring model features in an attempt to smooth responses and increase transferability, and then use equal weights for evaluation.

Figure 2. Principal components analysis (PCA) of four different Bactrocera spp. across different predictor variable sets. Light grey points represent 1000 random background points across the range of B. dorsalis s.s. and dark grey, B. invadens. a) PCA for “expert” predictor set. Proportion of variance for PC1 = 88.8% and for PC2 = 6.4%. b) PCA for ENFA driven predictor set (note: eight variables were loaded, most informative across the 4 “species”) Proportion of variance for PC1 = 68.4% and for PC2 = 24.6%.

doi:10.1371/journal.pone.0090121.g002

Range Expansion
To focus on the current range expansion into southern Africa we built ENMs (against using Maxent) with a combination of background (2), predictor set (2) and species datasets (4: the species boundary hypotheses), We sought to reduce ENM complexity through 'smoothing' predictor responses in an attempt to increase transferability and avoid possible underprediction [26]. We also only enabled hinge features and set the regularization parameter (β) at 1, 2 and 5 to examine how increases in β affected model fit and prediction. Regularization is a process of smoothing the model fit through making it more regular in an attempt to avoid fitting a too complex model [61]. All other settings were left at default and we employed 10 000 background points. Final models were run with 10 cross-validation replicates and the AUCTEST score examined. While AUCTEST was appropriate for the RDMs (ENMs using independent test datasets, not split-dataset approach), the use of AUC may be problematic as an evaluation of ENMs attempting to describe the potential distribution (e.g. [63,64]). So, to further evaluate model performance and rank complexity for each of the different ‘species’ datasets, we calculated sample size-corrected Akaïke information criteria (AIC,) (using ENMTools; [65,66]) to determine the lowest AICc value (coupled with a high AUCTEST value). We considered all combinations of background choice, predictor set (for ENFA – with and without correlated pairs identified and removed) and the different β values for all models. We performed paired t-tests across AICc scores between each model constructed on each species dataset. As a final check we examined correlation between variable pairs using Pearson’s correlation coefficient (r) for the chosen models across respective backgrounds and examined model performance when removing variables for any pair where r ≥0.75. Whilst Pearson’s r is only one measure of correlation between variables, it allowed for examination of linear correlations across the entire background area of our final predictor sets that may hamper model transferability.

To examine range expansion we projected the best performing ENM (selected through AICc approach) for each species boundary hypothesis to southern Africa and included a reconstructed De Meyer et al. [38] Maxent model. We evaluated the performance of these final models using TSS as before and measured niche breadth ($B = Levin’s measure of niche breadth (inverse concentration); see [67]), and niche overlap (Schoener's D) using ENMTools, for each of the ENMs below 14.78 on the African mainland (the most southern locality from the De Meyer et al. [38] dataset) across the logistic output grids from Maxent. We also acquired positive trap identifications from an area that has displayed recent incursion of B. invadens in South Africa. This translated into 11 trap points, but these only represented four grid cells at the resolution of our predictor layers. To test how each of the four ENMs predicted the recent invasion of B. invadens into South Africa we examined the test AUCTEST value using these trap data as an independent test dataset in Maxent.

Results
Bactrocera spp. Distributions
B. invadens and B. dorsalis s.s. are found across 10 different Köppen-Geiger climatic zones each, both occur in Asia, but B. invadens is also now widespread through Africa (Fig. 1a). Both B. papayae and B. philippinensis have restricted distributions in South East Asia, in tropical climate zones (Fig. 1a). For the GEnS background, B. dorsalis is found across 38 strata, B. invadens across 31 and B. philippinensis and B. papayae across 6 and 8, respectively. The climatic zones these strata fall into show that typically the
species are found in hot or extremely hot climates with varying rainfall regimes, from moist through to arid (Fig. 1b).

Background and Predictor Sets

The Koppen-Geiger defined backgrounds resulted in fewer climate zone classes and therefore wider geographic regions than did the backgrounds defined by occupied GEnS strata. The ENFA derived variables were different for each of the Bactrocera species (Table 1). There are no shared variables between the B. dorsalis and B. invadens datasets across both the Koppen-Geiger and GEnS backgrounds. Bactrocera philippinensis and B. papayae each share four variables with B. dorsalis and B. papaya shares four variables with B. invadens, while B. philippinensis only two (Table 1). Bactrocera invadens has the lowest scores for marginality and specialization (Table 1),

Figure 3. Reciprocal distribution models RDM for B. dorsalis s.s. + B. philippinensis + B. papayae (blue dots) and B. invadens (red dots). Ecological Niche Models shown here were constructed on ENFA-derived predictor sets as they had higher AUC_TEST and D scores than did those built on expert-driven predictor sets (see Table 2). Shading indicates suitability and solid grey areas are those that fall outside Asia and Africa. a) RDM trained on B. dorsalis + B. papayae + B. philippinensis distribution projected to the background of B. invadens, Model H (Table 2). b) RDM trained on B. invadens distribution projected to the background of B. dorsalis s.s. + B. philippinensis + B. papayae, Model E (Table 2).

doi:10.1371/journal.pone.0090121.g003
B. invadens though higher than Bactrocera dorsalis indicative of a widespread species across a variety of habitats. B. dorsalis the (represented as light and dark grey dots in Figs. 2a and b) across display high overlap across the four species. The accessible E-space predictor set (Fig. 2a) and the ENFA derived predictor set (Fig. 2b) component axes, though displays clear divergence along the two overlapping clouds when plotted on the first two principal axes, particularly for the light grey points depicting the background in Asia.

As well as being high overlap in E-space there is also high overlap in G-space, as demonstrated through RDM transferability (Figs. 3a, b) and supported in high AUCTEST; TSS and niche overlap scores (Table 2). The RDMs for B. invadens and B. dorsalis show that each species is able to project across to the distribution of the other, but in particular B. dorsalis s.s. over to B. invadens (ENFA: AUCTEST = 0.84, D = 0.86; Expert: AUCTEST = 0.80, D = 0.81) and this overlap even further enhanced by incorporating the points for B. philippinensis and B. papayae and projecting to Africa (ENFA: AUCTEST = 0.83, D = 0.91; Expert: AUCTEST = 0.845, D = 0.93). Combining the Bactrocera dorsalis species in Asia gives better prediction of the B. invadens range in Africa and gives high spatial congruence with this distribution. Schoener's D values for B. invadens projected to the Asian background range from 0.51–0.68, indicating moderate success in projecting to this background.

### Table 2. RDM performance.

| Model | Calibration | Project | Dataset | AUC\textsubscript{TRAIN} | AUC\textsubscript{TEST} | TSS | D |
|-------|-------------|---------|---------|----------------|----------------|-----|---|
| A     | B. invadens | B. dorsalis | ENFA | 0.888 | 0.762 | 0.559 | 0.51 |
| B     | B. invadens | B. dorsalis | Expert | 0.881 | 0.683 | 0.480 | 0.51 |
| C     | B. dorsalis | B. invadens | ENFA | 0.891 | 0.841 | 0.579 | 0.86 |
| D     | B. dorsalis | B. invadens | Expert | 0.894 | 0.804 | 0.461 | 0.81 |
| E     | B. invadens | DPP | ENFA | 0.888 | 0.787 | 0.568 | 0.76 |
| F     | B. invadens | DPP | Expert | 0.881 | 0.731 | 0.494 | 0.68 |
| G     | DPP | B. invadens | ENFA | 0.884 | 0.83 | 0.553 | 0.91 |
| H     | DPP | B. invadens | Expert | 0.886 | 0.845 | 0.563 | 0.93 |

Models were assessed on their ability to predict the distribution of the other species with the AUCTEST (area under the receiver operating characteristic curve) score (independent dataset not included in model construction). DPP = B. dorsalis + B. philippinensis + B. papayae. True Skill Statistic (TSS) values were calculated to evaluate model performance at the threshold of maximum training sensitivity plus specificity. Schoener's D values are the overlap of the given model in the projected range where the reciprocal model was calibrated.

doi:10.1371/journal.pone.0090121.t002

### Ecological Niche Model (ENM) performance for different Bactrocera dorsalis complex datasets.

| Species | AICc | Köppen-Geiger | GEnS | AUCTEST | Köppen-Geiger | GEnS |
|---------|------|----------------|------|----------|----------------|------|
|         | /    | Expert | ENFA | Expert | ENFA | Expert | ENFA | Expert | ENFA | Expert | ENFA |
| B. invadens | 1 | 10082.55 | 10115.73 | 10067.98 | 10161.30 | 0.870 | 0.879 | 0.848 | 0.857 |
|           | 2 | 10015.31 | 9948.31 | 10040.87 | 10016.62 | 0.863 | 0.872 | 0.838 | 0.85 |
|           | 5 | 10033.44 | 10024.97 | 10054.66 | 10084.71 | 0.855 | 0.861 | 0.827 | 0.837 |
| B. dorsalis | 5 | 15165.53 | 5778.47 | 5055.31 | 5691.30 | 0.869 | 0.846 | 0.877 | 0.852 |
|           | 2 | 4847.52 | 5271.84 | 4869.70 | 5640.72 | 0.855 | 0.856 | 0.845 | 0.845 |
|           | 5 | 4785.07 | 3570.73 | 4799.10 | 3529.23 | 0.868 | 0.818 | 0.873 | 0.828 |
| DPP       | 1 | 6330.44 | 6654.84 | 6233.28 | 6628.09 | 0.867 | 0.907 | 0.867 | 0.892 |
|           | 2 | 5975.67 | 5695.53 | 6008.80 | 6495.63 | 0.863 | 0.900 | 0.864 | 0.884 |
|           | 5 | 5942.12 | 6569.79 | 5977.70 | 6583.93 | 0.858 | 0.892 | 0.860 | 0.874 |
| All       | 1 | 16698.46 | 16095.50 | 16239.09 | 16514.54 | 0.841 | 0.851 | 0.816 | 0.826 |
|           | 2 | 16044.53 | 16136.19 | 16185.38 | 16497.96 | 0.836 | 0.843 | 0.810 | 0.819 |
|           | 5 | 16016.01 | 16170.28 | 16131.59 | 16471.56 | 0.831 | 0.830 | 0.805 | 0.804 |

DPP = B. dorsalis + B. philippinensis + B. papayae, All = B. dorsalis + B. invadens + B. papayae + B. philippinensis AICc = sample size corrected Akaike information criteria across 10 replicates, bold values represent significantly lowest AICc score (p<0.05); AUCTEST = area under the receiver operating characteristic curve; mean across 10 cross-validated replicates. / = regularization parameter.

doi:10.1371/journal.pone.0090121.t003
range, though not predicting the northern extent of *B. dorsalis* in Asia (Figs. 3b).

**Range Expansion**

Our final models for the four datasets were selected on significantly lowest AICc (coupled with a high AUC\textsubscript{TEST} score) (Table 3). Generally, the Köppen-Geiger background with the expert-driven predictor set yielded ENMs with higher performance, only separated on regularization changes (*B. dorsalis* $\beta = 2$, $p<0.05$; All $\beta = 5$, $p<0.05$; *B. dorsalis* + *B. papaya* + *B. philippinensis* $\beta = 2$, $p<0.005$), except for *B. invadens* where the ENFA variables gave the lowest AICc value ($\beta = 2$, $p<0.001$) (Table 3). However, variables describing minimum temperature of the coldest month and annual temperature range are highly correlated therefore generally, by increasing $\beta$ to values of 2 or 5, the AICc values were also significantly lowered – further reducing model complexity (beyond selecting only hinge-features) increased model performance (Table 3). Coupled with significantly different AICc scores for all model selections ($p<0.05$) the mean AUC\textsubscript{TEST} was $>0.80$, indicating high predictive ability given model conditions (Table 3). In addition our final models (bold in Table 3) all performed well with TSS values of: *B. invadens* = 0.602, *B. dorsalis* = 0.596, *B. dorsalis* + *B. philippinensis* + *B. papaya* = 0.607, All species = 0.532.

Niche breadth in southern Africa was significantly highest for the *B. dorsalis* s.s. ENM (B = 0.59, $p<0.001$) (Fig. 4a). Niche breadth for the combined dataset (B = 0.47 and the dataset of *B. dorsalis* + *B. philippinensis* + *B. papaya* (B = 0.55) were significantly higher than for *B. invadens* (B = 0.36, $p<0.001$ in both cases). Our *B. invadens* ENM also had higher niche breadth than the De Meyer et al. [38] *B. invadens* ENM in southern Africa ($p<0.001$) (Fig. 4a). Pairwise comparisons of niche overlap in southern Africa between the final *B. invadens* ENM and three other models revealed that the highest overlap was with the model considering all four species simultaneously (Comparison D, $D = 0.68$, $p<0.001$, Fig. 4b). Niche overlap between *B. invadens* and *B. dorsalis* was also high (Comparison B, $D = 0.66$, $p<0.01$) and consistent with niche breadth, there was higher overlap between *B. invadens* and the model with the other three species combined (Comparison C, $D = 0.67$, $p<0.01$). The De Meyer et al. [38] ENM and our *B. invadens* ENM had the lowest overlap (Comparison A, $D = 0.61$, $p<0.001$, Fig. 4b).

Overall, the final models for the *B. invadens* dataset and the all species combined dataset predict slightly different geographic area in Africa, particularly in the northern parts of the African range for *B. invadens* and in the southern parts of the range for the combined dataset (Fig. 5a). The De Meyer et al. [38] model predicts a more conservative distribution than these two models (Fig. 5a). The 11 points (4 grid cells) from the recent invasion of *B. invadens* in South Africa, all fall within a small area in the Limpopo province (hatched area, Fig. 5a). Consistent with the results for niche breadth, the AUC\textsubscript{TEST} values for these points were low for *B. invadens* (AUC\textsubscript{TEST} = 0.547), but then high for all species combined (AUC\textsubscript{TEST} = 0.844) and very high for *B. dorsalis* (AUC\textsubscript{TEST} = 0.937) and *B. dorsalis* + *B. philippinensis* + *B. papaya* (AUC\textsubscript{TEST} = 0.924) ENMs. While these AUC values should be interpreted cautiously given the low number of test points they do provide an indication of ENM performance for predicting this recent range expansion. The predicted global invasion potential of *B. invadens* and all four species combined is shown in Figure 5b.

**Discussion**

The recent range expansion and invasion of *Bactrocera invadens* into South Africa is a major concern for fruit growing industries within the country. Through ENMs and niche-exploration methods, we elucidated species-environment relationships and likely drivers of the geographical expansion of *B. invadens*. In answer to the questions posed by our study aims, *B. invadens* displays a highly overlapping niche in terms of both E-space and G-space with *B. dorsalis* s.s. (and *B. philippinensis* and *B. papaya*), supporting evidence that these species may indeed be conspecific. Secondly, the range expansion and invasion of *Bactrocera invadens* into South Africa is better explained through incorporating the species-environment relationships of these other members of the *B. dorsalis* complex. Thirdly, these results provide important information to predict the ongoing invasion of these *Bactrocera dorsalis*

---

**Figure 4. Niche metrics calculated for Bactrocera spp. Ecological Niche Models.** a) Niche breadth (Levin's B) for 10 replicates of each final ENM projected to mainland southern Africa (see Fig. 5a). Note: DPP = *B. dorsalis* + *B. philippinensis* + *B. papaya*. b) Niche overlap (Schoener's D) between ENMs projected to mainland southern Africa (see Fig. 5a): A = *B. invadens* & *B. invadens* De Meyer et al. (2010); B = *B. invadens* & *B. dorsalis*; C = *B. invadens* & *B. dorsalis* + *B. philippinensis* + *B. papaya* (DPP); D = *B. invadens* & All four species combined. doi:10.1371/journal.pone.0090121.g004
complex members and help direct recommendations for global management of these high risk species.

High overlap in both E- and G-space, and for both predictor sets used, is consistent with the hypothesis for *Bactrocera invadens*, *B. philippinensis* and *B. papayae* to be conspecific with *B. dorsalis* s.s. It is evident however, that E-space changes between ranges, as climatic variables are often anisotropic across large geographic extents like the backgrounds employed here [68]. This was largely visible through our PCA biplots, and may help explain the low transferability of the *B. invadens* RDM to Asia, rather than a niche shift as concluded elsewhere (e.g. [13–15]). The incomplete transferability may also be due to *B. invadens* being in a state of range expansion: that *B. dorsalis* s.s. is found in more strata from the GEnS analysis may be further indicative of this suggestion.
The advantages of updating distribution data is demonstrated by geographic differences and lowest niche overlap between the De Meyer et al. [36] model and the ENMs explored herein. Information from trap catches (there are now over 3000 Methyl Eugenol traps throughout South Africa [69]), including seasonality and abundance, should provide essential data to construct dispersal models, revisit ENMs, and further understand the rate at which B. invadens is spreading.

Without having true absence data to calibrate our ENMs, we are providing an assessment of invasion potential rather than the actual distributions for B. invadens/dorsalis [16]. By incorporating information from other members of the B. dorsalis complex into the B. invadens ENMs, some insight into the recent range expansion into South Africa can be achieved. Importantly, rather than a niche shift for B. invadens, range expansion is likely to be a single conspecific invader filling its potential niche. The differences in overlap and geographic extent between the B. invadens and the combined models may be due to sub-taxon consideration of datasets [23,30]. The B. invadens model and the combined model of the four species may reflect differences in ecology and thus provide complementary information for determining invasion potential [22]. To describe invasion potential we also attempted to increase transferability and minimize false negative predictions through reducing model complexity (e.g. feature selection). Associated error is thus more likely to fall on the side of over-prediction (commission error) rather than under-prediction (omission error) and this is likely to be a more desirable outcome when predicting the spread of a rapidly expanding species, though caution is required when translating this to management practices [18].

Invasive species that occupy large geographic extents may be modelled effectively through generalised bioclimatic backgrounds, as we found that the Koppen-Geiger was less restrictive than the GEnS background, resulting in higher model performance (or presence/background discrepancy). While use of wide backgrounds has typically been found to show lower transferability [70], model performance is affected by either too wide or too narrow a background [47]. A background based on dispersal would likely provide a useful test against these bioclimatic backgrounds, but quantifying and accurately modelling both active and passive dispersal remains challenging at present, due partly to the dispersal of tephritids through factors such as human-assisted dispersal [71]. It is likely that the GEnS selected backgrounds are suited to ENM applications for niches that are not under rapid change, such as conservation and biogeography monitoring-type analyses [52]. The fact that ENMs that were constructed on the expert-driven predictor variable set generally performed better than our ENFA one(s) provides good support for variable selection to be based on knowledge of physiological (or other functional) limits that define distributions [72]. However, often such knowledge is not present for an invasive species, and as our Bactrocera ENMs built on ENFA selected variables gave high performance, transferability and spatial congruence with the expert-driven predictor sets, we recommend that ENFA provides a valid alternative where such functional information is lacking, given that correlated predictors are identified.

Ecological niche models are useful tools for understanding invasion potential on condition that the weaknesses are identified and future research plans are centred on testing processes outside model capabilities (e.g. biotic interactions, dispersal and adaptation) (see [10]). For instance, competition has been observed between Bactrocera invadens and the indigenous Ceratitis cosyra, although in this case B. invadens was able to outcompete C. cosyra [73]. Likewise, thermal tolerance traits have been shown to differ between closely related tephritids, Ceratitis capitata and C. rosa, and this may translate into a competitive advantage to the former or a broader thermal niche [74]. By using established thermal tolerance and desiccation protocols it should be possible to test whether overlaps in E-space are related to a high degree of physiological similarity between the species [74], or if there are any shifts in physiological traits [27]. Testing for local adaptation in functional traits (such as physiological tolerances or host plant switching) can also reveal evolutionary processes that facilitate range expansion (e.g. [26]). Phenological studies and abundance data could be used to predict outbreaks and persistence of B. invadens across the geographic area of invasion potential (e.g. Ceratitis rosa [75]). For example, such information could be used to revise the existing Bactrocera dorsalis CLIMEX model [37] to examine invasion processes of B. invadens.

From previous climate-based models [37,38], both Bactrocera invadens and B. dorsalis s.s. appeared to have the potential to independently invade large geographic areas and, given the global invasion of other tephritids to date (e.g. C. capitata [53]), this seems like a reasonable assertion. Our results support a growing body of evidence that species boundaries in the B. dorsalis complex may require revision (e.g. [32,33,35,36]). Thus, we suggest that considering these B. dorsalis complex members separately has led to the underprediction of the invasive potential in both South Africa and globally. Proper management of pest invertebrates relies on correct identification of species, and due to the economic importance of these species, quarantine and management recommendations for B. invadens and B. dorsalis s.s. may need to be revised [32,36]. However, we agree with Shutze et al. [33,36] that behavioural and cytogenetic studies need to be completed before complete taxonomic revision.

Acknowledgments

The authors thank Matthew Addison for valuable comments whilst preparing this study, and to Mark Robertson and two anonymous referees for constructive criticism of an earlier version of this manuscript. Andrea Stephens provided distribution data for B. dorsalis and Mark De Meyer provided distribution data for B. invadens. Mark Shutze provided additional distribution information. ENFA analysis was assisted through a script provided by Jeremy VanDerWal. Trap locality data was supplied by farmers in Limpopo Province.

Author Contributions

Conceived and designed the experiments: MH JT. Performed the experiments: MH. Analyzed the data: MH. Contributed reagents/materials/analysis tools: JT MH. Wrote the paper: MH JT.

References

1. Ziska LH, Blumenthal DM, Runion GB, Hunt ER, Diaz-Soltero H (2010) Invasive species and climate change: an agronomic perspective. Clim Change 105: 13–42.
2. Lounibos LP (2002) Invasions by insect vectors of human disease. Ann Rev Entomol 47: 253–266.
3. Benedict MQ, Levine RS, Hawley WA, Lounibos LP (2007) Spread of the Tiger: Global risk of invasion by the mosquito Aedes albopictus. Vector-borne Zoon Dis 7: 46–83.
4. Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geog 30: 409–431.
5. Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, et al. (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26: 333–339.
6. Soberón J (2007) Grinnellian and Ehlerian niches and geographic distributions of species. Ecol Lett 10: 1115–1123.
32. Khamis FM, Masiga DK, Mohamed SA, Salifu D, de Meyer M, et al. (2012) Ecological niche and potential geographic distribution of the invasive fruit fly, Bactrocera invadens (Diptera: Tephritidae). Bull Ent Res 97: 369–378.

34. Drew RAI, Tsuruta K, White IM (2005) A new species of pest fruit fly (Diptera: Tephritidae) and the association with increased thermal resistance in an invasive mite, Tetranychus urticae (Acari: Tetranychidae). J Appl Ent 28: 272–278.

37. Stephens AEA, Kriticos DJ, Leriche A (2007) The current and future potential geographic distributions of Mediterranean fruit fly, Ceratitis capitata (Diptera: Tephritidae). Acta Trop 105: 131–145.

41. Drew RAI, Hancock DL (1994) The Mediterranean fruit fly, Ceratitis capitata, as an example. Div Dist 17: 1001–1014.

45. Wan X, Liu Y, Zhang B (2012) Invasion history of the Oriental fruit fly, Bactrocera dorsalis, in the Pacific-Asia Region: Two main invasion routes. PLoS One 7: e36176.

51. Hijmans RJ, Cameron S, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25: 1965–1978.

57. Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis of space and habitat use by animals. Ecol Mod 197: 516–519.

63. Lam BD, Khamis FM, Bobst RL (2005) The fruit fly, Bactrocera invadens, in northern Belgium using an ecological niche modelling approach. Biol Invas 7: 1153–1162.

64. Peterson AT, Papes M, Soberón J (2008) Rethinking receiver operating characteristics of ecological niche models. Methods Ecol Evol 3: 53–64.

65. Phillips SJ (2008) Transferability, sample selection bias and background data in species distribution modeling. Ecol Mod 222: 1810–1819.

66. Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species distribution: effects of climate change. Ecol Mod 190: 231–259.

68. R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org/. Accessed 2014 Feb 14.

69. Strible D, Mattyslen E (2009) Predicting the potential distribution of invasive ring-necked parakeets Psittacula krameri in northern Belgium using an ecological niche modelling approach. Biol Invas 11: 497–513.

70. Hirzel AH, Hauser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis: How to compute habitat suitability maps with absence data? Ecol Mod 163: 2027–2036.

73. Phiri SE, Schipper RE, Phillips SJ (2009) A maximum entropy approach to species distribution modeling. Proceedings of the 21st International Conference on Machine Learning. Banff, Canada.

74. Phillips SJ, Anderson RP, Schipper RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Mod 190: 731–750.

75. Phillips SJ (2008) Transferability, sample selection bias and background data in presence-only modeling: a response to Peterson et al. (2007). Ecol Mod 214: 35–50.
65. Jiménez-Valverde A (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Global Ecology and Biogeography, 21, 498–507.
66. Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33: 607–611.
67. Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol Appl 21: 335–342.
68. Nakazato T, Warren DL, Moyle LC (2010) Ecological and geographic modes of species divergence in wild tomatoes. Am J Bot 97: 680–693.
69. Soberón J, Peterson AT (2011) Ecological niche shifts and environmental space anisotropy: a cautionary note. Rev Mexicana Biodiv 82: 1348–1355.
70. Manrakhan A, Venter JH, Hattingh V (2013) The battle against an invasion: The case of the African invader fly, Bactrocera invadens. XVII Congress of the Entomological Society of Southern Africa, Potchefstroom, South Africa.
71. Anderson RP, Raza A (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus Nephelomyia) in Venezuela. J Biogeogr 37: 1378–1393.
72. Karsten M, Jansen van Vuuren B, Barnaud A, Terblanche JS (2013) Population genetics of Ceratitis capitata in South Africa: Implications for dispersal and pest management. PLoS One 8: e54291.
73. Sánchez-Fernández D, Aragón P, Bilton DT, Lobo JM (2012) Assessing the congruence of thermal niche estimations derived from distribution and physiological data: A test using diving beetles. PLoS One 7: e48163.
74. Ekési S, Billah MK, Nderitu PW, Lux SA, Rwomushana I (2009) Evidence for competitive displacement of Ceratitis capitata by the invasive fruit fly Bactrocera invadens (Diptera: Tephritidae) on mango and mechanisms contributing to the displacement. Environ Entomol 102: 981–991.
75. Nyamukondiwa C, Kleynhans E, Terblanche JS (2010) Phenotypic plasticity of thermal tolerance contributes to the invasion potential of Mediterranean fruit flies (Ceratitis capitata). Ecol Entomol 35: 565–575.
76. de Villiers M, Hattingh V, Kritzios EJ (2013) Combining field phenological observations with distribution data to model the potential distribution of the fruit fly Ceratitis rosa Karsch (Diptera: Tephritidae). Bull Ent Res 103: 60–73.