Ecological overlap between *Bactrocera* species helps explain recent expansion of *B. invadens* into South Africa

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Fruit flies are major economic pests through the world, causing huge economic losses to production of a wide range of commercial fruits. Some of the most notorious invasive species are found in the family Tephritidae, many of which cause widespread damage through puncturing fruit during egg laying and then larvae subsequently developing within the fruit. Climatic suitability is a major driver of invasion success and helps to determine ecological overlap between similarly related species. As many of the tephritids are highly invasive, we need tools to understand the role that climate plays in their pest status and determining spread.

Africa is already home to a large number of the tephritid fly species, including the Mediterranean fruit fly (*Ceratitis capitata*), Natal fly (*Ceratitis rosa*) and mango fruit fly (*Ceratitis cosyra*). A new tephritid fly was detected in Kenya in 2003. This fly was thought to have come from Sri Lanka (Drew *et al*., 2005; Khamis *et al*., 2012) and was described as a new species, *Bactrocera invadens*, commonly known as the African invader fly (Drew *et al*., 2005) (Fig. 1). *Bactrocera invadens* is part of the economically important *Bactrocera dorsalis* complex, comprising ~75 species. It is highly polyphagous, reported to have over 43 host plants (Khamis *et al*., 2012) and has spread rapidly through Africa, recently established in northern South Africa, in the Limpopo province (Venter, 2013) after repeated incursions and eradication reported from 2010 (Manrakhan *et al*., 2011).

Throughout Asia and elsewhere in the Pacific, including the USA, the oriental fruit fly, *Bactrocera dorsalis* s.s. (the species named *B. dorsalis* within a group of species called the *B. dorsalis* complex), is a major established pest with 250 identified plant hosts (Shi *et al.*, 2012). *Bactrocera invadens* is very hard to tell apart from *B. dorsalis* s.s. and the original description of *B. invadens* only separates the two species on subtle morphological characters (Drew *et al*., 2005) (Fig. 1). The similarities between the two species have increasingly led to the identity of *Bactrocera invadens* being called into question. Recent work has tested species similarities through a range of methods to try and determine the taxonomic status of these species. For example, Khamis *et al*. (2012) examined wing 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*. (2010) found no difference between sex pheromones in *B. invadens* and *B. dorsalis* males. Such studies have suggested the original description of *B. invadens* needs revisiting and that these two species are in fact the same. The species identification problem extends to other species within the *B. dorsalis* complex too. While *B. dorsalis* complex members are considered separate species, recent molecular information has revealed little or no tangible species boundaries between some other members of the complex (e.g. Khamis *et al*,. 2012; Shutze *et al*., 2012) and random mating occurs readily between the investigated pairs (Shutze *et al*., 2013).

Recent studies have examined the invasion potential of both *B. dorsalis* s.s. (Stephens *et al*., 2007) and *B. invadens* (De Meyer *et al*., 2010) separately, using different types of distribution models. De Meyer *et al*. (2010) 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 (the occurrence of the pest in Limpopo, for instance, as a case in point). In our recent paper (Hill & Terblanche, in review), we aimed to see if environmental overlap is high between *B. invadens* and *B. dorsalis* s.s. to support the current hypothesis that they are in fact the same species. As it may be that some other members of the *B. dorsalis* complex may also be part of this single species, we included two other members of the *Bactrocera dorsalis* complex in our study, namely *B. philippinensis* and *B. papayae*. By

Figure 1. *Bactrocera invadens* (left) and *Bactorcera dorsalis* (right).
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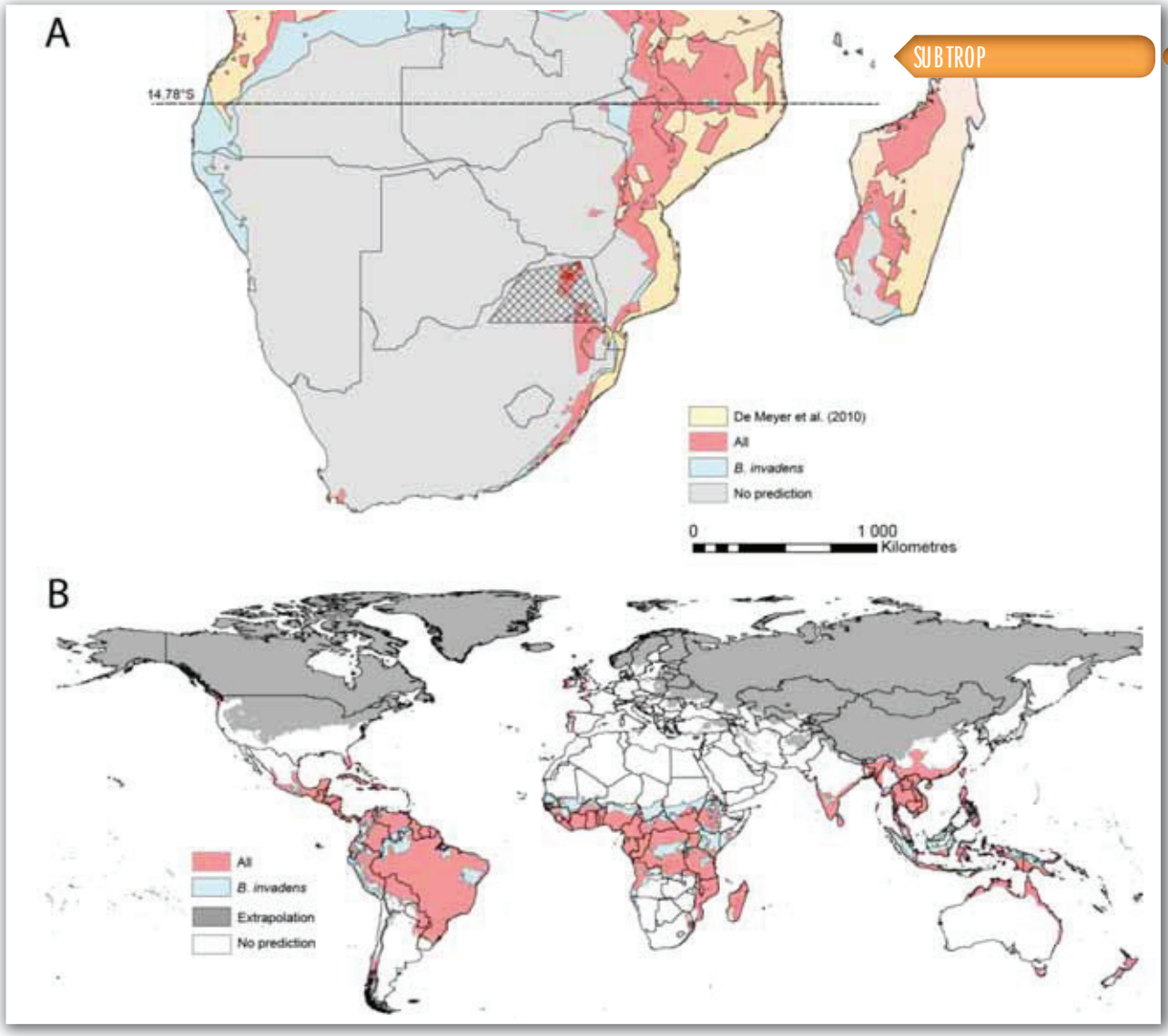

Figure 2. a) Ecological Niche Models (ENMs) projected to southern Africa to predict the range expansion of *B. invadens*. Hatched area = area affected by *B. invadens* incursions. Red points are known localities of trapped flies. b) Final ENMs projected to show global invasion potential of *Bactrocera invadens* and when considered as a single species with *B. invadens*, *B. philippinensis* and *B. papayae*. The grey shading indicates variables outside training range and extrapolation – regions where model interpretation needs to be taken cautiously (in this case, excluded).

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understanding some of the overlap between these species, it should be possible to then investigate invasion potential for these four flies considered together and separately so that a reasonable indication of spread may be ascertained.

To do this, we examined differences in the relationships between climatic variables such as temperature, rainfall and humidity, in relation to what we know about the distributions of these flies. We first tested for overlap in the ranges for sets of environmental variables between *Bactrocera invadens* and *Bactrocera dorsalis* s.s., as well as the two other putative conspecific species, *Bactrocera philippinensis* and *B. papayae*.

We then constructed predictive distribution models incorporating different species combinations. In doing so, we wanted to quantify the potential distribution of these species to understand overlap and also the future invasion potential of *B. invadens* in southern Africa and globally. One of the most common methods to do so is called an "ecological niche model". We explored different model parameters and complexity and looked to see how our models captured the current geographic distributions, and how well they performed in projecting to the invasive ranges of the different *Bactrocera* species. We tested how well the *B. dorsalis* model could predict the distribution of *B. invadens* and vice versa. Additionally, we tested how well the different models could capture distribution points for the recent establishment in the Limpopo province.

Consistent with other studies, we found that *Bactrocera invadens* has a high degree of overlap with *B. dorsalis* s.s. (and *B. philippinensis* and *B. papayae*) in terms of climatic suitability. The ecological niche models built for *Bactrocera dorsalis* s.s. were able to describe the range of *B. invadens* well, and *B. invadens* is able to project to the core range of *B. dorsalis* s.s. The models of both *Bactrocera dorsalis* and *B. dorsalis* combined with *B. philippinensis* and *B. papayae* were significantly higher in predictive ability to capture the distribution points in South Africa than for *B. invadens* alone (Fig. 2a). These results then allowed us to look at the global invasion potential of these species together (Fig. 2b).

In line with other studies that proposed *Bactrocera invadens* and *B. dorsalis* as the same species, we found that the measured ecological similarity and overlap between these species is high. Including the other two *Bactrocera dorsalis* complex species better describes

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Tawwe personeel laat Subtrop se vlag wapper

Annemarie de la Port
SUBTROP

Baanbrekerswerk het op die eerste Saterdag van April plaasgevind toe 'n groepie SUBTROP-personeel aan die "Tuffy Fun Race" deelgeneem het. Saam met Derek Donkin het vier dames die oefenskoene aangetrek: die twee jongste dames, Elsje Kleynhans en Nomvuyo Matlala, en die twee mees senior personeellede, Annemarie en Christa de la Port. Bonnie Buthelezi het as spanleier die nodige reëlings getref en gesorg dat die spannetjie spoggerig in helder oranje SUBTROP t-hemde uitgedos was. Sy het saam met die ander vroegoggend die warm vere prysgegee om ligdag die pad van Tzaneen na Coach House EN TERUG aan te durf.

Nie almal was fisies ewe voorbereid vir die steiltes wat in misreën aangedurf moes word nie. Douvoordag was nie die lekkerste tyd van die dag nie – berg op en berg af in digte mis.

By die draaipunt is deelnemers ingelig dat die aflos van 2 km afgestel is en dat almal die volle 5 km sou moes voltooi. Derek, 'n kranige hardloper, het vinnig weggespring en voor enige van sy kollegas die eindstreep oorgesteek. Elsje het ook gedraf en was in 'n goeie tweede plek, terwyl die ander drie gestap het.

Om hierdie afstand onder sulke toestande af te lê gee veel meer betekenis aan "stap". Die eerste been van die tog was 2,5 km opdraande!

Van die drie dapper stappers was Annemarie eerste terug. Christa het haar ná die draaipunt oor 'n jong meisietjie ontferm wie se gô uit was nadat sy die eerste helfte met kaal voete gedraf het, en het saam met haar teruggestap. Nomvuyo het saam met 'n klompie mammas geloop en gehelp stootkarretjie stoot.

Almal het die tog voltooi en behalwe vir 'n stywe spier of twee was daar geen ongevalle nie en was almal Maandag flink op kantoor.

Vanjaar se SUBTROP-deelnemers daag die ander uit om die volgende pretloop op volle sterkte aan te pak.

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the range expansion and invasion potential of *B. invadens* in South Africa. We therefore suggest that these species should be considered the same – at least functionally – and global quarantine and management strategies applied equally to these *Bactrocera* species.

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