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Alien species and public health impacts in Europe: a literature review

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Abstract

Impacts of alien species on human health have recently become a major issue in medical research and invasion ecology, but comprehensive assessments of this subject are largely lacking. Here, we provide a literature review of alien species with public health impacts in Europe based on a systematic search in the Thomson Reuters Web of Science. We detected 77 relevant articles, of which 21 were reviews and 56 were original research articles. The taxonomic focus was on vascular plants (n=31 articles) and dipterans (n=25 articles). The original research articles mainly covered the spread of the study species, while early invasion stages (introduction, establishment) as well as impact and management were less investigated. Alien species of health concern in Europe are mostly introduced as contaminants, and mostly originate from climatically similar regions of the Northern Hemisphere. In those cases (36% of all articles) when information on the trend in range and abundance was provided, this trend was mostly increasing. We detected little information on the severity of the impacts (two articles) and the interaction with climate change (three articles). In 15 original articles (28%) specific management measures were suggested, in only one article the socioeconomic costs were assessed. We conclude that European research on human health impacts of alien species is biased towards few species, and that several important aspects such as early invasion stages, severity of impact and its temporal trends, and the scale of the socioeconomic costs caused are poorly understood. Interdisciplinary projects bridging gaps between ecologists medical researchers, socioeconomists and public health authorities are required to link alien species to severity and trends of impacts, which is a crucial requisite for risk assessment and decision making.

Keywords

Aedes, *Ambrosia*, climate change, human health, management, vector

Introduction

Alien species invasions cause a multitude of impacts on environment (Vilà et al. 2010, 2011, Jeschke et al. 2013, Simberloff et al. 2013, Blackburn et al. 2014), and socioeconomy (Pimentel et al. 2000, Pimentel 2002, Gren et al. 2009). In particular, there is evidence for an increasing magnitude of human health impacts by alien species (Kenis and Branco 2010, Vilà et al. 2010, Richter et al. 2013, Conn 2014, Hulme 2014, Mazza et al. 2014), as globalization increases the likelihood for the movement of disease vectors (e.g. *Aedes* spp.), and has facilitated the transmission of tropical and subtropical pathogens to temperate regions (Paupy et al. 2009, Medlock et al. 2012, Bonizzoni et al. 2013). There, alien species may also benefit from climate change (Takumi et al. 2009, Walther et al. 2009, Thomas et al. 2011, Caminade et al. 2012, Dobson et al. 2013), causing additional pressure on human health (Keller et al. 2011, Strayer 2012).

Health impacts of a few alien species have already received much attention in research related to public health and invasion ecology (e.g. Smith et al. 2007, Tsetsartsin et al. 2007). In Europe, common ragweed (*Ambrosia artemisiifolia*) has become notorious for its highly allergenic pollen (e.g. Vilà et al. 2010, Bullock et al. 2012, Richter et al. 2013), giant hogweed (*Heracleum mantegazzianum*) for causing contact dermatitis (Pyšek et al. 2007), and the Asian tiger mosquito (*Aedes albopictus*) for serving as vector of several pathogens (Medlock et al. 2012). However, the human health impacts of many other alien species are far less recognized. Consequently, the taxonomic and geographic biases in understanding the impacts of alien species at large (Pyšek et al. 2008, Hulme et al. 2013) may prevail also for alien species of human health concern and may hinder a balanced understanding of the scale, patterns and trends of these impacts (Hulme 2014).

Based on a literature search, we here provide a review of the state of knowledge and associated research gaps on alien species impacting human health in Europe. In particular, we ask the following questions: (1) What is the taxonomic and geographic coverage of literature on human health impacts in Europe? (2) Which invasion stages (sensu Blackburn et al. 2011, Jeschke et al. 2013) are studied? (3) Where are the regions of origin and what are the introduction pathways of alien species of human health concern? (4) Which knowledge is currently available on issues such as severity and trends of impacts, interactions with climate change, and the scale of the socioeconomic costs?

Material and methods

Inclusion criteria

We included peer-reviewed articles dealing with species alien to Europe or being native in parts of Europe but alien to others that cause negative impacts on human health. We here define alien species as species being transported by direct or indirect human agency beyond the biogeographic limits of their past or present geographic ranges into areas in which they do not naturally occur (Richardson et al. 2000, Blackburn et al. 2011). For our purposes, we included alien species of direct health impact (e.g. allergenic plants), but also alien vector species (e.g. mosquitos, ticks, sandflies), which carry and transmit infectious pathogens to humans, and alien reservoir species (e.g. mammals), which are long-term hosts of pathogens of infectious diseases (cf. Mazza et al. 2014). In contrast, we excluded (i) emerging pathogens (e.g. virus, bacteria, prions, pathogenic fungi and protozoans – e.g. smallpox, HIV, Anthrax, Candida, Toxoplasma), if they did not arrive with alien species and were exclusively transmitted by native vector or reservoir species, (ii) domestic animals that serve as vectors or reservoirs, (iii) evidence from the native range of the species, (iv) indirect health impacts that might be caused by agricultural pests or species causing traffic accidents and (v) European species that do not fall under the definition of alien species such as those recently colonizing new regions in Europe without evidence that their spread was fostered by human assistance, although it might have been enhanced by climate change or habitat change (e.g. *Ixodes ricinus*, *Cheiracanthium punctorium*).

Literature search

We conducted a standardized and reproducible search in Thomson Reuters Web of Science (formerly ISI Web of Knowledge) in June 2013. Thus, we excluded literature published in other sources (non-indexed journals, books and conference proceedings, reports), which might contain additional relevant information. However, as the rigorous publication criteria applied for indexed publications are not necessarily met by publications in other sources, we consider our conservative approach for inclusion of publications warranted. We applied twelve search strings combining three or four search terms that specified the (i) impacted population (i.e. humans, public health), (ii) the alien species, (iii) the outcome (diseases), and (iv) the geographical focus (i.e. Europe) (Table 1). We did not use scientific or vernacular names of particular species for the search strings nor did we use reference lists of detected articles for further relevant references to avoid bias towards particular taxa. We did not apply any other kind of restrictions, e.g. regarding the year of publication.

Analyses

Titles of detected articles and subsequently their abstracts were screened to eliminate unsuitable articles that dealt for instance with pests and diseases impacting agriculture, livestock or wildlife. After this screening, 115 articles remained. Of these, 15 full texts were not available (these ones were mostly published in local journals in non-English language), 23 were excluded after reading the full version (mainly because the focal species did not fall under our inclusion criteria of being alien) and the remaining 77 were considered for further analyses.

Table 1. Applied search strings. Search strings applied in Thomson Reuters Web of Science (formerly ISI Web of Knowledge, http://thomsonreuters.com/thomson-reuters-web-of-science/) for the literature search in this review.

Population	Geography	Exposure 1	Exposure 2	Outcome
“human (health)”	**“Europe”**	**“alien species”**	**“alien species”**	**“disease”**
health*	europe*	alien*	species	
	europe*	invasiv* species	alien*	allerg*
	europe*	invasiv* species		allerg*
human* health*	europe*	invasiv* species		pathog*
		invasiv*	species	vector* born* disease*
human* health*	europe*	naturali*	species	
human* health*	europe*	establ*	species	
human* health*	europe*	introd*	species	
public* health*	europe*	exotic*	species	
public* health*	europe*	globali*	species	
public* health*	europe*	invasiv* species		parasit*
human*	europe*	exotic*	species	disease*

First, we classified each article as original research article (full length article or short report) or as review article. Then we performed descriptive analyses based on data and meta-data extracted from the included articles. These descriptive analyses dealt with bibliographic information (year of publication), taxonomic and geographic coverage, invasion stages (sensu Blackburn et al. 2011 and Jeschke et al. 2013), and finally, impact and management of review and original articles.

For original articles, we analysed the native range (continents) and the pathways of introduction (following the classification of Hulme et al. 2008) of the species. We did not perform these analyses for review articles, because they often dealt with multiple species (Van der Weijden et al. 2007, Aspöck 2008, Keller et al. 2011, Mack and Smith 2011). Further, we assessed if information on temporal trends in species distribution and abundance and on public health impact were given, if the economic costs were evaluated, and if management measures were suggested. Finally, we assessed if information on the effects of climate change on future spread and impacts of the study species was considered. All articles included and all data used in the analyses are presented in Suppl. material 1.

Results

Number of publications and temporal trends in publication

The 77 analysed articles consisted of 21 review articles and 56 original research articles (42 full articles, 14 short reports). We found a strong increase in the cumulative number of articles published (Figure 1). Interestingly, the 77 included articles were exclusively published recently, i.e. from 2002 onward.

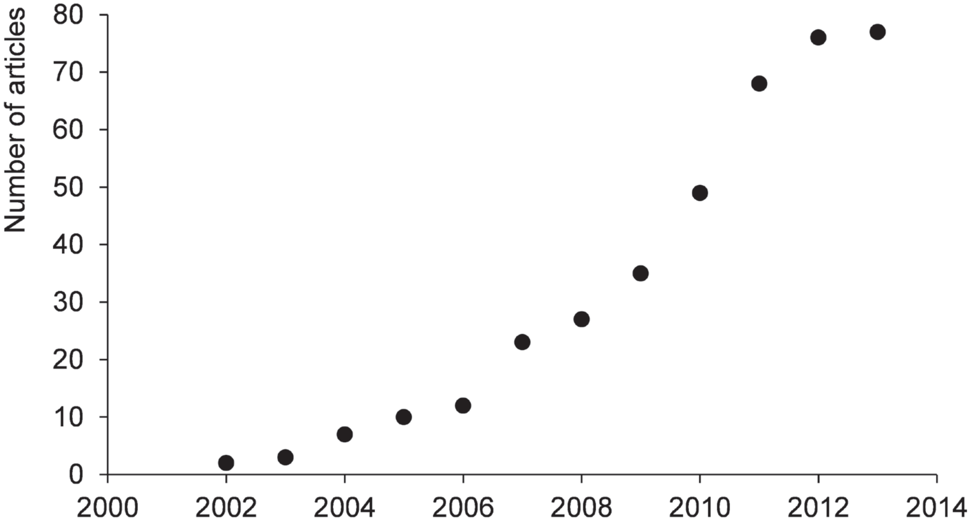

Figure 1. Temporal trend in European publications on alien species of health impact. Shown is the cumulative number of relevant articles detected by our search in Thomson Reuters Web of Science and included in this review (n=77). Note that articles published in 2013 were only partly included in Thomson Reuters Web of Science at the time of our search.

Review articles

With our search, we did not find any review article providing a complete coverage of alien species of human health impact with particular focus on Europe. Eight of the 21 review articles were dealing with dipterans (Table 2), with some of them focusing on a single mosquito species (Gratz 2004, Paupy et al. 2009), others on all alien mosquitos in Europe (Medlock et al. 2012), vectors of Arboviruses (Pfeffer and Dobler 2009), or vectors of West Nile Virus (Koopmans et al. 2007) and Leishmaniasis (Gramiccia et al. 2007, Dujardin et al. 2008, Ready 2010). Four reviews were dealing with vascular plants (Table 2), three with singles species focus (Brandes and Müller 2004, Sauerwein 2004, Gramiccia and Gradoni 2006) one considering all invasive plants of Ireland (Stout 2011). Other reviews focused on the raccoon (*Procyon lotor*; Beltrán-Beck et al. 2012) or presented short summaries on invasive birds (Brochier et al. 2010), amphibians and reptiles (Moutou and Pastoret 2010), or arthropods (Sanders et al. 2010). Aspöck et al. (2002) reviewed all human parasites and Aspöck (2008) all pathogens transmitted by arthropods, but without a dedicated focus on alien species. Further reviews on multiple taxa (Table 2, Suppl. material 2) included human parasites spreading by invasive plants (Mack and Smith 2011), vectors of vector-borne diseases (Van der Weijden et al. 2007), and a comprehensive work by Keller et al. (2011) covering all alien species in Europe, however health impacts played a very minor role in their assessment. The geographic scale of the reviews was mainly European (n=9) or global (n=6) (Table 3).

Table 2. Taxonomic coverage. The taxonomic affiliation of alien species with human health impacts in Europe detected in 77 articles. Shown is the number of alien species with human health impacts, and the number of original research articles and reviews per taxonomic group.

Taxonomic group	No of alien species	Original articles	Reviews	Total no of articles
Vascular plants (Tracheophytes)	28	27	4	31
Flies (Diptera)	6	17	8	25
Mammals (Mammalia)	2	3	1	4
Other arthropods (Arthropoda)	4	1	2	3
Mites and ticks (Acari)	7	2		2
Amphibians (Amphibia) and reptiles (Reptilia)	7	1	1	2
Birds (Aves)	53	1	1	2
Hymenoptera	1	1		1
Jellyfish (Cnidaria)	1	1		1
Multiple taxonomic groups	n.a.	*2*	*4*	*6*

Table 3. Spatial scale of relevant articles. Spatial scale of original and review articles on human health impacts of alien species in Europe.

Scale	Original articles	Review articles	Total
Global	3	6	9
European	6	9	15
Subcontinental	4	3	7
National	24	3	27
Subnational / local	16	0	16
Local lab / field trials	3	0	3

Original research articles

In the 56 included original articles, we found a strong bias in taxonomic coverage of alien species in Europe (Table 2; Suppl. material 2). Most articles were available for vascular plants of human health concern (n=27) and for dipterans (n=17) of human health concern, while only few articles dealt with other taxa such as mammals, ticks (acari), amphibians and reptiles, and birds. The single species most frequently studied were *Ambrosia artemisiifolia* (n=19) and *Aedes albopictus* (n=12) (See Suppl. material 2).

Most of the original research articles dealt with the national and regional scale (Table 3). Western, southern and central European countries had higher coverage by research articles, whereas little information was found for eastern and northern Europe (Figure 2, Suppl. material 3). Invasion stages were represented in an unbalanced manner (G test with Williams correction G=39.02, df=3, p<0.001; Figure 2). Most articles had a strong focus on spread (n=31 original articles), fewer on introduction (n=6), establishment (n=7), and transport (n=2). Similarly, a moderate number of publications studied impact (n=5) or management (n=5). Fourteen articles dealt with two or more invasion stages, impact or management. A large fraction of publications dealing with establishment (71%) and impact (50%) were short reports (See Suppl. material 1).

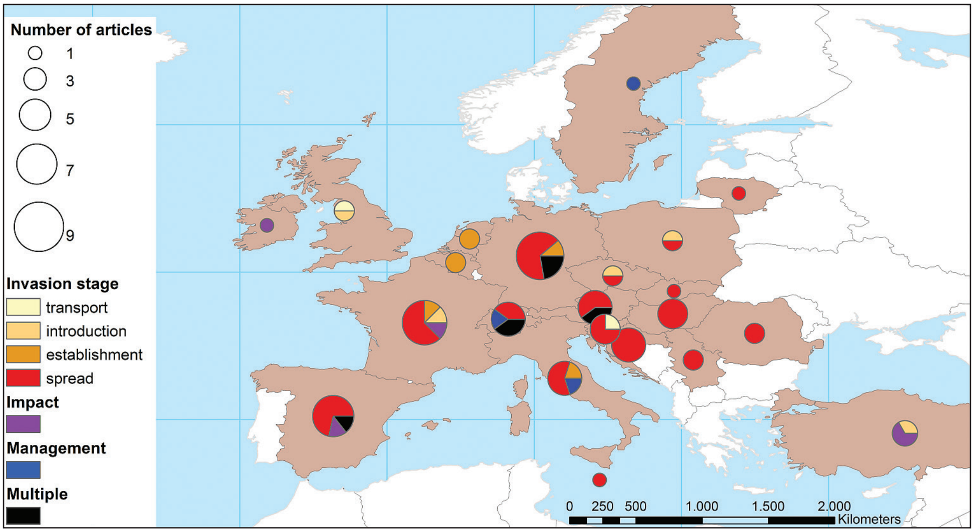

Figure 2. Geographical coverage of the original research articles. The map shows the geographical distribution of the detected original research articles on human health relevant alien species, broken down into invasion stages, impact and management. Articles dealing with several countries were assigned to each study country, whereas articles dealing with the European or global scale were not included in this map.

Geographic origins and pathways of introduction

Most of the 56 included original articles were dealing with alien species native to North America (n=20) and Asia (n=18), less with species from Africa (n=2) and the marine environment (n=2). The 56 articles covered 111 taxa (Suppl. material 2), of which 53 bird species were only listed in a single table of one article because of detected microsporidia infection (Kašičkova et al. 2009) and not considered for further analyses. The remaining 58 taxa also originated predominantly from North America (n=22) and Asia (n=11), but several articles dealing with multiple taxa also considered alien species from the Southern Hemisphere (Figure 3, Suppl. material 2).

Thirty-five articles dealt with contaminants and eight articles with released and escaped species. The two articles on the marine environment dealt with introductions by stowaway (ballast water) and corridors (Lessepsian migration). Fourteen articles dealt with taxa of multiple origins or multiple pathways. Again, the covered species were predominantly introduced as contaminants (total n=21 taxa), however some articles (e.g. Hidalgo-Vila et al. 2008, Hulina 2010) covered several taxa which escaped (n=19 taxa) or were released (n=9 taxa) (Figure 3, Suppl. material 2).

Severity of health impacts, temporal trends, and interaction with climate change

In only two of the 56 original articles (De Haro et al. 2010, Öztürk and İşinibilir 2010) the severity of the impact was quantified and only in one of them the trend in

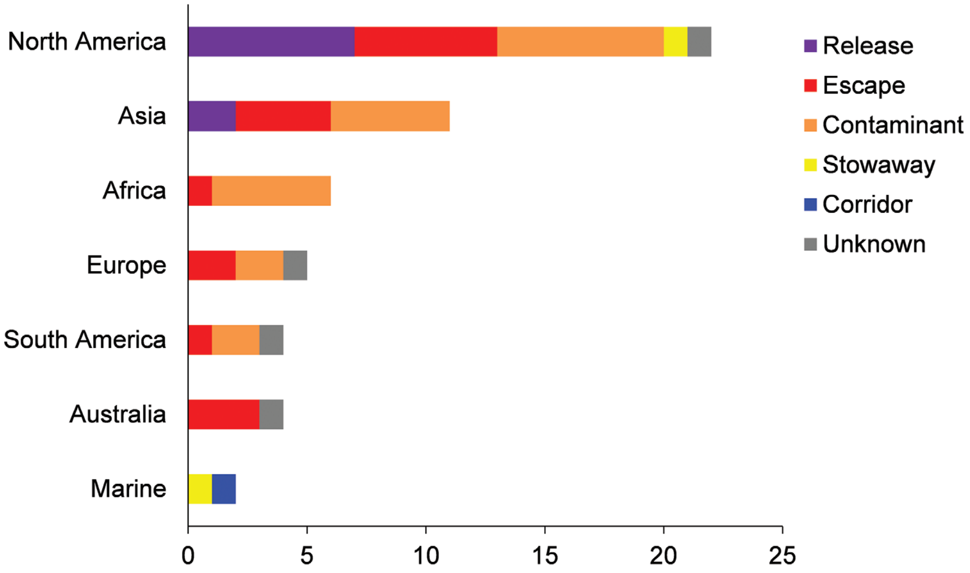

Figure 3. Pathways of introduction and native ranges (continents). Presented for 58 alien taxa of human health concern. Hybridogenous species which have arisen in the native range (e.g. anecophytes) or such native on several continents are not included (See Suppl. material 1).

Table 4. Temporal trends in distribution and impacts. Information on observed or projected changes of species range, species abundance or impact provided in the original research articles on alien species of human health concern in Europe (n=56).

Criteria	Temporal trend				Total
	Not assessed	Decreasing	Stable	Increasing	
Introduction rate	3				**3**
Species abundance	1		1		**2**
Species distribution	18		2	15	**35**
Impact	5		1		**6**
Management effectiveness	4				**4**
Infection rates of vectors or reservoir species	5		1		**6**
Total	**36**	**0**	**5**	**15**	**56**

impact was quantified by showing that no change occurred in the number of hymenoptera envenomations (i.e. stings or bites by a venomous animal including injection of venom) in the areas affected by Asian hornet (*Vespa velutina*) invasion (De Haro et al. 2010). In 36% of all articles, mainly those related to species distribution, also information on temporal trends was provided (Table 4). In most cases there was evidence of an observed or projected increase in distribution or impact (15 out of 20 articles, i.e. 75%), whereas no evidence was provided on decreasing distribution or impacts.

Table 5. Consideration of climate change in original research articles. Climate change effects were mainly discussed or assessed in articles on the spread of health relevant alien species. Only original research articles (n=56) have been analysed.

Invasion stage	**Climate change**		
	Assessed	Discussed	Not considered
Transport		1	1
Introduction		1	5
Establishment		1	6
Spread	3	13	15
Impact			5
Management		2	3
Total	**3**	**18**	**35**

Most of the 56 primary original articles did not consider potential effects of climate change (Table 5). Only three articles (Fischer et al. 2011, Thomas et al. 2011, Caminade et al. 2012) assessed climate change impacts, and further 18 discussed potential impacts of climate change.

Management experience and costs of management or medical treatment

In 15 original articles (27%) specific management measures were proposed, which were usually derived from the presented research. In further 20 articles (36%), general management measures were discussed or proposed. In the remaining 21 articles (38%), management measures were not mentioned. In only one original article the socioeconomic costs were assessed (Gren et al. 2009), in five articles management costs or socioeconomic costs of impact were discussed.

Discussion

We found that the analysed European literature on alien species of human health concern is biased towards few well studied species of only two taxonomic groups, allergenic plants of the family Asteraceae and disease vectors of the order Diptera. On the other hand, we did not detect literature focusing on some taxa of global human health relevance (e.g. snails, bivalves, crayfish) (Mazza et al. 2014), and comparably few information on disease vectors of the subclass Acari, or on vertebrates as reservoirs of alien pathogens. This demonstrates that a few organisms are dominating the literature and that the pronounced taxonomic bias in understanding the impacts of alien species at large (Pyšek et al. 2008, Hulme et al. 2013) also prevails for alien species of human health concern in Europe. This is of concern as lessons learned from few species not necessarily hold true for other species, and thus the risks posed by emerging pathogens may not be fully recognized.

Also the severity of the health impact is poorly covered by the literature, and temporal trends of impacts can almost only be estimated by proxy information. It would be desirable to know to what extent alien species introduced to Europe led to increased rates of disease incidents, but this is difficult, because original hosts or vectors are rarely identified (Hulme 2014). For instance, most articles dealing with the spread of species are explaining the type of impact (e.g. allergenic plant, disease vector), but analytic assessments of trends of numbers of impacted persons hardly occur. Öztürk and İşinibilir (2010) specify 815 hospitalizations after the arrival of the alien scyphomedusa *Rhopilema nomadica* in the Eastern Mediterranean (Turkish coast). One French article reports no increase of total hymenoptera envenomations after the establishment of alien *Vespa velutina* (De Haro et al. 2010), but the reported envenomation data do not differentiate *Vespa velutina* stings from those of native hymenopteran species, and the study therefore cannot be considered as evidence for no impact. This lack of quantitative information on severity and trend of impacts is problematic, because species impact and its severity is crucial for risk assessments (D'hondt et al. 2015) and commonly considered as the best criterion for prioritizing its management (e.g. Blackburn et al. 2014). In this context it is also important to note that estimates of monetary costs of alien species on human health in Europe are scarce, although such figures are decisive to steer decision making (Kettunen et al. 2009, Vilà et al. 2010). Kenis and Branco (2010) mention that economic studies on the impact of alien arthropods worldwide are numerous, with most of them have been undertaken in North America, South Africa and Oceania (Born et al. 2005), but less so in Europe.

Spatial patterns and temporal trends

The risks posed by alien species of human health concern are not equally distributed across Europe. Currently, evidence on human health impacts in Europe has mostly been documented in central and southwestern Europe, whereas little evidence is available for other European regions (Fig. 2). Whereas for northern Europe this lack of evidence most likely truly reflects a lower level of impacts, it is probable that it reflects for southeastern Europe a poor documentation of impacts. For instance, the first record of *Aedes albopictus* in Europe has been made in Albania (Adhami and Reiter 1998), but most articles are dealing with countries such as Spain (Eritja et al. 2005), Italy (Neteler et al. 2011) and the Netherlands (Takumi et al. 2009). Similarly, the highest infestation levels of common ragweed, the alien plant species with the strongest human health impacts in terms of costs and people affected (Vilá et al. 2010), are found in the Pannonian Basin of eastern Europe (Chapman et al. 2014), whereas most articles are from France (Dessaint et al. 2005, Genton et al. 2005, Fumanal et al. 2007, Chauvel and Cadet 2011). Thus the detected East-West divide seemingly does not reflect health impact, but mirrors research intensity. It is less biased towards Western Europe than in other medical and environmental research topics such as infectious diseases (Bliziotis et al. 2005, Durando et al. 2007), public health and preventive and environmental medicine (Soteriades and Falagas 2006), and farmland bird biodiversity (Báldi and Bátary 2011).

Although often lacking direct evidence, the European literature on alien species relevant to human health suggests that the magnitude of the impacts is increasing. This is mainly concluded indirectly from widespread evidence of increasing ranges and abundances of the species (Essl et al. 2009, Paupy et al. 2009, Walther et al. 2009, Keller et al. 2011, Neteler et al. 2011, Thomas et al. 2011, Caminade et al. 2012, Follak et al. 2013, Mazza et al. 2014). Velocity and rate of future spread are often dependent on the trajectories of globalization and climate, as these drivers act in concert in fostering the spread of most alien species of human health concern. Whereas climate change modulates habitat suitability, globalization increases propagule pressure and therefore the likelihood of introduction and establishment and thus range filling. Many species which are currently limited by temperature in Europe are projected to expand into currently climatically unsuitable regions mostly to the north (Chen et al. 2011). This projected northward and upward shift of most alien species under climate change will modify the location of those regions which are affected most by alien species of human health concern. For instance, the allergenic plants annual mugwort (*Artemisia annua*) and *Ambrosia artemisiifolia* are expected to increase their range and abundance due to rising temperatures (Essl et al. 2009, Follak et al. 2013). Thermophilic alien mosquito species, such as the yellow fever mosquito (*Aedes aegypti*) are assumed to establish in Mediterranean Europe (Thomas et al. 2011). Alien mosquito vectors from temperate Asia (e.g. *Aedes albopictus*) are projected to spread throughout central and northern Europe under climate change, whereas in the most arid parts of southern Europe the climatic suitability for their establishment might deteriorate (Eritja et al. 2005, Fischer et al. 2011, Caminade et al. 2012), as these species require ephemeral standing water bodies for their reproduction cycle. Additionally to range shifts due to climate change, habitat shifts might increase potentially suitable habitat as shown for *Ambrosia* and for mosquitos (Essl et al. 2009, Becker et al. 2010).

The increasing numbers of publications published per year might be an indirect indication of increasing relevance of health impacts of alien species in Europe. Interestingly, the detected literature on human health impacts and biological invasions published in refereed journals has been surprisingly recent as we found with our search criteria no publication which was published before 2002. Many of the alien species with human health impacts are either relatively recent arrivals (e.g. *Aedes albopictus*, *Ae. japonicus*, *Ae. koreicus*, *Ochlerotatus atropalpus*) (Medlock et al. 2012) or have strongly spread in the last decade (e.g. *Ambrosia artemisiifolia*) (Bullock et al. 2012, Chapman et al. 2014). Consequently, the attention devoted by scientists, funding agencies and the wider public has increased only recently. Furthermore, some of our selected keywords (e.g. "alien*", "invasiv*") are only rarely used in older literature. In addition, we have included only publications published in journals indexed in the Thomson Web of Science. This conservative approach, which we have chosen to ensure consistency in selecting the literature, excludes a substantial fraction of literature published in other outlets. Finally, there is a well-known publishing delay between conducting the research and publishing the results (publication lag) (Björk and Solomon 2013).

Regions of origin and the role of pathways

Most alien species of human health concern in Europe are native to North America or to East Asia, including the most common studied species, *Ambrosia artemisiifolia* (North America) and *Aedes albopictus* (East Asia). The predominance of species from these two regions, with climates similar to Europe, reflects their high relevance as source regions for alien species in Europe in general (Lambdon et al. 2008, Roques et al. 2010).

Recently, an emphasis on the contributions of specific pathways to the rates of invasion, and on the temporal changes in pathway importance has emerged (e.g. CBD 2014, Essl et al. 2015). In our review, the contaminant pathway was the most important for alien species of health concern. This is in agreement with general introduction patterns of alien arthropods to Europe that are mainly associated with horticultural trade and unintentional escapes of pests (Rabitsch 2010). However, the dominance of introductions as contaminants likely mirrors the favorable species traits of the most relevant taxonomic groups. Diptera of the genus *Aedes* spp. have drought-resistant eggs able to withstand long journeys and enter Europe associated with used tires or Lucky bamboos, which are imported from Asia (Medlock et al. 2012). For common ragweed, medium- and long-distance spread are driven by human agency (e.g. bird feed; EFSA 2010), whereas local population growth and short-distance spread are dependent on natural seed dispersal (Bullock et al. 2012).

Invasion stages and implications for management

While most articles focus on spread, the first invasion stages such as transport, introduction and establishment are poorly covered, a pattern that is even more pronounced for articles assessing temporal trends. The difficulties to gain research funding for basic monitoring activities and that research targeting early invasion stages may not allow for quantitative analyses resulting in research articles, but only FOR descriptive short notes, are probably important reasons for this result (Pietzsch et al. 2006, Scholte et al. 2009, Versteirt et al. 2009).

The publication bias in favor of spread and against early invasion stages indicates that the precautionary principle is not sufficiently embedded in scientific inquiry, as incipient invasions can be easier controlled (Bohren et al. 2006, Galzina et al. 2010, Neteler et al. 2011, Fernández-Llamazares et al. 2012, Hulme 2014, Mazza et al. 2014). Similarly, articles assessing management effectiveness are underrepresented (Bayliss et al. 2012). It should be taken seriously that many studies recommend a comprehensive surveillance of the studied species, which is a prerequisite for rapid management response (e.g. Paupy et al. 2009, Takumi et al. 2009, Versteirt et al. 2009, 2012, Galzina et al. 2010, Capelli et al. 2011, Fischer et al. 2011, Kalan et al. 2011, Marsot et al. 2013, Thomas et al. 2011, Fernández-Llamazares et al. 2012, Medlock et al. 2012). An appropriate tool to avoid invasions already at the earliest stage is certainly the application of trade restrictions, as proposed e.g. for the pet trade (Hidalgo-Vila et al. 2008, Moutou and Pastoret 2010), but as highlighted in Mazza et al. (2015), online trade is poorly regulated and some species, such as the Indo-Pacific lionfish *Pterois volitans*, are sold despite being potentially harmful to humans. A crucial role for guiding European policy on invasive alien species will be exerted by the new European Regulation 1143/2014 (EU 2014), which entered into force in 2015; this legislation, however, focuses on biodiversity impacts and human health will only be considered as aggravating factor.

In terms of management, genetic techniques to eradicate mosquitos (strains with wingless females, transgenic strains) have recently received much attention (Paupy et al. 2009, Sutherland et al. 2011, 2014, Alphey et al. 2013). Some methods developed for mosquitos spread genes through a population despite the genes conferring a reproductive disadvantage, and are meanwhile also explored for alien plants (Hodgins et al. 2009). In principle, the use of such genetic methods may reduce the need for periodic releases of carriers of the desired traits. Beyond effects on the target alien species, the potential side-effects such as unintended dispersal of target species to other localities, horizontal gene transfer, and unforeseen ecological persistence of heritable control elements, have not been investigated in detail (Sutherland et al. 2014).

Gaps in knowledge and research priorities

We found substantial gaps in the literature on human health impacts of alien species in Europe. Most conspicuously, taxonomic and geographic coverage are biased towards few well-studies species and regions while early invasion stages and severity and trends of impacts are poorly studied. Finally, the role of climate change was rarely integrated in predictive assessments. For this study, we have extracted the available articles from the most important literature database for natural sciences. Additional literature on human health impacts of alien species will be available in complementary repositories for medical research publications (e.g. Pub Med). A test run with the search string »“alien species” AND “public health” AND “Europe”« resulted in 38 articles, with the large majority of them being not relevant to this review or redundant to articles that we obtained with our principal search in Web of Science. To ensure repeatability and to avoid that outcomes are biased regarding their relative taxonomic and geographic coverage, we did not perform specific searches at specialist sources, for particular species, or snowballing in reference lists of detected articles. We are aware that this approach may have negatively affected the comprehensiveness of the review. However, such systematic search effort covering several environmental and medical databases, relevant specialist sources, as well as the most relevant scientific and vernacular species names should be a promising alternative for obtaining a more comprehensive set of articles on the topic (Bayliss et al. 2015).

The existence of disciplinary frontiers in publishing and archiving may limit the exchange and uptake of knowledge on human health impacts of alien species generated in different scientific fields. This situation will hopefully improve, e.g. by the "One Health" initiative, an interdisciplinary approach for combating threats to the health of animals, humans, and the environment (Dantas-Torres et al. 2012, Conn 2014). Currently, research projects combining ecology and medical research on and management of alien species hardly exist in Europe. However, this kind of interdisciplinary research would be desirable to assess the direct implications and possible indirect consequences of alien species risks posed for human health now and under foreseeable changing environmental conditions (Conn 2014, Bayliss et al. 2015). Therefore, interdisciplinary projects bridging gaps between ecologists, medical researchers, socioeconomists and public health authorities such as the on-going EU-funded Atopica-project (www.atopica.eu), which focuses on common ragweed, are exemplary and should be taken as a model.

Conclusion

Knowledge on human health impacts of alien species in Europe is still scattered. The review articles detected in this synthesis cover particular species or species groups, whereas a complete coverage of alien species of human health impact in combination with a strong focus on Europe was lacking (but see Hulme 2014 for a recent essay on this topic). Detected original research articles were biased towards few species, mainly vascular plants and dipterans. Alien species of health concern in Europe are mostly introduced as contaminants of products originating from climatically similar regions of the Northern Hemisphere such as North America and Asia. Original articles most commonly deal with the spread of species, while knowledge gaps prevail for early invasion stages, severity and trends of impacts, interactions with climate change, and the scale of the socioeconomic costs. Research projects combining invasion ecology and medical research on alien species would be desirable to assess the consequences of alien species risks posed for human health now and under foreseeable changing environmental conditions. Comprehensive surveillance and monitoring for alien species of health concern are prerequisites for risk assessments and urgent management response and an important baseline for assessing the impact of alien species on severity and frequency of diseases and other types of health impacts.

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Supplementary material 1

Literature on human health impacts by alien species in Europe used in this review (n=77 articles)

Authors: Stefan Schindler, Bernadette Staska, Mildren Adam, Wolfgang Rabitsch, Franz Essl

Data type: categorized literature

Explanation note: Literature on human health impacts by alien species in Europe used in this literature review (n=77 articles). Given are article type, full citation, authors, publication year, journal (source) name, species under concern, taxonomic group, spatial scale, country / region, invasion stage-impact-management, climate change impact, criterion, trend in criterion, severity of impact, trend of impact, management measures, costs, origin, and pathway of first introduction.

Supplementary material 2

Alien species studied in the 56 original articles.

Authors: Stefan Schindler, Bernadette Staska, Mildren Adam, Wolfgang Rabitsch, Franz Essl

Data type: categorized species list

Explanation note: Alien species studied in the 56 original articles, their regions of origin (continents) and their introduction pathways.

Supplementary material 3

Spatial scale and location of the original and review articles

Authors: Stefan Schindler, Bernadette Staska, Mildren Adam, Wolfgang Rabitsch, Franz Essl

Data type: Table summarizing geographical coverage of the considered literature

Explanation note: Spatial scale (global, continental, subcontinental, national, subnational, Local lab/field trials) and location of the original (n=56) and review (n=21) articles.

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RESEARCH ARTICLE

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Assessing the flexibility of the Analytic Hierarchy Process for prioritization of invasive plant management

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Abstract

Decision tools have been advocated to assist the prioritization of management areas for preventing and mitigating exotic invasions into native ecosystems. Currently, most tools have been created for specific invaders/regions and are thus often not sufficient to address the complex range of invasion scenarios that managers encounter. As exotic invasions continue to be a major issue, science-based, information-driven tools are pressingly needed. In this study, we explore the potential of utilizing the Analytic Hierarchy Process (AHP), one of the information-driven tools, to flexibly prioritize various invasion scenarios by incorporating a broad spectrum of management data. We tested the flexibility of the AHP management tool with two distinct invasion-stage-specific prioritizations for Amur honeysuckle (*Lonicera maackii*). The AHP tool successfully created two management prioritizations from contrasting invasion scenarios of established Amur honeysuckle invasion versus a hypothetical scenario of newly invading populations. The flexibility of AHP allowed users to alter input based on the stage of invasion in each scenario. In the established scenario, management priority was assigned to removing Amur honeysuckle from the most ecologically significant areas. For the new invasion scenario, priority was shifted to removing the invader from areas of most recent invasions. The two contrasting prioritizations demonstrate the flexibility of AHP as a management tool. We conclude that the flexible AHP tool could be useful for prioritizing management of exotic plant invasions.

Keywords

Analytic Hierarchy Process, modeling, invasive plant management

Introduction

Invasive species are a growing problem both economically and ecologically. As these species continue to spread and invade new regions, managing to reduce their impacts becomes crucial (Byers et al. 2002, Ricciardi et al. 2013). Managers often face a suite of invasive species and large infested areas, making it a necessity to prioritize management actions (Hiebert 1997, Skinner et al. 2000). Many studies have examined the characteristics, spread, and potential impacts of invasive species, leading to generalizations about invasion ecology (e.g., Ehrenfeld 2010, Simberloff et al. 2012, Fei et al. 2014). Yet, effective management guidelines can be limited as the extensive knowledge and data associated with invasion ecology at the landscape scale can result in complex management scenarios. There is a need for science-based, information-driven tools to assist management decision-making.

Frameworks that analyze relevant information to facilitate the decision making process are known as decision tools. While decision tools have been used for a number of management purposes, such as prioritizing various conservation efforts (Sarakinos et al. 2001, Moilanen et al. 2005, Pert et al. 2013, Peterson et al. 2013), they have received less attention in the field of invasive species management. Moreover, existing applications of decision tools in invasion management were built to address a specific stage of the invasion process. For instance, certain models focus on preventing the introduction of high impact invaders (Cunningham et al. 2004) while others prioritize management areas based on detection, spread, or impacts of the invaders (Taylor and Hastings 2004, Mehta et al. 2007, Cook et al. 2007). Individually, these static models are not suitable to address the complex range of invasion scenarios that managers often encounter.

One such tool capable of incorporating a range of invasion data for prioritization modeling is the Analytic Hierarchy Process (AHP). In broad terms, AHP leads users through the decision making process by comparing input data in a pairwise manner that leads to priority (Saaty and Vargas 2001). By reducing complex decisions to a series of pairwise comparisons, expert judgement is incorporated into the decision process resulting in an objective ranking of the data. AHP has been applied in various fields and successfully produced prioritization outputs for forest conservation (Valente and Vettorazzi 2008) and landfill site selection (Zelenović Vasiljević et al. 2012).

However, there has been limited use of AHP for invasive plant management. Existing applications of AHP in invasion management are often region or species-specific (e.g., Roura-Pascual et al. 2009, Forsyth et al. 2012, Hohmann et al. 2013). Moreover, these studies do not directly demonstrate to managers that the AHP tool is adaptable to their specific management scenarios. Therefore in order to test the flexibility of AHP, we assessed if one tool could adapt to different management scenarios. We used two contrasting invasion scenarios, early versus late stage invasion of an exotic plant, for AHP assessment. We also assessed how the flexibility of the AHP management tool altered management priority between scenarios and further discussed how this flexibility could be useful for managers.

Methods

Model species

Amur honeysuckle (*Lonicera maackii*) (Rupr.) Herder, a widely distributed and high-impact invasive exotic plant, was used as our study species to assess the AHP management tool. Amur honeysuckle is native to eastern Asia and is found in most states of the eastern United States. Amur honeysuckle forms dense understory patches with thick canopies and often results in a monocultural system that impacts native species, alters nutrient cycling, prohibits natural regeneration processes, and degrades the habitat for wildlife (Gorchov and Trisel 2003, McKinney and Goodell 2010, Dutra et al. 2011, Watling et al. 2011). Many forested areas have been or will be impacted by the invasion of Amur honeysuckle.

Study area

The Inner Bluegrass physiographic region of Kentucky, USA served as the general study area and covers approximately 5,000 km^2 (Figure 1a). The Inner Bluegrass region is largely defined by limestone formations and phosphate rich silt loam soils (Wharton and Barbour 1991). The regional climate is characterized as temperate, humid, and continental (Wharton and Barbour 1991). Amur honeysuckle is widespread and found in thick patches throughout this region.

AHP management tool

In general, there are two initial steps in AHP workflow. In the first step, a manager sets a goal, such as prioritizing areas for the removal of an invasive exotic plant. As is often the case, complete removal from all locations isn't feasible, and management must be prioritized based on a preset of information. The second step of AHP is gathering the data (parameters) that will be used in the decision making process. Spatial data representing different characteristics of the invasion process and relevant to invasive plant management were selected for our analysis. To fit the structure of AHP, the parameters were placed into a hierarchy system that organizes the data into groupings at various levels. At the highest level, the parameters were grouped into one of three categories: Invasive Exotic Plant (IEP) Attributes, Ecological Impacts, or Land Use Characteristics. At the lowest level of the hierarchy, the descriptive information (attributes) of each parameter is assigned to individual management units (e.g. density level of plant infestation – low, medium, or high). The data organized into categories, parameters, and attributes, along with descriptions and data sources can be found in Table 1.

AHP outputs were generated by using two different scenarios of Amur honeysuckle invasion, one actual and one hypothetical, in order to examine AHP flexibility. The first

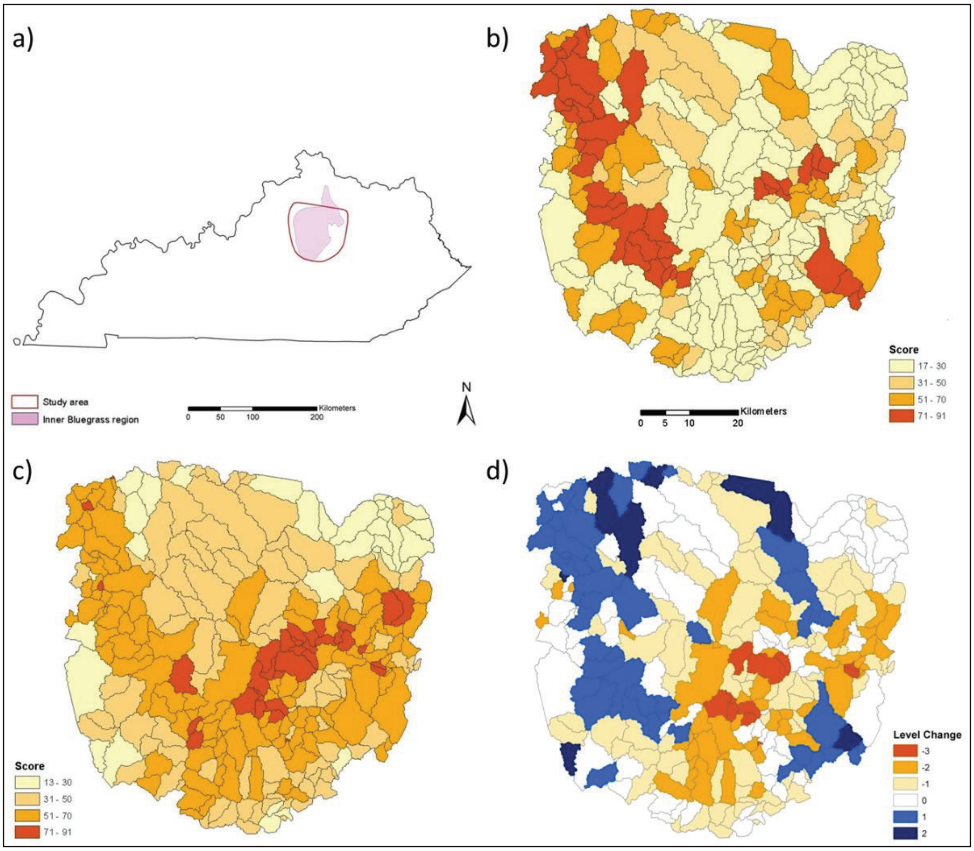

Figure 1. a Location of study area created to fit the general outline of the Inner Bluegrass region of Kentucky. The priority scores calculated for **b** established invasion output and **c** new invasion output **d** The change in priority level between the established and new invasion scenarios.

output examined prioritization under the current stage of Amur honeysuckle invasion within the Inner Bluegrass region of Kentucky. This output was labeled the "established invasion scenario" (EIS) because Amur honeysuckle is widely established and distributed throughout this region, having high ecological and economic impacts. The second output examined prioritization under a hypothetical scenario, in which Amur honeysuckle was new to the region and only beginning invasion and early establishment. This output was labeled "new invasion scenario" (NIS) because it represented a hypothetical stage of invasion in which the density levels of Amur honeysuckle are much lower than what the region is currently experiencing. By using one tool to generate two outputs, we were also able to compare how a perceptual change in the stage of Amur honeysuckle invasion could alter parameter importance and management priority between outputs.

Parameters were organized into AHP using the software program Expert Choice decision software (Version 11.5, Arlington, VA). AHP analyzes the data by gather-

Table 1. Detailed description of data used in the AHP management tool. Parameters are organized into one of three categories, Invasive Exotic Plant (IEP) Attributes, Ecological Impacts, or Land Use Characteristics. The Description column gives details of data sources and how parameters were generated. The Attributes column details how parameters were divided and assigned to management units.

Category and Parameter	Description	Attributes
IEP Parameters		
Amur honeysuckle density	Estimated Amur honeysuckle density from a supervised classification of a 2009 Landsat satellite image	5 density levels: lowest, low, medium, high, highest
Young Amur honeysuckle density	Estimated young Amur honeysuckle density by subtracting the 2005 distribution from the 2009 distribution	5 density levels: lowest, low, medium, high, highest
High invasion pressure	Calculated average density of Amur honeysuckle per watershed. Higher densities relate to higher invasion pressure on neighboring watersheds	Is the watershed neighboring a unit with a higher than average density of Amur honeysuckle? Yes or no
Ecological Impacts		
Rarity-weighted species richness index	Presence/absence of rare species. Index created by the Kentucky State Nature Preserves Commission. Index incorporates the rare species distribution and number of populations within the state to create a rarity index score	5 index levels: High = high concentration of rare species present Medium = rare species present Low = may support rare species, though no occurrences are known Historic = occurrences that have not been observed for over 20 years Absent = no rare species present or historically documented
Ecologically important sites	Ecologically significant areas as identified by the Kentucky State Nature Preserves Commission	Does the watershed contain an ecologically important area? Yes or no
GAP diversity	Generalized habitat diversity levels as modeled by the GAP analysis program	3 diversity levels: low, medium, high
Land Use Characteristics		
Land usage	General land usage of each watershed derived from Population Interaction Zones for Agriculture (PIZA) created by the USDA	3 zones: agricultural land, less impacted land, highly urbanized land
Road density	Road dataset produced by the Kentucky Transportation Cabinet	5 density levels: lowest, low, medium, high, highest

ing the parameters in a pair-wise manner, asking the user to rate which parameter is more important (and by how much) in meeting the assigned goal. For instance, the user would answer the question, “when prioritizing watersheds for Amur honeysuckle management, are the ecological impacts or the invader’s attributes more important?” In this pairwise manner, all categories, parameters, and attributes were weighted. We used a natural resource manager and an ecologist to provide responses to the pairwise comparisons for both invasion scenarios.

Calculating management priority

Attributes of each parameter were overlaid onto individual management units by using ArcGIS 10 Geospatial Modeling Environment (ESRI Inc., Redlands, CA). The 14-digit hydrological unit code (HUC), which refers to the finest scale for watershed delineation, was used to divide the study area into 286 management units. A priority score for each management unit was calculated by converting attribute weights into a point value and then totaling the points of all attributes within each unit (Ou et al, 2008). A total of 100 possible points was assigned among the three categories of the hierarchy based on the user generated weights. Points were then allocated to parameters and attributes based on user generated weights of importance. Management units with high total scores were deemed higher priority than those receiving lower scores. Management units were organized into one of four priority levels based on their total points (Table 2). Differences in distribution of priority between the two outputs allowed us to

Table 2. Scoring intervals organized into management priority levels. The higher the score, the higher the priority level assigned to the management unit.

Scoring interval	Priority rank	Priority level
0–30	Lowest	1
31–50	Low	2
51–70	Medium	3
71–91	High	4

Table 3. The AHP results of the established invasion output. Weighted percentages of importance were assigned at the category level (IEP Parameters 24%). Percentage points were further divided among parameters within each category (IEP density – 14). Points were then assigned to individual attributes that represented the characteristic of each management unit (Lowest – 14).

1. IEP parameters (24%)	2. Ecological impacts (66%)	3. Land use characteristics (10%)
1.1 IEP density (14)	2.1 Rarity-weighted richness (32)	3.1 Land usage (6)
Lowest 14	High 32	Agriculture 1
Low 10	Medium 28	Less impacted 6
Medium 5	Low 14	Highly urban 2
High 2	Historic 7	
Highest 0	Absent 0	3.2 Road density (4)
		Lowest 4
1.2 Young IEP density (6)	2.2 Ecologically important site (27)	Low 3
Lowest 1	Yes 27	Medium 2
Low 2	No 0	High 1
Medium 3		Highest 0
High 4	2.3 GAP diversity (7)	
Highest 6	Low 1	
	Medium 4	
1.3 High invasion pressure (4)	High 7	
Yes 4		
No 1		

analyze how altering user input based on invasion stage impacted priority. The results of the two prioritizations were analyzed in ArcGIS by comparing changes in each management unit's score and priority level between the outputs.

Results

The AHP successfully produced two distinct prioritizations from one tool, demonstrating a useful flexibility. Between the two invasion scenarios, users were able to weight the importance of the parameters differently dependent upon the stages of Amur honeysuckle invasion. For the EIS output, the Ecological Impacts category was weighted the highest (66%), followed by IEP Parameters (24%), and Land Use Characteristics (10%) (Table 3). Parameters listed in the order of deemed importance were the rarity weighted species richness index, followed by ecologically important sites, and Amur honeysuckle density. The remaining five parameters had limited influence, with high invasion pressure and road density deemed the least important when considering management priority.

For the hypothetical NIS output, the IEP Parameters category was weighted highest (62%), followed by Land Use Characteristics (29%), and Ecological Impacts (9%) (Table 4). Within the categories, the five highest parameters were Amur honeysuckle density, followed by young Amur honeysuckle density, land cover, road density, and

Table 4. The AHP results of the new invasion output. Weighted percentages of importance were assigned at the category level (IEP Parameters 62%). Percentage points were further divided among parameters within each category (IEP density – 30). Points were then assigned to individual attributes that represented the characteristic of each management unit (Lowest – 6).

1. IEP parameters (62%)	2. Ecological impacts (9%)	3. Land use characteristics (29%)
1.1 IEP density (30)	2.1 Rarity-weighted richness (4)	3.1 Land usage (17)
Lowest 6	High 4	Agriculture 1
Low 14	Medium 3	Less impacted 12
Medium 19	Low 2	Highly urban 17
High 25	Historic 1	
Highest 30	Absent 0	3.2 Road density (12)
		Lowest 1
1.2 Young IEP density (21)	2.2 Ecologically important site (4)	Low 4
Lowest 4	Yes 4	Medium 7
Low 10	No 0	High 10
Medium 15		Highest 12
High 19	2.3 GAP diversity (1)	
Highest 21	Low 1	
	Medium 1	
1.3 High invasion pressure (11)	High 1	
Yes 11		
No 1		

high invasion pressure. The remaining three parameters had little influence on the prioritization, with GAP (Gap Analysis Program) diversity being weighted the lowest.

Clear differences in the spatial distribution of priority areas were observed between the two outputs (Figure 1b–d). For the EIS output, the top priority units were generally found within a western strip of the study area (Figure 1b). For the NIS output, the top priority units were in a tight cluster within the center of the study area (Figure 1c). Because of these distinct differences in priority, we quantified the changes in priority distribution (Figure 1d). The greatest change in priority score between outputs was 58 points. The majority of changes in priority level were from instances where units that received low scores in the EIS output received high scores in the NIS output.

Discussion

Comparison of invasion scenarios

The ability of a user to compare parameter importance within each respective category is vital to producing a flexible tool for management. Users altered which parameters they believed were most important for prioritizing management sites dependent upon the stage of invasion. In the EIS output where Amur honeysuckle has long been established and widespread, priority was weighted towards removing the invader from the most ecologically significant areas. After deeming the Ecological Impacts category as most important, users decided that the presence/absence of rare species and ecologically important areas should receive more weight than the GAP diversity parameter.

Outside of the Ecological Impacts category, users also deemed that the distribution and density of Amur honeysuckle as important information. User input suggested that management units with lower Amur honeysuckle density were most important because these sites would be easier to manage, resulting in a better possibility for control. The other parameters, which related to spread and establishment, were not as important in this output because of the widespread establishment of the invader.

In the NIS output, priority was shifted from primarily protecting ecologically important areas to relying on parameters that would lead to monitoring of high risk sites and quick removal of new invasions. The IEP Parameters category was most important in this output because it would allow managers to locate such areas of new establishment and remove the invader before it spreads. In addition, users weighted the Land Use Characteristics category higher because its parameters may lead to monitoring and prevention of introduction. For instance, the land usage and road density parameters identify areas of increased disturbance, which may relate to a higher probability of introduction or establishment. Rather than focusing on potential impacts in a scenario of newly invading Amur honeysuckle, users suggested that in an effort to eradicate the invader, it was more important to focus activities on removing current stands while also directing operations to monitor and/or prevent new introductions.

AHP management tool

For this assessment, we chose to demonstrate the AHP management tool at the landscape scale and used watersheds as management boundaries. It is important to address the landscape level because the risk of invasion is often related to its environmental factors (With 2002). We are acknowledging that certain landscapes may be more vulnerable to invasion and experience various levels of impacts. Likewise, prioritization at the this level can facilitate eradication of the most ecologically damaging populations, while creating a system that uses limited labor in areas of most need. Furthermore, watersheds are highly recognizable by managers and make realistic boundaries at this scale. By operating at a landscape scale, we were able to use readily available GIS data to create many of our parameters. Many state agencies have websites dedicated to sharing ecologically relevant data at this scale. Finally, changes in parameter importance between the two outputs demonstrate the importance of using data that broadly cover the entire invasion process.

We acknowledge that the AHP outputs were only generated from two users. While the management tool was not demonstrated by multiple user groups we believe that our results show that AHP is capable of producing flexible outputs for prioritizing management. Our assessment of AHP flexibility, along with other region and species-specific AHP frameworks (e.g., Skurka Darin et al. 2011, Hohmann et al. 2013, Robison et al. 2013) will greatly enrich managers options in invasive species management decision making.

Management implications and conclusion

Our results demonstrate the flexibility of the AHP management tool, which is important for managers. Managers can create a unique AHP framework around their management scenario and needs by incorporating appropriate data that best fit the target invader. The tool could also be adjusted to meet various management scales by changing data sources between county, state, or regional levels. The AHP management tool may be especially useful for managers in situations where work proposals are required before implementation. In such cases, a manager could use one basic tool to propose multiple prioritizations based upon the various goals within the organization. Managers could also demonstrate how management might change dependent on potential budgets, priority between ecological protection or economic feasibility, or preference between eradication or control of spread. Equipped with more information, comparisons and decisions can be made that best meet each unique management situation.

Overall, there is a need for information-driven tools to assist management decision-making. Invasive plant management at the landscape scale is often complex and should include data relevant from all stages of the invasion process. AHP as a tool is guided by the user's expert knowledge and allows the user to assess large amounts of data in a structured environment. In addition, AHP provides valuable transparency to the decision making process. Various frameworks have been constructed that successfully demonstrate the usefulness of the AHP tool for addressing specific management questions. By successfully demonstrating the flexibility of AHP across two different invasion scenarios, our results indicate that AHP has the potential to meet management needs for prioritizing invasive plant management.

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Site-specific temporal and spatial validation of a generic plant pest forecast system with observations of *Bactrocera dorsalis* (oriental fruit fly)

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Abstract

This study introduces a simple generic model, the Generic Pest Forecast System (GPFS), for simulating the relative populations of non-indigenous arthropod pests in space and time. The model was designed to calculate the population index or relative population using hourly weather data as influenced by developmental rate, high and low temperature mortalities and wet soil moisture mortality. Each module contains biological parameters derived from controlled experiments. The hourly weather data used for the model inputs were obtained from the National Center of Environmental Prediction Climate Forecast System Reanalysis (NCEP-CFSR) at a 38 km spatial resolution. A combination of spatial and site-specific temporal data was used to validate the GPFS models. The oriental fruit fly, *Bactrocera dorsalis* (Hendel), was selected as a case study for this research because it is climatically driven and a major pest of fruit production. Results from the GPFS model were compared with field *B. dorsalis* survey data in three locations: 1) Bangalore, India; 2) Hawaii, USA; and 3) Wuhan, China. The GPFS captured the initial outbreaks and major population peaks of *B. dorsalis* reasonably well, although agreement varied between sites. An index of agreement test indicated that GPFS model simulations matched with field *B. dorsalis* observation data with a range between 0.50 and 0.94 (1.0 as a perfect match). Of the three locations, Wuhan showed the highest match between the observed and simulated *B. dorsalis* populations, with indices of agreement of 0.85. The site-specific temporal comparisons implied that the GPFS model is informative for prediction of relative abundance. Spatial results from the GPFS model were also compared with 161 published observations of *B. dorsalis* distribution, mostly from East Asia. Since parameters for pupal overwintering and survival were unknown from the literature, these were inferred from the distribution data. The study showed that GPFS has promise for estimating suitable areas for *B. dorsalis* establishment and potentially other non-indigenous pests. It is concluded that calibrating prediction models with both spatial and site-specific temporal data may provide more robust and reliable results than validations with either data set alone.

Keywords
Risk analysis, invasive species, modeling, climate

Introduction

The increase in international trade has exacerbated the problem of non-indigenous species moving between continents (Lenzen et al. 2012) and causing economic damage. Phytosanitary regulatory agencies aim to prevent non-indigenous pest entry and establishment and attempt to mitigate their impact when they become established. Pest risk maps are used by phytosanitary agencies to support risk analysis, pest surveillance, and emergency programs. One of the most important types of risk maps are those that estimate potential distribution based on climate suitability, which are usually created with bioclimatic models. Risk maps for non-indigenous species are generally created under two main constraints, limited time to produce the risk map product and sometimes gaps and uncertainties in the biological data needed to fit and validate the model. These constraints suggest that a suitable model for phytosanitary applications should be both generic and simple to use. One widely used approach is species distribution modeling, where a pest's potential distribution is inferred from a mathematical relationship between climate variables and the known distribution. One popular example is MaxEnt, which uses distribution data in combination with derived background observations (Phillips et al. 2006). However, MaxEnt and other species distribution models may not extrapolate reliably especially into novel climates (Elith and Leathwick 2009; Elith et al. 2012; Kriticos et al. 2014). An alternative is CLIMEX-Compare Locations (Sutherst and Maywald 1985), which uses literature and distribution data to fit the model parameters. CLIMEX is a simple process-based model that unlike a spatial distribution model, contains functions that explicitly define biological processes. CLIMEX is very widely used, partly because if there is insufficient literature data to parametrize the model it can be inferred from the distribution data itself. One disadvantage of CLIMEX is that it has many parameters and can be relatively labor intensive and subjective to fit, although an improved algorithm for auto-fitting could relieve some of these issues.

In addition to the need for potential distribution maps, other phytosanitary applications of weather or climate-based models include predictions of: i) the frequency of years favorable to crop losses or epidemics (Pinkard et al. 2010b); ii) the timing of life stages to deploy surveys or treatments; iii) the duration of mitigation treatments designed to achieve control or eradication based on historical or forecast weather; and iv) the extent of crop damage or injury to specific hosts (Magarey et al. 2014; Magarey et al. 2007; Pardey et al. 2013; Pinkard et al. 2010b). These kinds of applications are also relevant to the management of indigenous pests. Process-based models have an advantage over the species distribution modeling approach in that they can be used to make these kinds of predictions. Though this does push the modeling process towards greater complexity as additional host and management factors are included. As evidence of this many process-based models developed for management of endemic pests, especially plant diseases can become quite complicated (Rossi et al. 2007). However, there is a trade-off. As models become more complex, they are increasingly difficult to adapt to a new species. As evidence of this there are hundreds of publications for CLIMEX a simple process model but for its sister product DYMEX a more complex generic model, there are far fewer published examples.

In order to address this problem, there is benefit in creating a simple generic model framework that is a compromise between ease of use and capabilities for additional phytosanitary and pest management applications. In this study, we introduce the Generic Pest Forecast System (GPFS), for simulating relative pest populations in space and time. The GPFS model presented in this study has the following components: i) Developmental rate estimated from cardinal temperatures (Sutherst et al. 1999); ii) Mortality from cold (Kaliyan et al. 2007), heat (Dentener et al. 1996), and soil moisture; iii) Population index based on developmental rate and mortality. Although these are the basic model components, the GPFS model also includes components for: iv) Infection and sporulation modules for plant pathogens; v) Pest and host growth stages based on degree days; and vi) Potential damage based on predicted pest population and host and pest growth stages (Magarey unpublished data), however these last three components will not be presented in this study. The GPFS model is designed to run within a pest information platform such as NAPPFAST (Magarey et al. 2014; Magarey et al. 2007) which would supply the required hourly weather inputs. The NAPPFAST system (used by the U.S. Department of Agriculture's Animal Plant Health Inspection Service between 2002 and 2014) included an interactive template to allow users to create simple degree day, disease infection, and flexible models from U.S. and global weather databases for phytosanitary applications. The GPFS model is a process-based model of the pest-host interaction and is not designed to simulate factors that may limit host distribution such as aridity. As a consequence these kinds of factors must be considered separately using additional climate layers inside a geographic information system.

The oriental fruit fly (OFF) (*Bactrocera dorsalis*) was chosen as a study pest to test the GPFS model because there is an extensive amount of literature data available for model development and validation. *B. dorsalis* lays eggs below the skin of the host fruit and develops from egg to adult in as little as 17 days but development can be substantially delayed under cooler conditions (Christenson and Foote 1960) The larvae feed on fruits and mature larvae drop to the ground and pupate in the soil. Adults typically live for up to 3 months but may live longer in cooler conditions. Like other fruit flies, *B. dorsalis* requires favorable temperature and soil moisture conditions (Yang et al. 1994) and is one of the key pest groups of southeast Asia and Hawaii, causing damage to fruits and vegetables by larval feeding (Clarke et al. 2005). *B. dorsalis* is considered to be a species complex and *B. invadens* have recently been determined to be the same species (Schutze et al. 2014). *B. dorsalis* can be a major threat to agricultural crops because of extreme polyphagous behavior and is known to be highly invasive (Clarke et al. 2005). We conducted two types of evaluations of the GPFS predictions against *Bactrocera dorsalis* observations. The first was what we termed site-specific temporal validation to refer to the comparison of model predictions with observations from specific locations where data are collected at regular intervals over multiple years. This kind of validation is recommended by the developers of CLIMEX (Sutherst et al. 1999) and has been conducted in several CLIMEX studies (de Villiers et al. 2013; Legaspi and Legaspi 2010; Pinkard et al. 2010a). The second type of validation was a comparison of predicted suitability based on 10-years of weather data against the known distribution of *B. dorsalis*.

In summary, the objective of this study is to introduce the GPFS model and validate it for *B. dorsalis* using site-specific observations and distribution data. In addition, we wished to use the GPFS model to investigate the potential for establishment in the United States. No information collected on site was used to parameterize the model with the exception of food availability. In addition, no local weather data were used as input into the models to investigate the potential for gridded global hourly weather data to be used for historical pest predictions.

Materials and methods

Pest observations. Site-specific temporal pest observations were obtained from three studies in which adult oriental fruit fly were trapped (Han et al. 2011; Jayanthi and Verghese 2011; Vargas et al. 2010). The studies were selected because they contained multiple years of data and the observations could be obtained from the authors or read from the figures. No pesticides were believed to have been applied at these sites. The study sites include Hawaii in the United States, Wuhan in China, and Bangalore in India (Table 1). Hawaii has a subtropical climate with temperatures and humidity moderated by trade winds blowing oceanic air over the islands. Monitoring was conducted on Hawaii Island, HI, from September 2007 to March 2008 once every two weeks using methyl eugenol traps (Vargas et al. 2010). Wuhan has a humid subtropical climate with abundant rainfall and four distinct seasons. Observations were collected at an experimental farm in which various fruits and vegetable crops were growing. Adult male flies were sampled with methyl eugenol-baited traps from January to December in 2008 and 2009 at 10-day interval with replacement of lures every 20 days. The oriental fruit fly population data in Figure 1 of Han et al. (2011) were used for site-specific validation in China. Bangalore has a tropical

Table 1. Locations of case studies.

Reference	Location	Latitude	Longitude	Data period
Vargas et al. 2010	Hawaii Island, HI, USA	19.42942 (19°25'45.912")	-154.882 (-154°52'55.2")	2006–2008
Han et al. 2011	Wuhan, China	30.42915 (30°25'44.9394")	114.3639 (114°21'50.04")	2007–2009
Jayanthi and Verghese 2011	Bangalore, India	12.93686 (12°56'12.6954")	77.62111 (77°37'15.996")	1999–2002

savanna climate with distinct wet and dry seasons. Observations were collected in a guava orchard at the Indian Institute of Horticultural Research, Bangalore. The guava orchard was chosen to provide a food source for oriental fruit fly during the off-season for mango. Traps baited with methyl eugenol were used to monitor the insect population from June 2000 to June 2002. Population observation data from Figure 3 of Jayanthi and Verghese (2011) were used.

The Hawaii data were obtained from the authors whereas the observations for Bangalore and Wuhan were extracted directly from figures in the papers. Data extraction was conducted using a spreadsheet program (Excel 2010, Microsoft, Redmond, WA). The figure from the paper was scanned and copied into the spreadsheet and overlaid with a finer scale transparent grid-shaped graph with the same range of x- and y-axes to improve the ease of reading the data.

In addition to the site-specific observations, pest distribution data were also obtained from the literature (Suppl. material 1). *B. invadens* has recently be shown to be the same species as *B. dorsalis* (Schutze et al. 2014) so these observations were also included.

GPFS model. The GPFS model is designed as a simple generic tool for pest prediction for both arthropods and pathogens. The model is designed to run from hourly weather data inputs and to make predictions of the influence of weather on the relative pest population (population index) and phenological stages. For oriental fruit fly, GPFS only utilizes modules for development rate, high and cold temperature mortality, wet soil moisture mortality, and population index (Table 2). The first step in the GPFS model is to calculate the developmental rate in each hour. Next, the mortalities due to high temperature, cold temperature, and wet soil are calculated from hourly temperature and precipitation. The next step is to calculate the population index. The population index each hour is based on the sum of a development rate (scaled by the number of generations to reach maximum population) while removing the proportions of the population killed by high and low temperatures and by wet soil moisture. The population index is not sub-divided into individual life stages. Finally, the population index is adjusted by a simple function to account for lack of host availability.

Developmental rate. The hourly developmental rate (D) was estimated from four parameters: minimum temperature (T_{min}), lower optimum temperature (T_{opt1}), upper optimum temperature (T_{opt2}), and maximum temperature (T_{max}), describing the rate

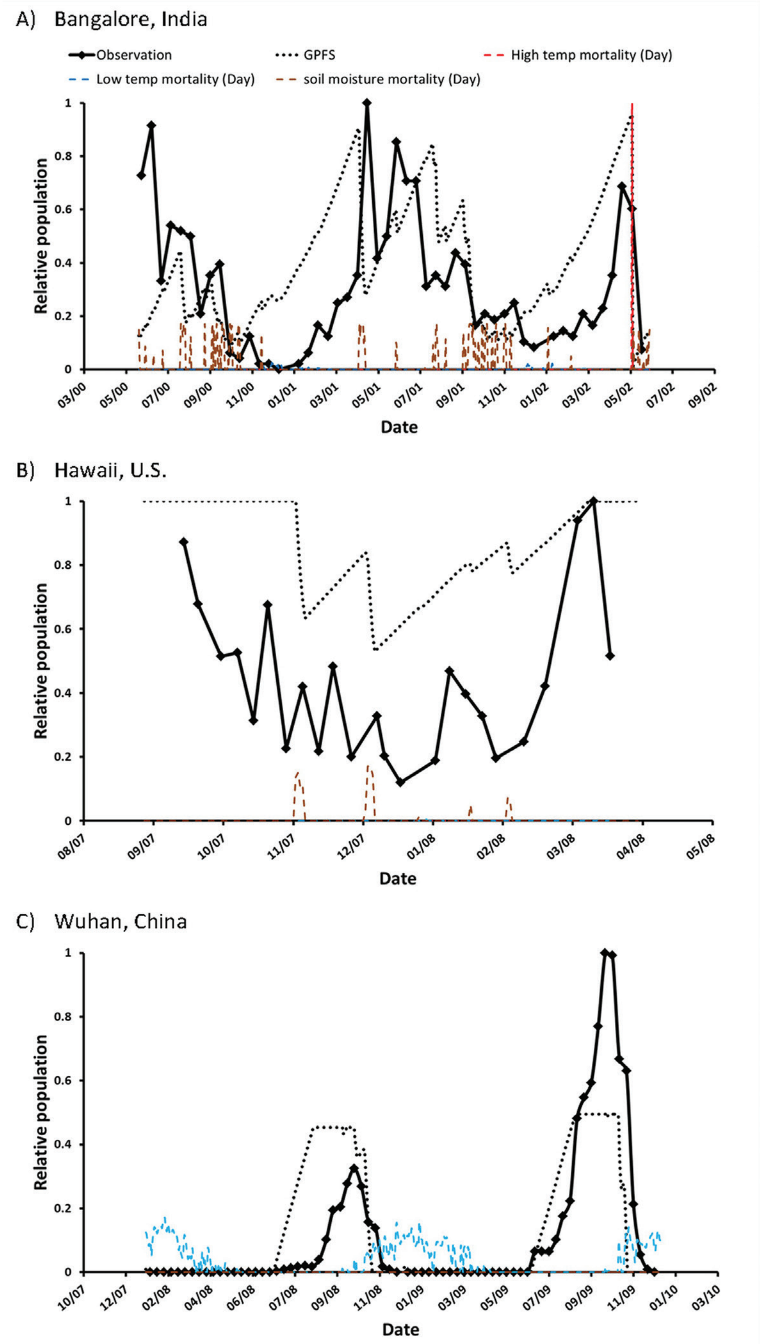

Figure 1. Comparison of observed (straight line with markers) and GPFS predicted (dashed line without markers) population of the adult oriental fruit fly, *Bactrocera dorsalis*, at three locations: **A** Bangalore, India **B** Hawaii, USA; and **C** Wuhan, China. Raw data of *B. dorsalis* field observations were converted to a population index (range: 0 to 1) to facilitate the comparisons

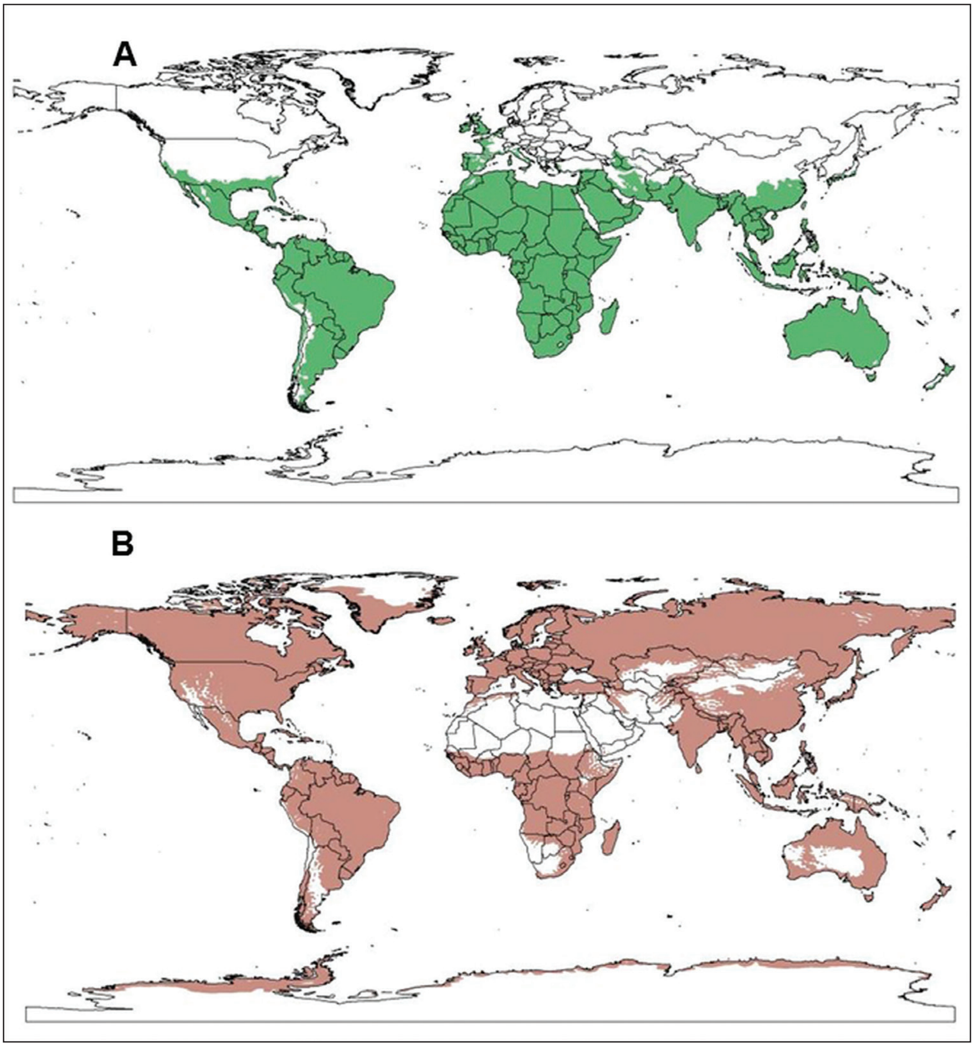

Figure 2. Cold and dry exclusions based on one or more occurrence of minimum temperatures of -10 °C (**A**) and annual precipitation less than 254 mm (**B**).

of development or population growth (Sutherst et al. 2007; Sutherst et al. 1999). We assumed that oriental fruit fly followed linear or constant development rates between these temperature thresholds. Developmental rates at each range obtained from the following equations.

$$\text{If } T < T_{min}\text{; or } T > T_{max} \text{ then } D = 0 \tag{1A}$$

$$\text{If } T_{min} < T <{}_{Topt1} \text{ then } D = (T - T_{min}) / ((T_{opt1} - T_{min})*24) \tag{1B}$$

$$\text{If } T_{opt1} < T < T_{opt2} \text{ then } D = (1/24) = 0.041677 \tag{1C}$$

$$\text{If } T > T_{opt2} \text{ and } < T_{max} \text{ then } D = (T- T_{opt2}) / ((T_{opt2} - T_{max})*24) \tag{1D}$$

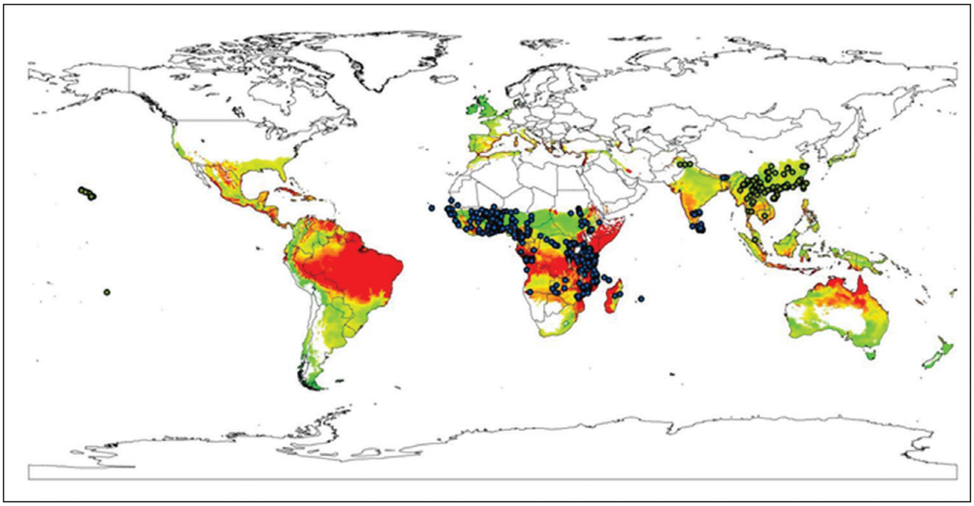

Figure 3. GPFS model prediction of potential global population index of oriental fruit fly, *Bactrocera dorsalis (*including observations of *B. invadens)*, based on most recent 10 years (2003–2012) weather data from National Centers for Environmental Prediction – Climate Forecast System Reanalysis (NCEP-CFSR) at a 38 km resolution. The predictions are on a scale of 0-1 and do not account for the presence or absence of suitable hosts. The map is the highest population index of any month averaged over ten years with initial populations in each year being independent. The map also includes the cold and dry exclusions from Figure 2.

where T is the hourly air temperature, °C. Threshold temperatures of four developmental rate parameters were obtained from refereed papers: T_{min} = 13.3 °C (Christenson and Foote 1960), T_{opt1} = 24 °C (Vargas et al. 2000), T_{opt2} = 34 °C (Vargas et al. 1996; Yang et al. 1994), and T_{max} = 41 °C (Christenson and Foote 1960). When hourly temperature is between $\mathrm{T}_{\mathrm{opt1}}$ and $\mathrm{T}_{\mathrm{opt2}}$, the rate of development reaches the maximum value of 1.0 per day or 0.041677 per hour.

Low temperature mortality. The hourly low temperature mortality was estimated from an exponential equation (Kaliyan et al. 2007). Although this equation was developed for Indian meal moth (*Plodia interpunctella)* it is based on the influence of temperature on the rate of chemical reaction and as such is a generic equation that can be adapted to other species. For temperatures less than T_{Mlt}

$$M_{lt} = [1/(EXP(\beta_1 + \beta_2/(T + 273.2) + \beta_3 *LN(T + 273.2))\,] \qquad (2)$$

where M_{lt} = the proportion of the population dying from low temperature mortality in an hour at temperature T in °C. To estimate parameters (β_1, β_2, and β_3), published data for lethal time (LT_{100}) of *B. dorsalis* were obtained (Burikam et al. 1992). However, due to the lack of information, additional data was included from *B. invadens* (now considered to be the same species) (Grout et al. 2011) and another species *B. tryoni* (De Lima et al. 2007; Heather et al. 1996; Jessup 1992; Jessup et al. 1993; Jessup et

Table 2. Parameters and abbreviation used in the GPFS model for oriental fruit fly.

Symbol	Parameter name	Value	Reference
D	Development rate		
T	Ambient temperature, °C		
T_{min}	Minimum temperature	13.3	Christenson and Foote (1960)
T_{opt1}	Low optimum temperature	24	Vargas et al. (1996)
T_{opt2}	High optimum temperature	34	Vargas et al. (1996)
T_{max}	Maximum temperature	41	Christenson and Foote (1960)
M_{lt}	Low temperature mortality		
T_{Mlt}	Threshold	13.3	Burikam et al. (1992), Grout et al. (2011), De Lima et al. (2007), Heather et al. (1996), Jessup (1992), Jessup et al. (1993, 1998)
β_1	Constant for M_{lt}	1101.7	
β_2	Coefficient for $1/(T+273.2)$ in M_{lt}	-49892	
β_3	Coefficient for $\mathrm{LN}(T+273.2)$ in M_{lt}	-162.9	
M_{ht}	High temperature mortality		
T_{Mht}	Threshold	33	Armstrong et al. (2009), Jang et al. (1999), Xie et al. (2008)
β_4	Constant for M_{ht}	25.9595	
β_5	Coefficient of degree one for M_{ht}	-0.4959	
β_6	Coefficient of degree two for M_{ht}	0	
M_{wsm}	Wet soil moisture mortality		Eskafi and Fernandez (1990), Hou et al. (2006), Xie and Zhang (2007)
β_7	Constant for M_{wsm}	50.4	Eskafi and Fernandez (1990), Xie and Zhang (2007)
P	Proportion of population in soil inhabiting life stages for M_{wsm}	0.36	
$P_{(n)}$	Population index		
β_8	Reciprocal of number of hours required to reach maximum population for $P_{(n)}$	0.008	
β_9	Generations to reach maximum population under optimum conditions for $P_{(n)}$	4	
β_{10}	Hours to complete one generation under optimum conditions for $P_{(n)}$	30.4 d	
β_{11}	Extinction threshold	0, 0.0001	

al. 1998) were also used to estimate the parameters for low temperature mortality. The fit for low temperature mortality is shown in Suppl. material 2 and Suppl. material 5 (using Celsius units for ease of interpretation).

Puparia of *B. dorsalis* can survive freezing conditions and overwinter at low levels in China (Han et al. 2011); however, there were no experimental data available for parameter estimation. Instead, the threshold temperature for overwintering survival for creation of a cold exclusion mask was derived from comparisons of oriental fruit fly distribution records with extreme annual minimum temperatures. This analysis was done outside of the GPFS model in a geographic information system and is described below. It also did not take into account the insulating influences of snow cover.

High temperature mortality. The hourly high temperature mortality is given by a polynomial equation with parameters β_4, β_5 and β_6 fitted from observations of mortality under controlled conditions using an exponential function that has be shown to have utility for predicting heat mortality for light brown apple moth (*Epiphyas postvittana*) and Long tailed mealy bug (*Pseudococcus longispinus*) (Dentener et al. 1996). For temperatures greater than T_{Mht},

$$M_{ht} = (60/[EXP(\beta_4 + \beta_5 *T + \beta_6*T^2)]) < 1 \qquad (3)$$

where M_{ht} = the proportion of the population dying from high temperature mortality in an hour at temperature T. To estimate parameters (i.e., β_4, β_5, and β_6) of high temperature mortalities, LT_{100} of oriental fruit fly in response to extreme high temperatures, ranging from 43 to 50 °C, were obtained from published data (Armstrong et al. 2009; Jang et al. 1999; Xie et al. 2008). The studies were conducted in either a heating block system (HBS) or a forced-air chamber. LT_{100} data were fitted to the model of the denominator part in the equation (3). All parameters ($\beta_{1\text{-}6}$) were fitted using PROC NLIN in SAS software 9.3 (SAS Institute, Cary NC). The fit for high temperature mortality is shown in Suppl. material 2 and Suppl. material 4.

Wet soil moisture mortality. Excessive soil moisture i.e. flooding can reduce the populations of some fruit flies including *B. dorsalis* (Xie and Zhang 2007). The hourly wet soil moisture mortality M_{wsm} is given by a simple empirical relationship. If soil is flooded then,

$$M_{wsm} = P*(1/\beta_7);\ else\ M_{wsm} = 0 \qquad (4)$$

where M_{wsm} = the proportion of the total population dying from soil moisture mortality in an hour, and P = the proportion of the population in soil-inhabiting life stages. This was assumed to be a constant 0.36 based on the pupal proportion of total degree days. The parameter β_7 is the number of hours that the life stage will survive in flooded soil. In the absence of soil moisture data, the soil was defined as flooded if more than 10 mm of rain had fallen in the previous 24 hours. Parameter (β_7) for soil moisture was also estimated by calculating LD_{100} in flooded soil from published data with *B. dorsalis* (Xie and Zhang 2007) and *Ceratitis capitata* (Wiedemann), Mediterranean fruit fly (Eskafi and Fernandez 1990). Mortality (LD_{90}) was 2.49 d for third instar *B. dorsalis* larvae in flooded conditions at 25 °C (Xie and Zhang 2007); however, no information for the pupae was available, so it was assumed that pupae would respond similarly to flooding like larvae. *Bactrocera dorsalis* pupae did not survive at soil moisture greater than 80% (Hou et al. 2006), although the survival time in saturated soils is unknown. A study with Mediterranean fruit fly showed that survival under similar conditions were 4 and 3 days for larvae and pupae, respectively (Eskafi and Fernandez 1990). We used this data to estimate approximate LD_{100} of *B. dorsalis* pupae under saturated conditions and calculated LD_{100} as (2.49/0.9)*(3/4) = 2.1 day. Thus, (β_7) = 50 hours. Wet soil moisture mortality does not account for increased pupal survival that occurred with increased soil humidity (Vargas et al. 1987), but only mortality was associated with flooding. Since this version of the GPFS model did not calculate the proportion of the population in each pest stage, we assumed a fixed proportion (0.36 based on stage duration) of the population was present in the pupal stage at any point in time.

Population index. The population index is a measure of relative population as influenced by weather conditions and is a function of the developmental rate, the mortality rates and the population index in the current hour (n).

$$P_{(n)} = [P_{(n-1)} + (\beta_8 * D)] * (1- M_{lt}) *(1-M_{ht})) *(1-M_{wsm}) \leq 1 \qquad (5)$$

where $P_{(n)}$ = the population index (0-1) at hour *n*. The parameter β_8 is the reciprocal of the number of hours required to reach the maximum value of the population index. It can be estimated from

$$\beta_8 = 1/(\beta_9 * \beta_{10}) \qquad (6)$$

where β_9 = generations to reach maximum population index under optimal conditions and β_{10} = days to complete 1 generation under optimal temperature conditions. The variable β_9 was arbitrarily chosen based on the assumption that a minimum of four generations would be required to reach the maximum value of the population index. The model also includes an extinction value, β_{11}, which if the final population falls below due to mortality, the population would remain at 0 even when favorable conditions returned.

Host fruit availability. The period when host fruits are available is an important factor in determining *B. dorsalis* population increase (Chen and Ye 2007). Monthly status of fruit availability (1: food, 0: no food) was implemented into the GPFS model to adjust population size based on fruit tree phenology. If food was not available for a given month, then the population was allowed to decrease during unsuitable periods, but not increase. In Wuhan, China, we set food as available from July to December (Han et al. 2011). Peaches were the only fruit available during May and June, but no oriental fruit fly larvae were found in peaches, so these months were not included as having an available food source. No food limitation was applied to Bangalore, India where the combination of mango and guava likely provides a near year round source of food and Hawaii, USA, where there are primary hosts, such as strawberry guava and common guava, as well as other fruits and vegetables (Cornelius et al. 2000; Vargas et al. 1983; Vargas et al. 1990).

Pupal cold mortality. There is evidence to suggest that pupae survive lower cold temperatures than larvae. In Wuhan, pupae were shown to successfully overwinter although survival was dependent upon the time of year when pupae where placed in the soil (Han et al. 2011). In addition, the authors also found occasional pupae in the field. Although, the authors did not definitively demonstrate these occasional pupae may give rise to overwintering populations, there is reason to err on the side of caution when constructing models of potential distribution, especially those for phytosanitary applications. Since there were insufficient data to parameterize the cold mortality of pupae, this was simulated outside of the GPFS model framework by comparing the extreme annual minimum temperature with the oriental fruit fly distribution maps, assuming this would represent the range of OFF cold survival or seasonal migration. A probability map showing the frequency of -10 °C or less each year was used as the exclusion layer and to mask out areas where oriental fruit fly would not overwinter. The Extract by Mask function in ArcGIS was used to create a global map showing likely maximum population and areas where oriental fruit fly would not survive. In NAPPFAST (Magarey et al. 2014), a probability map for one or more occurrences of minimum temperatures of -10 °C or less from the period January 1 to December 31 was made using ten years of hourly CFSR weather data (2003-2012). A frequency of 2 or more years in 10 was considered to be likely to eliminate oriental fruit fly populations (since populations might recover by re-introduction if killing periods occurred only once in every ten years). The grids were imported into ArcGIS and compared with oriental fruit fly distribution records. The grid included all the distribution records in the zone with values of 1 year or less. A mask of unsuitable area (2 years or more) was created and then multiplied by the maximum population grid to create the final global oriental fruit fly map. Large lakes including the Caspian Sea were excluded from the final product.

Dry exclusion. In addition to cold exclusion, a dry exclusion map was generated to mask dry/desert areas from the global distribution map using the ArcGIS. If annual precipitation was less than 254 mm, then the areas were defined as arid and unsuitable for oriental fruit fly habitats. This limit is commonly defined as limit for aridity (Maliva and Missimer 2012) and represents areas on the map that are likely not to have suitable habitat for OFF.

Model runs. The hourly weather data used for the model comparison and the creation of maps were produced by the National Center of Environmental Prediction Climate Forecast System Reanalysis (NCEP-CFSR) at a 38 km spatial resolution (Saha et al. 2010). A commercial weather data company (ZedX Inc., Bellefonte, PA) provided hourly weather data for specific years and locations from the gridded CFSR data sets created by NCEP. The input variables for the GPFS model were hourly air temperature, and precipitation. For the site-specific comparisons, the model was run in MS Excel. For spatial comparisons, a version of the model was coded into the GNU Compiler Collection (Free Software Foundation, Inc. http://gcc.gnu.org). Risk maps were created by running the GPFS model from January 1 to December 31 using ten years of CFSR weather data. To investigate the maximum climate suitability, the model was run using the same initial population index value in each year and populations did not carry over from one year to another, The model was run with the extinction value (β_{11}), set at 0. A map of final population in the middle of each month for each year was created and the average was calculated for each month over the ten year period. Each of these monthly maps was imported into a Geographic Information System for further processes (ArcGIS, ESRI, Redlands, CA) including incorporation of cold and dry masks. Since populations may peak at different times of the year depending on climate, a summary grid reporting the maximum population was created. For a risk map specific to the conterminous United States, Real-Time Mesoscale Analysis (RTMA) hourly data at 5 km spatial resolution (Benjamin et al. 2007) were used instead of CFSR. The main component of RTMA is the Gridpoint Statistical Interpolation (GSI) system derived from over 14,000 weather station observations, radar and satellite observations in NCEP (De Pondeca et al. 2011). Observations are ingested each hour and a 1-hour forecast is used as background layer to supplement observations for the next iteration. To look at the potential for pest establishment, the GPFS model was run from 2007 to 2012 with an initial population index in January 2007. In each subsequent year, the initial population index was the final population index in the previous year. The final map represented the maximum population index of any month in the final year (2012) and included the cold mask.

Site-specific temporal comparisons. Several accuracy measurements were calculated to determine how well GPFS predictions fit the observed population changes at the study locations. To facilitate comparisons with the predicted populations, the trap catch data were scaled between 0 and 1. The scaled values were calculated by dividing each observation by the 99th percentile of data from all years at each location. The statistical tests included mean error (*ME*), mean absolute error (*MAE*), mean square error (*MSE*), square root of *MSE* (*RMSE*), and index of agreement (*d*). Definitions and interpretations of these indices are well described in Legates and McCabe (1999) and Moriasi et al. (2007) and the equations for computing these indices were adopted or modified from these literatures. *ME*, *MAE*, *MSE*, and *RMSE* are indices for error that describe the difference between model prediction and observations in the units (or squared units) of the variable. Equations for computing these indices are expressed as:

$$ME = \left[\frac{\sum_{i=1}^{n}\left(Y_i^{obs} - Y_i^{pred}\right)}{n}\right] \tag{7}$$

$$MAE = \left[\frac{\sum_{i=1}^{n}\left|Y_i^{obs} - Y_i^{pred}\right|}{n}\right] \tag{8}$$

$$MSE = \left[\frac{\sum_{i=1}^{n}\left(Y_i^{obs} - Y_i^{pred}\right)^2}{n}\right] \tag{9}$$

The index of agreement (*d*) measures the degree of how observed values are accurately estimated by the simulation. The index of agreement is different from a measure of correlation or association in that it measures the degree of error-free of the model's predictions (Legates and McCabe 1999; Willmott 1981). Like correlation coefficients, it ranges between 0 and 1, where a value of one indicates a perfect match between observed and simulated variables while zero value suggests a complete disagreement. The index of agreement (*d*) is expressed as:

$$d = 1 - \left[\frac{\sum_{i=1}^{n}\left(Y_i^{obs} - Y_i^{pred}\right)^2}{\sum_{i=1}^{n}\left(\left|Y_i^{pred} - Y^{mean}\right| + \left|Y_{i=1}^{obs} - Y^{mean}\right|\right)^2}\right] \tag{10}$$

Spatial distribution comparisons. Model accuracy measures, modeled prevalence and sensitivity, were estimated using the final GPFS risk map. Raster cell values were extracted using ArcGIS. No data values (i.e., -9999), mainly assigned to oceans, were excluded from the analysis. The modeled prevalence is the proportion of raster cells classified as suitable. To estimate prevalence, the least presence threshold was used to classify raster cells as suitable or unsuitable. In species distribution modeling, the lowest presence threshold (LPT) is commonly defined as the predicted value of lowest training observation (Webber et al. 2011). We used the predicted value of 1st percentile in the training observations so the threshold is not influenced by an individual outlier. The modeled prevalence was estimated by dividing the number of cells with values greater and equal to LPT value by total number of raster cells. The model sensitivity is the proportion of test locations falling in suitable raster cells.

Results

Site-specific temporal validations. At the China and India sites, the GPFS model populations went extinct due to cold and/or heat mortality with the extinction threshold set at 0.0001. Since the parameters for pupal cold mortality were unknown, the cold mortality threshold was not able to be estimated. Instead the model was run with an extinction threshold set to 0. For high temperature mortality, a correction was made to the threshold, T_{Mht} to 39 °C from the literature value of 33 °C, which improved accuracy and allowed populations to persist in Bangalore. This may indicate that OFF individuals can move to find more favorable microclimates and thus avoid the highest temperatures. All other parameters remained the same from their literature values. The highest index of agreement was 0.85 at Wuhan. Regardless of modeling systems, the mean errors between the scaled adult populations and the predictions were smallest at Wuhan, followed by Bangalore and Hawaii.

The GPFS population predictions at Bangalore, India matched relatively well with the observed population (Figure 1A). The GPFS model correctly simulated the major peak populations in 2001 (April 2) and 2002 (April 22). Although the first peak in 2000 (June 19) was not correctly simulated, it may be due to increased food availability associated with mango harvest. In 2000, the GPFS modelled a peak in April 21 (Data not shown in figure). The main drivers of population decline in the GPFS model run at Bangalore were cold mortality during the cooler months and soil moisture mortality during the wetter summer months (including the monsoonal months, typically August to September). Heat stress mortality did not seem to be a population limiting factor.

For Hawaii, USA, the GPFS model simulated population dynamics relatively poorly compared to the other two locations (Figure 1B). There are several reasons for this. The first is that temperatures never reach extremes that cause steep population declines. Second, even by Hawaii standards this area has high populations due to the presence of many hosts throughout the trapping area. Methyl-eugenol traps, because they draw from a very broad area, can be difficult to interpret under these conditions. Consequently, distinct peaks in trap captures did not occur like the other sites (Figure 1). The GPFS model predicted a population decline during the wettest part of the year but underestimated the magnitude of the decline. The reduced climate suitability was driven mostly by excessive soil moisture. The model also had food as available all year round in Hawaii, although it is possible that there is less food available in the winter months. Another factor is that there are more uncertainties in weather data in Hawaii due to few stations and topographical influences.

The GPFS predictions matched the observed oriental fruit fly population comparatively well in Wuhan (Figure 1C) compared to the other two study locations (i.e., Bangalore and Hawaii). The GPFS model overestimated the mean population in 2008, but underestimated it in 2009. In 2008, the simulated population increased faster and had a higher peak compared to the observations. This may be due to the fact that surviving overwintering population levels are very low. The model concordance might be improved by a finer temporal representation of food availability. For example, the first host that supported oriental fruit fly oviposition, pears, did not ripen until mid-July, while the model allowed food to be available throughout July. This consideration is balanced by the fact that some OFF oviposition may occur before this period on unripe fruit. OFF prefer ripening fruit and survival is lower on unripe fruits (Chiu and Chen 1987). Declines in the GPFS simulated population in Wuhan were driven entirely by cold temperatures since heat mortality was not a factor.

Spatial distribution validations. The cold and dry exclusions eliminated large portions of Northern Europe, Asia and America and desert regions of Africa and Asia (Figure 2). The cold exclusion was based on the frequency of -10 °C or less each year and the dry exclusion was based on areas receiving less than 254 mm. The GPFS model was run globally at a 38 km grid resolution with extinction value β_{11} set at 0 (Figure 3) and 0.0001 and with January 1 in the Northern Hemisphere and July 1in the Southern Hemisphere (data not shown) start dates. For the locations where oriental fruit fly has been observed in Asia (Figure 4B), the mean and median of predicted maximum population were 0.404 and 0.338, respectively, with 25th and 75th percentiles of 0.197 and 0.577. With the threshold set at 0, the model predicted low levels of oriental fruit fly population surviving in Northern China in the middle of December, well beyond the range of the observed oriental fruit fly distribution. With the threshold set at 0.0001 the model greatly under predicted the range of oriental fruit fly in China. However, as discussed earlier, pupal mortality from cold temperatures may be much lower than larval mortality based on observations of pupal survival (Han et al. 2011).

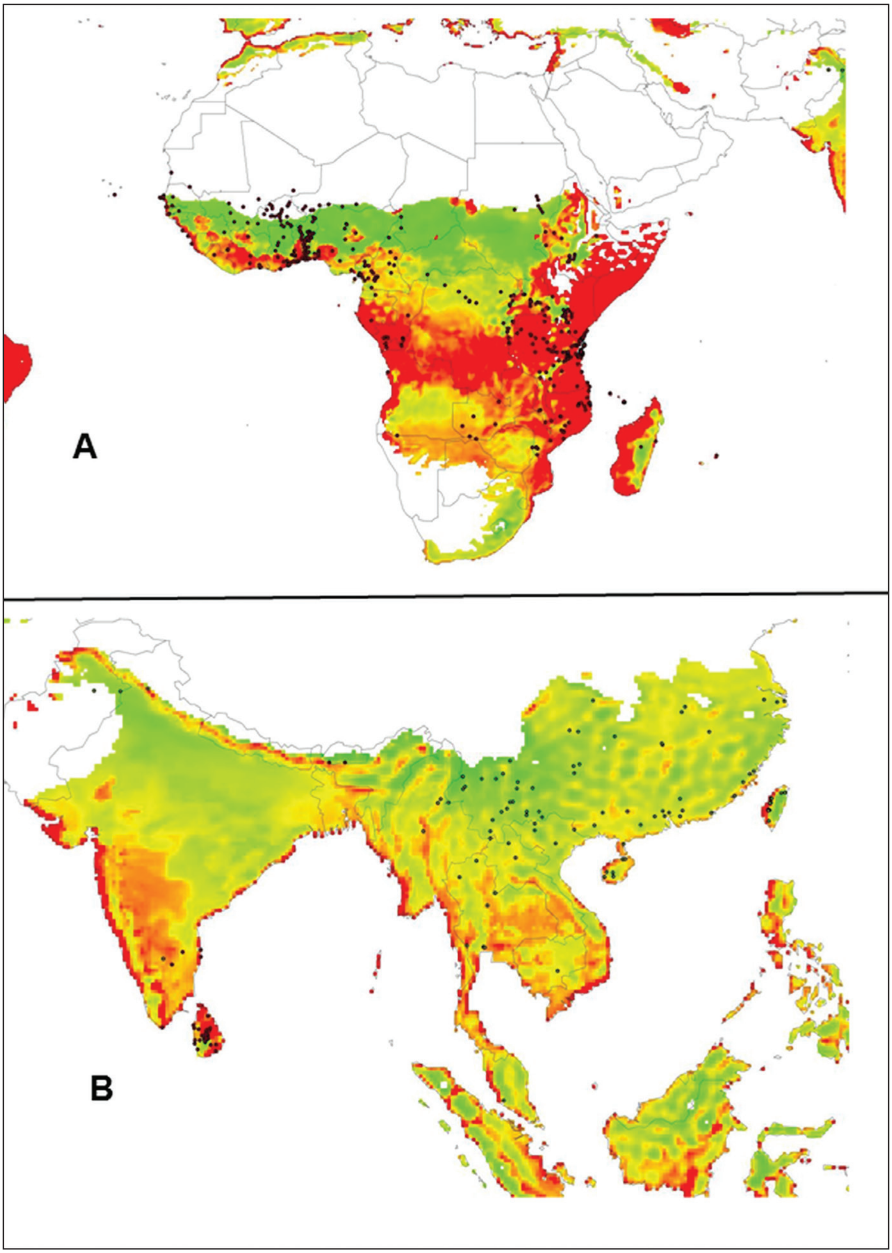

Figure 4. GPFS model prediction for potential population index of oriental fruit fly, *Bactrocera dorsalis* (including observations of *Bactrocera invadens*) in A) Africa and B) Asia based on most recent 10 years (2003-2012) weather data from National Centers for Environmental Prediction – Climate Forecast System Reanalysis (NCEP-CFSR) at a 38 km resolution. Locations where *B. dorsalis* or *B. invadens* has been observed in the literature are shown as black dots. The predictions are on a scale of 0–1 and do not account for the presence or absence of suitable hosts. The map is the highest population index of any month averaged over ten years with initial populations in each year being independent. The maps also include the cold and dry exclusions from Figure 2.

Since pupal survival parameters were not known the global suitability map included the cold and dry exclusions calculated independently and used to mask out unsuitable areas (Figure 2). Since most oriental fruit fly observations were in China, we show the map for this region (Figure 4B). The maps suggested that the Least presence threshold (LPT) based on the GPFS model output was 0.055, which was surprisingly low, although species distribution records are often collected for rare species (Bradley 2013). The model sensitivity was 0.99, i.e., over 99 % of observations (159 out of 161) were found within areas modelled as being climatically suitable (Figures 3 & 4). In Asia, the GPFS model predicted most oriental fruit fly occurrences in suitable regions except one in the northeastern Pakistan (Figure 4B). In Africa, the fit of the model against *B. invadens* observations was good with the exception of a number in the Sahel of Africa that were excluded from the suitable range because they were considered too dry. Globally, the modeled prevalence was 0.21, but without the cold and dry exclusion it was 0.95. The analysis assumed that host plants are available globally. The global climate suitability map indicates that oriental fruit fly may survive in most south parts of Africa and America, whereas only in limited areas of Europe, North America and North Africa are suitable due to cold or dry weather conditions (Figure 3). In parts of Europe, southern parts of South America and southern Australia, the climate for OFF is marginally favorable. Populations may not well survive in these areas during unfavorable years. Running the model in the establishment mode i.e. with population index change after five or more years may answer this question. However, it was not our objective to evaluate this question except for the United States where this was completed with RTMA data. The climate suitability map for the U.S. using 5 km resolution RTMA data suggests that potential fruit fly distribution may be limited to southern and western coastal areas in the United States (Figure 5).

Discussion

In this study, we introduced a new pest prediction model, the Generic Pest Forecast System (GPFS) and validated it against site-specific observations and spatial distribution. Importantly, no site-specific information was used to parameterize the model, with the exception of host fruit availability used in both models. In addition, no local weather data were used as inputs into the models to investigate the potential for a gridded global weather database to be used for historical pest predictions.

The goal of the team developing the GPFS model was to create a simple weather-based pest model that would have application for predicting potential distribution. In addition, the model was conceived also to have application to other risk based questions such as time of pest emergence and potential impacts in managed crop systems for both indigenous and non-indigenous pests. This additional information may enable decision makers to better understand the consequences of a newly established pest. One of the precedents for the GPFS model is weather-based pest forecast models which are routinely used in pest forecasting (Magarey et al. 2001). However, these

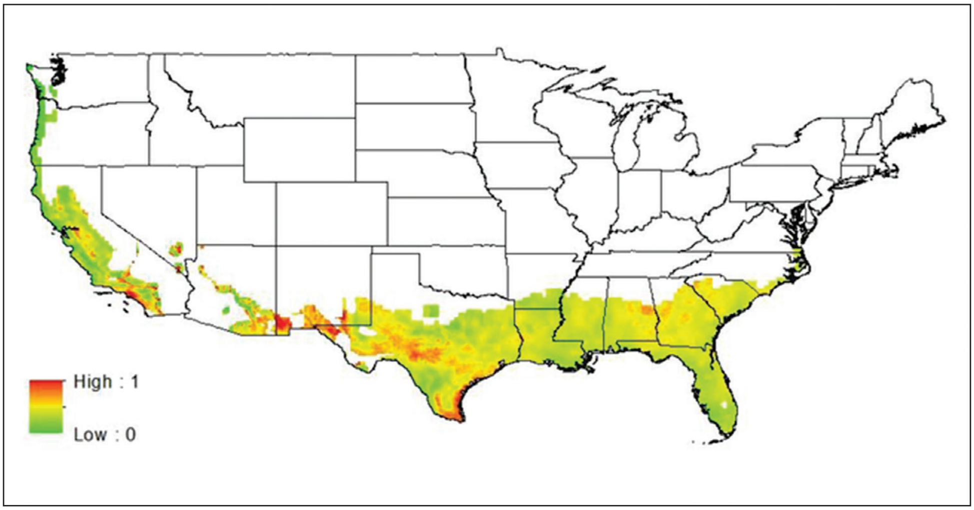

Figure 5. GPFS predictions of potential population index of oriental fruit fly, *Bactrocera dorsalis*, in the United States based on A. Real-Time Mesoscale Analysis weather data (2007–2012) with a 5 km resolution. The predictions are on a scale of 0-1 and do not account for the presence or absence of suitable hosts. The map is the final population index in December 2012 that resulted from the simulation of population change beginning with an initial population in January 2007. The map also includes the cold exclusion from Figure 2.

kinds of models do not typically include mortality factors since the pest is endemic and overwintering-survival is not usually in question. The GPFS also shares some similarities with CLIMEX-CL (Compare Locations), a widely used pest modeling software. CLIMEX is a relatively easy way to create a climate suitability map for a species since the generic nature of the growth and stress parameters enable the model to simulate the growth and survival of a species irrespective of the exact biological processes. This is probably one of the key reasons for the widespread use and adoption of CLIMEX-CL. In the GPFS, Eq. 1 is used to calculate developmental rate and in CLIMEX-CL, the same equation is also used in combination with a degree day formulation to calculate the temperature growth index (Sutherst et al. 2007). CLIMEX and GPFS both use stresses or mortality due to cold and heat but with different equations. The GPFS is designed to run from hourly weather inputs whereas CLIMEX runs from weekly indices usually estimated monthly climate averages. In GPFS, the population index accumulates each hour and is reduced by mortality factors. In CLIMEX, the Ecoclimatic Index (EI) value is calculated each week as the product of stress and growth indexes and then the EI is accumulated over the year. CLIMEX also includes additional types of stresses, and indices such as diapause and irrigation not considered in the GPFS. To compensate, the GPFS model may need to be used in combination with other GIS data sets when comparing pest distributions, such as those defining aridity.

The GPFS model appears to have a number of useful features. It has a relatively simple formulation, few parameters and can be used to investigate population changes during the seasons as well as produce overall suitability maps. The simplicity of the model makes it easy to adapt to a new pest, assuming these parameters are available or can be determined from a closely related pest (the latter which would increase the uncertainties associated with the simulation). Adaptability of a model to a new species is important since phytosanitary agencies must often develop risk assessments at short notice.

Although GPFS is a generic model, it is still not as flexible as the generic pest simulation model in the CLIMEX family, DYMEX (Maywald 2007), in building a model for a targeted species or adopting an already existing model to another new species. However, an experienced DYMEX user is required to use the model the development portions of DYMEX (DYMEX model builder), although the task may be simplified if a model exists for a related species. The GPFS represents a compromise in terms of model complexity. For example, to calculate the developmental rates, simple linear slopes at each temperature threshold range were used. Many other modeling tools use unique pest specific equations to represent developmental rates (Gutierrez et al. 2010; Maywald 2007). However, linear estimation of developmental rate seems appropriate when there is scarce information on pest development data, especially for exotic species. The GPFS model presented in this study has the potential to be improved with additional modules for diapause and pesticide timing.

The ease of parameterization is another key consideration for the use of a pest model. One limitation for the modeling of exotic species is the lack of published experimental data to parameterize the model. A useful feature of CLIMEX-CL is that parameter values can be estimated from the experimental literature, from the distribution data or as recommended using both in combination. A disadvantage of CLIMEX-CL is the weekly model time step, which can make the parameterization process more difficult since some experimental data such as mortality may have observations made at an hourly time step. The GPFS requires biological parameters, including information on development rate and mortalities due to heat, cold, and wet soil moisture. Consequently, it would not be possible to make a GPFS model for some pest species at present. One option is to parameterize the model from a related species, which increases the level of uncertainty associated with the modeling process. One possible solution is to use the distribution data to fit the parameters using an automated process. Such a method has been employed to fit a mechanistic model to predict forest species distributions (Higgins, Mullen et al. 2011).

Accuracy is another key consideration for evaluating models. The results from this study need to be kept in context with the limited amount of site-specific information (including weather data) that was used to inform the model. Information on other factors such as pest migration, food quantity, species competition and/or existing natural enemies, and management factors were not included. A more sophisticated simulation model may be able to have superior results using this kind of site-specific variables. When these kinds of site-specific parameters are included in a simulation model it is prudent to check the model is portable to other sites (Yonow et al. 2004).

The GPFS model might also be improved by adding modules to account for the population of individual pest stages. This would allow it to be used for other applications for example predicting the timing of a particular phenological stage for scheduling trapping or scouting applications. Another module that could be improved is the food supply model, which was highly simplistic and also relied on a monthly time-step. In some cases the phenological susceptibility of a host may be more precisely estimated from an observed biofix and a degree day model. In phytosanitary risk analysis, there is sometimes a need to simulate potential impacts and spread of pest in order to assess mitigation or response options (Waage et al. 2005). There is potential to improve the GPFS model to account also for factors such as host development, pesticide treatments, host resistance and natural enemies; factors that have been included in other pest forecast, simulation models or expert systems (Fitt et al. 1995; Gutierrez et al. 2010; Travis et al. 1992). Estimates of spread and impacts based upon a simulation model might improve upon those inferred from a pest's native range where climate, host and management conditions might be quite different. Examples of climate based simulation models being used in these kind of impacts assessments suggest there is benefit in adding this capability (Kriticos et al. 2003; Pinkard et al. 2010c).

One limitation with process models that require hourly weather inputs has been the lack of reliable, consistent, and dense global historical weather station data for use in validating models against published historical data of pest populations. This situation changed in 2010 when the National Center of Environmental Prediction (NCEP) introduced the Climate Forecast System Reanalysis (CFSR) (Saha et al. 2010). The CFSR database superseded the NCEP R2, which had a crude spatial resolution of 200 km, and included a more simplified description of atmospheric processes. The CFSR database provides a relatively high resolution (38 km) source of high quality gridded data from 1982 until the present at a 1-hourly time step. It is believed to be the most consistent and reliable source of global gridded historical data. The CFSR also has a much more detailed description of the atmosphere and atmospheric processes and improved accuracy, especially in the Southern Hemisphere. In a comparison with 28 weather stations in horticultural production areas, CFSR data had a mean relative and mean absolute errors of -0.3 °C/-4.3% and 2.4 °C/12.8% respectively for air temperature and relative humidity (Magarey, unpublished data). The reliability of CFSR data may also be dependent on other factors such as topographical complexity and the density of weather stations used as inputs into the reanalysis. It would have been informative to have compared CFSR weather data with those from local weather stations, but this was outside of the scope of the project. We did not do this in this study because of the complexity and some degree of spatial uncertainty around the exact locations of the field trials. CFSR data show promising performance for hydrological studies including stream flow and crop yield modeling (Dile and Srinivasan 2014; Fuka et al. 2013). The challenge for pest forecasting is potentially far greater due to the need for predictions data to be generated on finer spatial and temporal scales than those used for hydrology. To the best of our knowledge, this study is one of the first to use CFSR data for pest forecasting. The CFSR data set allows pest modelers not only to create high resolution global maps from hourly data but also to create historical predictions for which field observations at specific locations over multiple years have been published in the literature.

Utility of site-specific temporal validation

Site-specific temporal observations can play a useful role for model validation by providing an additional level of confidence that the model is providing realistic results. These types of validations may not be possible or can be difficult for some species due to pest and host phenology. That is that the number of individuals caught in a trap is a function of pest or host phenology and not just pest abundance. In this version of the GPFS model, we ignored pest phenology although it is incorporated into a newer version (Magarey unpublished data). However, including pest stages into the model greatly adds to complexity including the required parameters. In addition, for a pest with many generations and overlapping stages such as OFF it may not contribute much additional information. For example, including a stage specific model into the GPFS did not improve prediction accuracy for light brown apple moth (*Epiphyas postvittana*) (Hong and Magarey, unpublished data). The prediction of pest population index at specific sites can be revealing. For example, it might help identify sites where a pest is not expected to overwinter even if the summer climate is suitable. This is important since some distribution (spatial) records may be unreliable or the record may have corresponded with a rare or ephemeral observation of the species (Macfadyen and Kriticos 2012).

One important factor for site-specific validation is choosing representative locations. For example, predicted population indexes of *B. dorsalis* oriental fruit fly population in Wuhan, China were relatively superior compared to the two other locations (Figures 1C and Table 3). One likely cause of this is that cold winter conditions in Wuhan (absent at the other two sites) help synchronize population development. This also points out a limitation of site-specific validation in that it may not always be possible to obtain pest observations from locations that represent the potential range of suitable climates for an invasive pest. In addition, sites that have moderate climates such as Hawaii may not provide ideal validation sites for models to be deployed in continental climates because the populations are not primarily limited by climatic conditions. Another limitation of the site-specific validation is that the contribution of migration or human-mediated transport is not always clear. For example in Wuhan, populations potentially could overwinter at low levels (Han et al. 2011); however the contribution of fruit transported by humans may be a more important factor in the population cycle. Another limitation of site-specific validations is that observations lag predictions based on weather data. It might be possible to calculate a lag factor based on developmental time, however this could be complex depending on the biology of the pest. Since the fit was relatively robust without such a correction, we did not attempt to calculate a lag time. In addition, another limitation is population increases caused by abundance of food during periods such as harvest, Since the GPFS model is simple, it did not consider food quantity only the timing of food availability.

Utility of spatial distribution validation. Since site-specific temporal validation often includes relatively few locations, spatial validation is critical. Spatial validation of the GPFS showed the utility of the GPFS model but also the need for the cold exclu-

Table 3. Model accuracy measures between observation and predictions of GPFS.

	Bangalore, India	**Hawaii, USA**	**Wuhan, China**
Observation			
N	50	24	73
Mean	0.32	0.44	0.12
Standard deviation	1.75	1.18	1.77
GPFS			
Host/food availability	Jan–Dec	Jan–Dec	Jul–Dec
Prediction mean	0.40	0.85	0.13
Mean absolute error (MAE) (>= 0)	0.23	0.41	0.08
Mean error (ME) (-Inf to +Inf)	-0.08	-0.41	-0.02
Mean square error (MSE) (>= 0)	0.08	0.20	0.02
Index of agreement (d)	0.58	0.50	0.85

sion layer to prevent over-prediction in higher latitudes due to the lack of experimental data to parameterize the low temperature mortality. This shows that the combination of both complex (i.e., GPFS) and simple (i.e., exclusion) modeling techniques may be useful for defining the non-suitable areas (Figures 2 & 3). A recent study has shown that *B. dorsalis* is genetically indistinguishable from *B. invadens* (Jose et al. 2013). *B. invadens* is distributed from Senegal through the southern Congo with most occurrences in Benin and Cameroon along the equator in West Africa (Goergen et al. 2011). The GPFS model based on *B. dorsalis* parameters predicted these areas as suitable. The GPFS model also predicted that Angola and Namibia would also be suitable, although these countries likely have lower host densities. One note of caution is that populations of *B. dorsalis* from different localities may differ in their temperature and moisture requirements, so any predictions for an invading population should be treated with caution. This is especially the case since *B. dorsalis* is a species complex.

The GPFS predicted population can also be compared to a description of *B. dorsalis* populations found in an environmental chamber study in which temperature and humidity were maintained at levels representative of six U.S. cities (Flitters and Messenger 1953). This comparison of both the environmental chamber and the GPFS simulation showed that Fort Pierce, Florida and Oceanside, California were the most suitable for the oriental fruit fly, followed by Riverside, California. The chamber representing Fresno, CA, had low populations during the summer periods, while GPFS predictions were 0.13 and 0.17 in July 15 and Aug 15, respectively. In the chamber study and the GPFS model simulations using RTMA data (Figure 5), Vincennes (Indiana) populations could multiply in the spring and summer, but died out in the winter. In the Charleston (South Carolina) chamber, observed fly populations declined to zero during winter. The GPFS model suggests that oriental fruit fly could survive in Charleston, with the possible explanation that the model did not run through the end of winter, but stopped at December 31, prior to calculating averages for the ten year period. An alternative way to run the GPFS model is to begin with a founder population and then run the model for a ten year period. The disadvantage of this approach is that it may underestimate potential distribution as population extinctions might be caused by one or more extreme events. For a pest that may be frequently introduced, the average of a ten year prediction might be the most suitable. Alternatively, the analyst may choose to select individual years based on the occurrence of extreme weather conditions that might limit pest establishment.

Ideally, host abundance and phenology are also required for prediction of the population index (or relative abundance), but this information is very rarely available, especially on global scales. We investigated the use of global crop maps (http://capra.eppo.org/maps.php) (Monfreda et al. 2008); however, we chose not to use them due to the poor reliability in certain areas and the large host range of oriental fruit fly, which added to the complexity and uncertainties of making the maps. As a consequence of the lack of host availability data, the GPFS tends to over-predict fruit fly populations in some areas. Another cause of over prediction is the lack of host plants; for example, in much of semi-arid Australia host plants are likely to not be abundant. However, for a local scale map such as a pest detection map for California or Florida, it would be important to include maps of cropland or host distribution, rather than using the exclusion based on precipitation to define host areas.

Conclusions

The GPFS model was introduced as a simple weather-based model for predicting potential distribution. The model was shown to be able to simulate relative pest populations in some locations, which could have potential to estimate potential impacts of a pest when combined with other biological and management variables. The model requires literature data to estimate model parameters and as such will not be usable for all species unless alternative methods of parameterization are added in improved versions of the GPFS model. This study also shows the potential for improving pest risk models by conducting spatial and site-specific temporal validations against published observations. Although these kinds of temporal validations will not be possible for every species, they can provide insight into the spatial domain by suggesting why a species might not persist or provide an indication of the risk. It can also be helpful for calibrating model parameter values. Importantly, the arrival of high quality global gridded historical weather databases can make site-specific temporal validations from published observations easier for hourly weather-based models. The downloading and archival of gridded data sets are a large undertaking requiring considerable resources. However, smaller organizations have the opportunity to purchase hourly data sets from commercial weather providers for specific sites of interest. Ultimately as computer power improves these costs will decrease. Additionally, the model could be run in real time to support surveillance activities given the concern about low level or cryptic invasions escaping pest detection programs (Papadopoulos et al. 2013). We suggest that models be validated both spatially and temporally, when possible, in order to increase the confidence in their results. Caution is needed since in some locations a pest may not be coupled to climatic conditions and the population may be driven by other temporal factors, e.g., food availability. Spatial validation provides confidence that the model is working correctly in a range of climates, whereas site-specific temporal validation can offer insights to explain population increases or decreases. It could also provide evidence for including or discounting suspicious distribution records. We suggest that both of these types of validations should be included in inter-model comparisons. In conclusion, validating pest risk models with spatial and site-specific temporal data may provide more robust and reliable results than validations with spatial data alone.

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Supplementary material 1

Table S1

Authors: Seung Cheon Hong, Roger D. Magarey, Daniel M. Borchert, Roger I. Vargas, Steven K. Souder

Data type: distribution data

Explanation note: List of references for oriental fruit fly (*B. dorsalis*) distribution.

Supplementary material 2

Table S2

Authors: Seung Cheon Hong, Roger D. Magarey, Daniel M. Borchert, Roger I. Vargas, Steven K. Souder

Data type: distribution data

Explanation note: List of references for *B. invadens* distribution (Courtesy to Marc De Meyer, Royal Museum for Central Africa, Tervuren, Belgium).

Supplementary material 3

Table S3

Authors: Seung Cheon Hong, Roger D. Magarey, Daniel M. Borchert, Roger I. Vargas, Steven K. Souder

Data type: specimens data

Explanation note: Summary statistics of low and high temperature mortality of *Bactrocera dorsalis.*

Supplementary material 4

Figure S1

Authors: Seung Cheon Hong, Roger D. Magarey, Daniel M. Borchert, Roger I. Vargas, Steven K. Souder

Data type: specimens data

Explanation note: Fit of low temperature mortality function (line) to observations (diamonds).

Supplementary material 5

Figure S2

Authors: Seung Cheon Hong, Roger D. Magarey, Daniel M. Borchert, Roger I. Vargas, Steven K. Souder

Data type: specimens data

Explanation note: Fit of high temperature mortality function (line) to observations (diamonds).

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RESEARCH ARTICLE

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On the origin of South American populations of the common house gecko (Gekkonidae: *Hemidactylus frenatus*)

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Abstract

Hemidactylus frenatus is an Asian gecko species that has invaded many tropical regions to become one of the most widespread lizards worldwide. This species has dispersed across the Pacific Ocean to reach Hawaii and subsequently Mexico and other Central American countries. More recently, it has been reported from northwestern South America. Using *12S* and *cytb* mitochondrial DNA sequences I found that South American and Galápagos haplotypes are identical to those from Hawaii and Papua New Guinea, suggesting a common Melanesian origin for both Hawaii and South America. Literature records suggest that *H. frenatus* arrived in Colombia around the mid-'90s, dispersed south into Ecuador in less than five years, and arrived in the Galápagos about one decade later.

Keywords

Galápagos, Gekkonidae, *Hemidactylus*, invasive species, South America

Introduction

With more than 120 species occurring in warm regions worldwide, *Hemidactylus* accounts for nearly 13% of the total number of recognized species in the family Gekkonidae. It is one of the most species-rich and widely distributed reptile clades (Carranza

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and Arnold 2006). Nonetheless, species of *Hemidactylus* occur naturally only in Asia, Africa, the Mediterranean region, and South America (Carranza and Arnold 2006) and most of them have small distribution ranges confined to southern Asia and Africa. The enormous geographical range covered by *Hemidactylus* is in fact explained by the distribution of just a few species – *H. angulatus*, *H. brookii*, *H. flaviviridis*, *H. frenatus*, *H. garnotii*, *H. mabouia*, *H. parvimaculatus*, *H. persicus*, and *H. turcicus* (Bauer et al. 2010; Carranza and Arnold 2006; Kluge 1969). Most of them are frequently found in association with human settlements, and some have dispersed transoceanically either by human activity or natural rafting (Šmíd et al. 2013). As alien reptiles, species of *Hemidactylus* can achieve large densities leading to potential changes to food webs and ecosystem dynamics of the invaded areas (Kraus 2009).

The natural range of many of these widespread species is sometimes not clear. The common house gecko, *H. frenatus* Duméril & Bibron, 1836, is thought to have originated in tropical Asia and possibly the Indo-Pacific (Bansal and Karanth 2010; Bauer et al. 2010; Case et al. 1994) and has been introduced on many tropical and subtropical regions worldwide including the Eastern Pacific and mainland South America (Fig. 1), where it seems to be expanding its range. It has been recently reported from Venezuela (Rivas Fuenmayor et al. 2005), Colombia (Caicedo-Portilla and Dulcey-Cala 2011), and Ecuador (Jadin et al. 2009) including the Galápagos Islands (Torres-Carvajal and Tapia 2011). Despite this seemingly rapid range expansion, no attempts have been made to investigate the origin and spread of *H. frenatus*

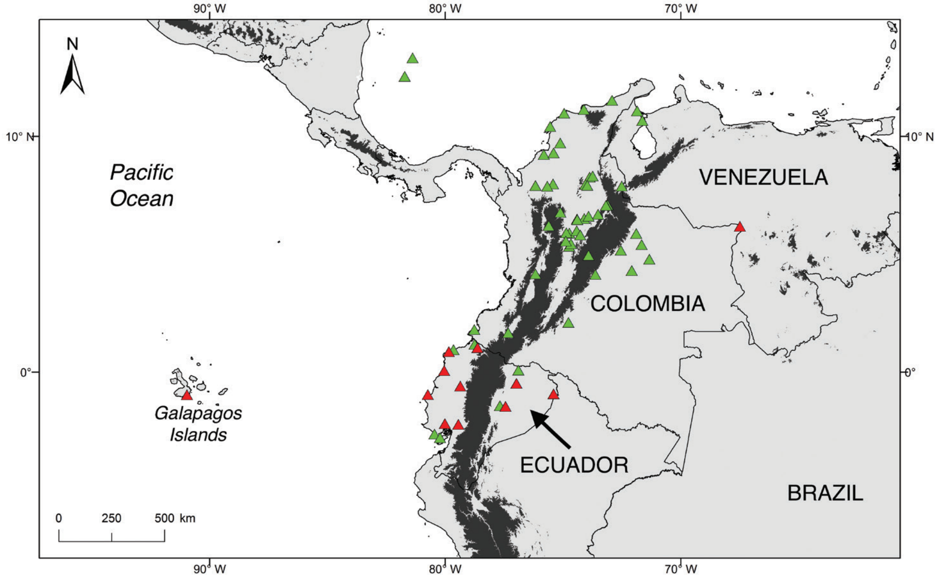

Figure 1. Distribution of *Hemidactylus frenatus* in South America and adjacent islands. Areas above 2000 m are shaded in dark grey. Localities of samples included in this study are shown in red. Locality data was taken from Rivas Fuenmayor et al. (2005), Jadin et al. (2009), Caicedo Portilla and Dulcey-Cala (2011), Torres-Carvajal and Tapia (2011), and the specimen database at Museo de Zoología QCAZ.

throughout the American continent and intervening islands. In this study, I use new mitochondrial DNA sequence data from individuals of *H. frenatus* occurring on mainland Ecuador and the Galápagos along with published sequences from Colombia, Hawaii and Asia to investigate the origin and colonization history of invasive populations of *H. frenatus* in South America. The objectives of my study are (i) to infer a phylogenetic tree of *H. frenatus* from South America, the Eastern Pacific (Galápagos), Hawaii, Melanesia, and Asia, and (ii) use that tree to infer the origin of *H. frenatus* from South America.

Materials and methods

Character and taxon sampling

I obtained nucleotide (nt) sequences of the mitochondrial ribosomal small subunit (*12S*, 370 nt) and cytochrome b (*cytb*, 303 nt) genes from 15 specimens collected on both sides of the Andes in Ecuador, as well as the Galápagos islands, and deposited in the herpetological collection of Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ). In addition, I retrieved sequences from GenBank representing samples of *Hemidactylus frenatus* from Colombia, Hawaii, India, Myanmar and Papua New Guinea. I used *H. brookii* and *H. flaviviridis* as outgroup taxa because they are closely related to *H. frenatus* (Carranza and Arnold 2006). GenBank accession numbers of specimens included in this study are presented in Table 1.

Laboratory protocols

Genomic DNA was isolated from frozen muscle or liver tissues using a guanidinium isothiocyanate extraction protocol. Polymerase Chain Reaction (PCR) amplification of gene fragments was performed in a final volume of 25 µl reactions using 1X PCR Buffer (– Mg), 3 mM $MgCl_2$, 0.2 mM dNTP mix, 0.2 µM of each primer, 0.1 U/µl of Platinum® *Taq* DNA Polymerase (Invitrogen, Carlsbad, CA) and 1 µl of extracted DNA. Negative controls were run on all amplifications to check for contamination. Gene fragments were amplified using the primers 12S1L, 12S2H and 12sb for *12S* (Blair et al. 2009; Kocher et al. 1989) and LGL765, GluDGL and H16064 for *cytb* (Bickham et al. 1995; Burbrink et al. 2000; Palumbi 1996). The amplification protocol consisted of 1 cycle of initial denaturation for 3–5 min at 96 °C, 30–40 cycles of denaturation for 30–40 sec at 92–94 °C, annealing for 30–40 sec at 48–57 °C, and extension for 40–110 sec at 72 °C, as well as a final extension for 7–15 min at 72 °C. Positive PCR products were visualized in agarose electrophoretic gels and treated with ExoSAP-it (Affymetrix, Cleveland, OH) to remove unincorporated primers and dNTPs. Cycle sequencing reactions were carried out by Macrogen Inc. (Seoul, Republic of Korea).

Table 1. Vouchers, locality data, and GenBank accession numbers of taxa and gene regions included in this study. Geographical coordinates in decimal degrees are provided for new localities sampled in this study.

Taxon	Voucher	Locality	GenBank accession number	
			cytb	12S
Hemidactylus brookii	E1109.10	India	DQ120276	DQ120447
H. flaviviridis	E912.2	Yemen	DQ120284	DQ120455
H. frenatus	CES07035	India	HM595655	HM595691
H. frenatus	E509.5	India	DQ120282	DQ120453
H. frenatus	E509.2	Myanmar	DQ120281	DQ120452
H. frenatus	E509.1	Myanmar	DQ120280	DQ120451
H. frenatus	NV	Papua New Guinea	AY217801	AY218005
H. frenatus	E509.7	Hawaii	DQ120278	DQ120449
H. frenatus	E509.6	Hawaii	DQ120277	DQ120448
H. frenatus	E509.3	Colombia	DQ120279	DQ120450
H. frenatus	QCAZ4524	Ecuador: Esmeraldas 1.0425; -78.6304	KT455016	KT455031
H. frenatus	QCAZ4875	Ecuador: Manabí -0.9505; -80.7423	KT455017	KT455032
H. frenatus	QCAZ5076	Ecuador: Esmeraldas 0.8740; -79.8450	KT455018	KT455033
H. frenatus	QCAZ8124	Ecuador: Pastaza -1.4529; -77.4425	KT455019	KT455034
H. frenatus	QCAZ8130	Ecuador: Pastaza -1.4529; -77.4425	KT455020	KT455035
H. frenatus	QCAZ8472	Ecuador: Guayas -2.2126; -79.4472	KT455021	KT455036
H. frenatus	QCAZ9111	Ecuador: Guayas -2.1822; -80.0181	KT455022	KT455037
H. frenatus	QCAZ10197	Ecuador: Pichincha -0.5888; -79.3627	KT455023	KT455038
H. frenatus	QCAZ10213	Ecuador: Orellana -0.4720; -76.9807	KT455024	KT455039
H. frenatus	QCAZ10215	Ecuador: Orellana -0.4720; -76.9807	KT455025	KT455040
H. frenatus	QCAZ11128	Ecuador: Galápagos -0.9573; -90.9674	KT455026	KT455041
H. frenatus	QCAZ11165	Ecuador: Galápagos -0.9573; -90.9674	KT455027	KT455042
H. frenatus	QCAZ11197	Ecuador: Galápagos -0.9573; -90.9674	KT455028	KT455043
H. frenatus	QCAZ11452	Ecuador: Manabí 0.0740; -80.0480	KT455029	KT455044
H. frenatus	QCAZ11593	Ecuador: Orellana -0.9167; -75.4000	KT455030	KT455045

Alignment, model selection, and phylogenetic analyses

Data were aligned in MAFFT under default settings (Katoh and Toh 2010). Genes were combined into a single matrix with four partitions (*12S* and 1st, 2nd and 3rd codon positions of *cytb*). Evolutionary models for each partition were selected using jMODELTEST (Posada 2008) under the Bayesian information criterion. Phylogenetic relationships were assessed under a Bayesian approach in MrBAYES 3.2.0 (Ronquist and Huelsenbeck 2003). The analysis consisted of ten million generations and four Markov chains with default heating values. Trees were sampled every 1000 generations resulting in 10000 saved trees per analysis. Convergence was confirmed by plotting the –ln *L* per generation. Adequacy of mixing was assessed by examining the acceptance rates for the parameters in MrBAYES; I verified that the average standard deviation of split frequencies between chains and the potential scale reduction factor (PSRF) of all the estimated parameters approached values of ≤ 0.01 and 1, respectively. Additionally, I used TRACER to verify that the effective sample sizes (ESS) had values above 200. After analyzing convergence and mixing, 1000 trees were discarded as "burn-in" from each run. We used the resultant 36,000 trees to calculate posterior probabilities (PP) for each bipartition on a 50% majority rule consensus tree. Intra- and interspecific sequence divergence for each gene was assessed with uncorrected distances, which were obtained in PAUP* (Swofford 2003).

Results

A total of 673 aligned sites of *12S* (370 nt) and *cytb* (303 nt) were obtained. Selected models were K80+G, 000010+F, TrN, and 012212+G+F for 1st, 2nd and 3rd codon positions of *cytb* and *12S*, respectively. Of the 25 aligned sequences, 17 contained missing data ranging between 1–65 sites, which together represented 2.6% of the total sites in the matrix.

All 15 new sequences obtained in this study from continental Ecuador and the Galápagos, as well as GenBank sequences of specimens from Colombia, Hawaii and Papua New Guinea were identical (missing data ignored). The clade formed by these sequences (PP=0.95) was recovered with high support (PP=0.91) as sister to a clade with two samples from Myanmar (PP=0.90); samples from India were nested in a clade (PP=0.78) sister to all other samples of *Hemidactylus frenatus* (Fig. 2). Monophyly of this species was not supported strongly (PP=0.65). The same phylogenetic analysis as described above, except that identical sequences were removed, yielded slightly higher posterior probability values.

Intraspecific genetic distances between individuals of *H. frenatus* from Papua New Guinea/Hawaii/South America and individuals from India and Myanmar included in the analysis varied between 0.069–0.132 and 0.047–0.078 for *cytb* and *12S*, respectively (Table 2).

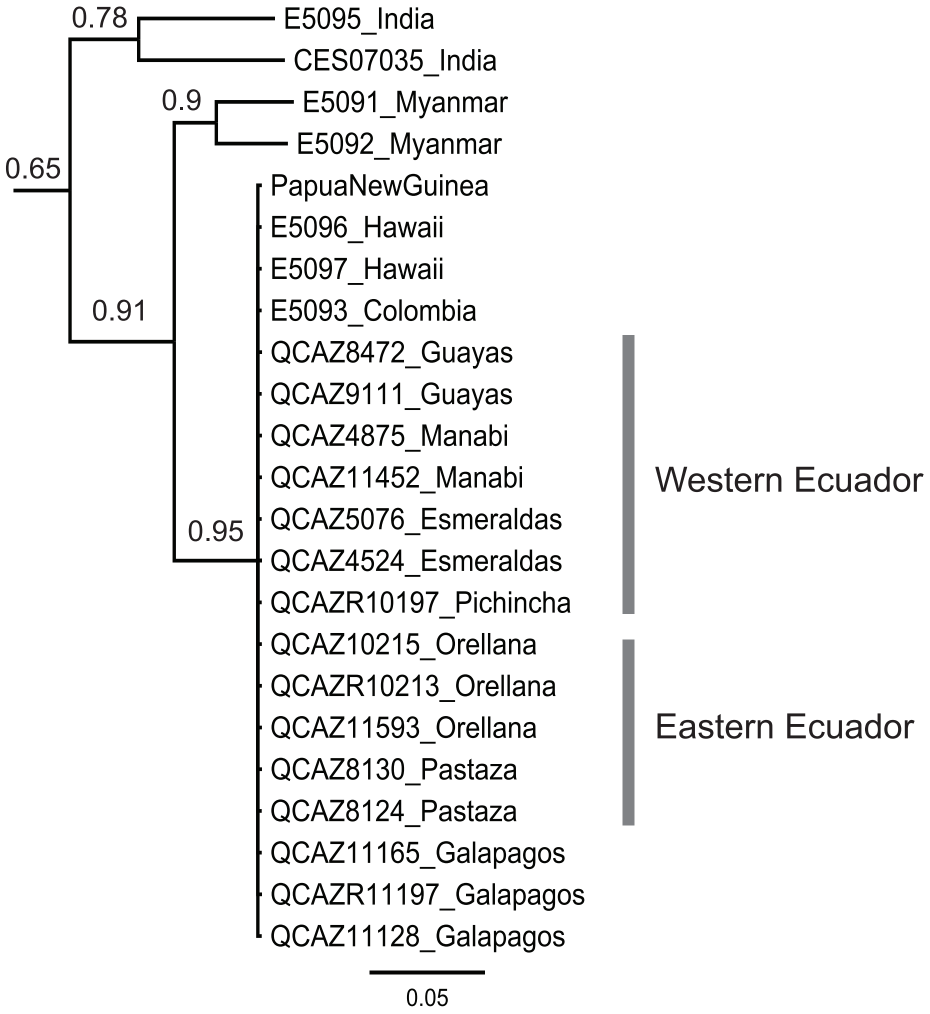

Figure 2. Majority rule (50%) consensus tree of 36,000 trees obtained from a Bayesian analysis of 25 specimens and 673 nucleotides corresponding to *cytb* and *12S* mitochondrial gene regions. Outgroup taxa *Hemidactylus brookii* and *H. flaviviridis* are not shown; all terminals correspond to *H. frenatus*. Numbers on branches are posterior probability values. Voucher numbers (if available) and country of collection are shown on each terminal. For samples collected in Ecuador, voucher numbers and province names are indicated.

Table 2. Uncorrected genetic distances among taxa included in this study for *cytb* (upper diagonal) and *12S* (lower diagonal) gene fragments. Taxon name along with voucher number and country of collection are indicated in first column. The sequence of *H. frenatus* from Colombia represents other sequences from South America, as well as those from Hawaii and Papua New Guinea included in this study.

Taxon sample	1	2	3	4	5	6	7
1: *H. flaviviridis* E912.2 Yemen		0.251	0.201	0.205	0.191	0.218	0.187
2: *H. brookii* E1109.10 India	0.208		0.178	0.195	0.162	0.185	0.189
3: *H. frenatus* E509.1 Myanmar	0.172	0.158		0.076	0.076	0.129	0.130
4: *H. frenatus* E509.2 Myanmar	0.174	0.160	0.025		0.069	0.135	0.105
5: *H. frenatus* E509.3 Colombia	0.175	0.158	0.047	0.047		0.132	0.105
6: *H. frenatus* E509.5 India	0.168	0.151	0.056	0.064	0.078		0.105
7: *H. frenatus* CES07035 India	0.177	0.164	0.078	0.081	0.070	0.061	

Discussion

The fact that *cytb* and *12S* haplotypes of *Hemidactylus frenatus* from Hawaii, the Galápagos, and mainland South America are identical to those in Papua New Guinea sheds some light on the origin and dispersal of this species from Melanesia to South America across the Pacific Ocean. The invasive populations in Hawaii and South America most likely originated from a single 'stock' in Melanesia; otherwise, we would expect more genetic variation among invasive samples. This is supported by the genetic variation that was observed only among the four samples from India and Myanmar included in this study. Although these four samples come from geographically close localities, their genetic distances vary between 0.076–0.135 and 0.025–0.064 for *cytb* and *12S*, respectively (Table 2). Had South American and Hawaiian haplotypes originated from two or more different Melanesian 'stocks', we would observe some degree of genetic divergence when comparing those haplotypes. This contrasts with the high genetic diversity of invasive *H. frenatus* recently reported from the remote Pacific island of Moorea, French Polynesia (Tonione et al. 2011), and shows that invasive species can have different colonization patterns (i.e., one versus multiple invasive haplotypes) across their non-native distribution ranges.

How *Hemidactylus frenatus* arrived in South America remains an open question given its ability for massive, human-mediated range expansion (Carranza and Arnold 2006). One possibility is that this species departed from the same site in Melanesia more than once, arriving both in Hawaii and South America independently. Although I did not investigate marine trading routes in detail, there is probably a better chance that *H. frenatus* first arrived in Hawaii and from there spread (directly or through Central America) to South America.

The common house gecko, as its name suggests, is easy to spot at human settlements feeding around light bulbs at night. Therefore, we can assume that the first time it is found as an invasive species in a certain location corresponds approximately to the colonization time at that location. Thus, based on the year *H. frenatus* was first reported from each site included in this study, it seems like its general colonization route after leaving Papua New Guinea or somewhere nearby was (first report year follows each site) Hawaii 1940s (Kraus 2009), continental Colombia 1996 (Caicedo-Portilla and Dulcey-Cala 2011), continental Ecuador 2000 (QCAZ 6098, 6111) and the Galápagos 2011 (Torres-Carvajal and Tapia 2011). However, colonization in Colombia was probably earlier than 1996 through harbors in the Atlantic Ocean (Caicedo-Portilla and Dulcey-Cala 2011). Regardless of colonization routes, literature data indicate that *H. frenatus* has colonized South America fairly recently, arriving in Colombia first and then spreading south into Ecuador and the Galápagos (Fig. 1). Furthermore, *H. frenatus* was first reported from Venezuela near the Colombian border in 2000 (Rivas Fuenmayor et al. 2005), suggesting that this population also arrived from Colombia.

Recent arrival of *Hemidactylus frenatus* to South America including iconic conservation sites as the Galápagos archipelago should be of concern. Given its great dispersal ability and potential distribution (Rödder et al. 2008), *H. frenatus* is expected to rapidly expand its range across South America. This is an aggressive species that tends to reach high densities and outcompete other lizard species. For example, exclusion of the alien species *Lepidodactylus lugubris* by more recently introduced *H. frenatus* has been documented in several Pacific islands (Bolger and Case 1992; Brown et al. 2002; Cole et al. 2005; Petren et al. 1993; Petren and Case 1998). This competitive exclusion seems to be the result of many factors including behavioral interference, predation on juveniles of *L. lugubris*, enhanced ability of *H. frenatus* to exploit food resources, and avoidance of *H. frenatus* by *L. lugubris* (Kraus 2009). Endemic lizard species can also be negatively affected by invasive common house geckos, as has been shown in the Mascarene islands, where the arrival of *H. frenatus* resulted in population declines and even some extinction events of the native *Nactus* geckos (Cole et al. 2005). Besides competition, invasive *H. frenatus* can have negative secondary trophic effects. For example, *H. frenatus* is one of the alien prey species that help the invasive snake *Boiga irregularis* maintain high densities in Guam (Fritts and Rodda 1998).

Only recently was *Hemidactylus frenatus* reported for the first time in Galápagos (Torres-Carvajal and Tapia 2011). It was collected on Isabela Island, where three other nocturnal lizards are known to occur. One of them is an endemic species of leaf-toed gecko (*Phyllodactylus* sp.; Torres-Carvajal et al. 2014), and the other two are alien nocturnal geckos, the mourning gecko, *Lepidodactylus lugubris*, and the South American leaf-toed gecko, *P. reissii* (Hoogmoed 1989; Phillips et al. 2012). As much as this offers a great opportunity to study ecological interactions among one endemic and three invasive species of gecko lizards, it also raises concerns about the conservation status of the endemic species in Isabela and other islands in the archipelago. In lieu of the potential negative impacts of introduced common house geckos presented above, their eradication from the Galápagos archipelago should be seriously considered.

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