

Chapter 4

Analysis of Invasive Insects: Links to climate change

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Abstract

Climate change is expected to alter the geographic distribution and abundance of many species, increase the invasion of new areas by exotic species, and in some cases leads to extinction of species and of whole ecosystems. This chapter reviews some of the links between species invasions and climate change. The effects of climate change on insect pest populations can be direct, through impacts on physiology/ behavior; or, indirect, through biotic interactions (i.e., bottom-up and top-down effects). Anthropogenic climate and global change will be a major driver in the introduction, establishment, distribution, impact and changes in the efficacy of management strategies. To address these problems we must be able to predict with accuracy the effects climate change will cause in species distribution and abundance, be they native or exotic species. The commonly used ecological niche modeling (*ENMs*) approaches have implicit assumptions about the biology of the target species, and characterize the ecological niche using aggregate weather and other factors in the area of its recorded distribution. More holistic physiologically based demographic models (*PBDMs*) approaches explicitly model the biological and physiological responses of species to weather and species they interact with at fine temporal and spatial scales.

The geographic distribution and relative abundance of four invasive insect pests are reviewed under observed and +2°C weather scenarios across the USA and Mexico: the tropical new world screwworm, pink bollworm on cotton, Mediterranean fruit fly (i.e., medfly) on a fruit tree hosts, and olive fly on olive. +2°C climate change will increase the distribution of screwworm and pink bollworm, reduce the geographic distribution of medfly and alter the distribution of olive fly. The model for olive fly is used to examine the distribution of the fly across the Mediterranean basin illustrating the transferability of the model.

1. Introduction

Climate change is expected to change the geographic distribution and abundance of many species, increase the invasion of new areas by exotic species and in some cases lead to extinction of some species and whole ecosystems. This chapter reviews some of the links between species invasions and climate change, with a focus on specific biological characteristics endemic of arthropods and insects. While we emphasize invasive species, the same arguments and methods of analysis apply to native species. In this regard we examine the role of weather/climate and biotic interactions on the distribution and relative abundance of the four species, and review GIS-based regional analyses of four invasive insects. Chapter 17 reviews methods of analysis used for studying invasive species.

Invasive species may be of any taxa, and collectively cause in excess of \$140 billion in losses annually in the United States (Pimentel *et al.* 2000) and a trillion worldwide (Oerke and Dehne 2004). This is nearly an order of magnitude higher than caused by natural disasters (see Ricciardi *et al.* 2011). Among invasive alien species, most exotic plant introductions have been intentional (e.g., crops, ornamentals) or as contaminants in seed and soil (e.g., yellow starthistle), whereas most arthropod / insect introductions have been accidental (Pimentel *et al.* 2005). Insects as a major taxonomic group have a long history of establishment and research focus due to their often high economic impact and visibility (Pyšek *et al.* 2008). Overall, a substantial share, 30% or more, of insect pests are introduced alien species, but they make up a small fraction of the total insect fauna (Ward and Masters 2007). A strong geographical bias exists in invasion biology with most efforts addressing invasive species occurring in the United States and other developed countries, with Africa and Asia being understudied, and likely reflecting differences in regional wealth (Pyšek *et al.* 2008). This bias has serious ecological and economic consequences for rapidly globalizing countries such as India that face high risk of biological invasions, with the potential consequences being felt globally as these understudied areas are not only recipient but also major global sources of invasive species (Khuroo *et al.* 2011). A review of 136 case studies of eradication efforts against 75 invasive species indicate that local campaigns were more successful than regional or national ones, whereas reaction time, level of knowledge, and insularity were unrelated to eradication success (Pluess *et al.* 2012).

2. Examining Links between Species Invasions and Climate Change

The effects of climate change on insect pest populations can be direct, through impacts on their physiology/ behavior; or indirect through biotic interactions (i.e., bottom-up and top-down effects; Bale *et al.* 2002). Hellmann *et al.* (2008) identified five potential areas affecting insect invasions with respect to anthropogenic climate and global change: (1) mechanisms of transport and introduction, (2) enhanced establishment, (3) changes in the distribution of existing invasive species, (4) the impact of established invasive species, and (5) changes in efficacy of management strategies.

2.1 Transport and introduction.

Global trade is generally recognized as the primary driver for the introduction and spread of exotic insect species (Mooney and Hobbs, 2000; Tatem and Hay 2007). On broad spatial scales and for a range of taxonomic groups including insects, Essl *et al.* (2011) posits that the consequences of current high levels of international trade on the extent of biological invasions will probably be completely realized only decades into the future, pointing out that the numbers

of alien species currently established correlate more closely to past indicators of socio-economic activity (e.g. trade). Current invasions may to some extent be seen as a socio-economic legacy of past economic activities.

Climate change may also alter the transport and introduction of species directly. For example, like many other insects, wind is a significant factor in the distribution and colonization of many species, and projected increases in storm severity are likely to augment the number of species and distance traveled by invasive insect pests. The longest weather associated migration of an insect occurred in 1988 when desert locusts from Africa were found on Caribbean islands and the east coast of South America (Rosenberg and Bert 1999). The locusts were transported 4500km on a sub-tropical low pressure wave and a resulting hurricane. Increasing storm frequency and severity may therefore be a separate means for increases in new invasive species introductions.

2.2 Establishment

Surface warming may be a key factor in the establishment of new invasive species. For example, using the first record of occurrence for 394 invasive and noninvasive alien insect species introduced in China, United States, and United Kingdom during the period 1900-2005, Huang *et al.* (2011) found a significant positive association between establishment rates of invasive insects and the increase in mean annual temperature. This association was significant even when adjusted for changes in international trade, suggesting that climate warming can boost the establishment rates of invasive insects even without an increased probability of introduction. For example, climate warming is projected to expand the range of the globally invasive tiger mosquito (*Aedes albopictus*; see Benedict 2007) into new alpine areas in Europe from its current range in northern Italy (Roiz *et al.* 2011). Warmer nights are increasing flight activity of the winter pine processionary moth (*Thaumetopoea pityocampa*) enabling them to disperse greater distances (Battisti *et al.* 2006).

2.3 Distribution

A common problem in biological control is that invasive insect and other pests in new geographical ranges are likely to have few natural enemies and as a result tend to be limited in distribution more by climate than biotic interactions (Schermer and Coakley 2003). A warming climate may alter the distribution of existing invasive insects by helping their successful spread into new areas (Robinet and Roques 2010), but may restrict the spread in areas close to the upper range of favorability (e.g. Gutierrez and Ponti 2009). The rate of climate change (i.e., geographic shifts of isotherms over time; see Loarie *et al.* 2009) is of concern for biodiversity conservation as the dispersal rates of many species, especially perennial plants, are up to an order of magnitude slower than for many annual plant species (Burrows *et al.* 2011), increasing the risk of extinction of perennials. The rate of climate change is less of a problem for invasive insects (Hulme 2012) because their rates of spread are often an additional order of magnitude higher (Liebholt and Tobin 2008), partly releasing them from climatic constraints. For this reason, Ohlemüller (2011) posited that invasive insect species are less likely to run out of suitable climatic conditions (i.e., areas within the species' climatic niche space) than native species in the face of climate change. Climate change affects physiology and behavior of insects (and plants), and even modest warming can dramatically affect the energy budget of insects in diapause, and affect the species' geographic distributions and success of invasion (Hahn and Denlinger 2011). Warming could affect all stages via increased respiration and decreases in growth, reproduction and survival.

2.4 Impact of established invaders

Established insect invaders may impact ecosystems both directly via trophic interactions (herbivory, predation or parasitism), and indirectly via more complex mechanism such as competition for resources, disease transmission, apparent competition, or pollination disruption, and in other ways (Kenis *et al.* 2009). Pollination is a key ecosystem service in natural and agricultural systems, and adapted local pollinator may be prone to disruption by the interaction of climate change and invasive species (Schweiger *et al.* 2010). The impact of invasive insect pests may also be mediated by the effects of climate change on their natural enemies (Thomson *et al.* 2010) and via species interactions (Yang and Rudolf 2010). The effects of climate change on the majority of invasive species and their biotic interactions have not been considered and conceal significant unforeseen vulnerability (Burkett *et al.* 2005).

2.5 Management efficacy

Effectiveness of management strategies for invasive species are mostly a function of the capacity to assess the dynamics of the invaded biological systems, with the difficulty likely increasing in the face of climate change (see Gilman *et al.* 2010) and rapid change in abiotic factors, insect migrations and demographic pressures.

In addition, on a more pragmatic basis, climate uncertainty related to temperature, rainfall, wind speed, and other factors, is also likely to alter current pest control practices, by altering the timing of pesticide applications and effectiveness (e.g., longevity, drift and deposition). Although experimental data are lacking, statistical evaluations suggest increased pesticide usage for many crops in response to temperature and/or precipitation (Chen and McCarl 2001). Rising CO₂ per se may also reduce the efficacy of certain herbicides (Ziska *et al.* 1999) increases competition between plants (Manea and Leishman 2011), however, indirect roles of CO₂ on insecticide and/or fungicide applications and efficacy have not been characterized.

3. Assessing Climate Change Effects: geographic distribution and abundance of invasive insects

Plants and animals in the Phylum Arthropoda (e.g., Class Insecta) are heterothermic implying that their developmental rate varies with the temperature of their immediate environment but also other factor such as measures of moisture and nutrition. In the short run, their phenology, dynamics and abundance in an area are largely determined by both weather and interactions with species in their food webs and chains. Climate (i.e., long run weather) and interactions with other species determine average abundance and geographic range. Climate change, specifically changes in surface temperatures, precipitation and rising [CO₂] on plant hosts are likely to alter the distribution and abundance of many insect species directly and via significant impacts on trophic interactions and the potential for extinction.

[CO₂] (Ziska 2003, Ziska *et al.* 2011, George *et al.* 2007) and warming (Meineke *et al.* 2013) are known to be higher in urban areas, with temperatures being of similar magnitude to global warming predicted in the next 50 years. These conditions provide a microcosm climate warming experiment. For example, Meineke *et al.* (2013) found that the scale insect *Parthenolecanium quercifex* was 13 times more abundant on willow oak trees in the hottest parts of Raleigh, NC, in the southeastern United States, than in cooler areas despite similar parasitism rates. Furthermore, scale collected from trees in hot urban areas became more abundant in hot greenhouses than in cool greenhouses, whereas the abundance of scale

collected from cooler areas remained low in hot and cool greenhouses, and suggest that some scale demes had adapted to high temperatures. The synergism of climate with biotic and human-mediated components, including habitat modification is illustrated by the ubiquitous distribution of the invasive Argentine ant (*Linepithema humile*) (Roura-Pascual *et al.* 2011).

The direct effect of global climate and environmental change is thought to add considerable uncertainty to the structure, function and stability of native and invaded ecosystems (*sensu* Tylianakis *et al.* 2008). However, although biological implications of climate change are often posited, exactly how climate change will alter the risk, spread and impact of invasive species is poorly understood (see Yemshanov *et al.* 2009). Ziska *et al.* (2009) posed the following questions related to the potential impact of invasive species on food and fiber production in the face of climate change: how vulnerable is agriculture to invasive species, are current pest management strategies sufficient to control invasive outbreaks in the future; what are the knowledge gaps, and can we provide initial recommendations for scientists, land managers and policy makers in regard to available resources? We note that the same questions and methods of analysis should apply to species in natural ecosystems that will also be affected by climate change.

It is generally acknowledged that the impact of climate change on native and invasive species biology can best be understood via holistic analysis (e.g., Sutherst and Bourne 2009, Gilman *et al.* 2010), but rarely is this done, and further, the question of what methods should be used in the analyses remain largely unresolved (Gallien 2010). A critical first step to assess the invasiveness of a species is to predict accurately changes in its population in space and time. Commonly used methods to predict the geographic distribution of species are classed as ecological niche models (*ENMs*), but more holistic realistic physiologically based demographic models (*PBDMs*) have been developed that offer a larger suite of insights. *ENMs* and *PBDMs* are introduced below with an emphasis on their ecological and bio-economic applications, and in greater detail in chapter 17.

3.1 Ecological niche models (*ENMs*)

ENMs are used to characterize the ecological niche space of species based on aggregate weather and other factors in extant areas of the species, and then to use the model to determine the potential geographic/climatic range in new areas. *ENMs* assume the current geographic distribution of a species is the best indicator of its climatic requirements, that the distribution is in equilibrium with current climate, and climate niche conservatism is maintained in both space and time (Beaumont *et al.* 2009, see Elith. & Leathwick 2009).

But *ENMs* have important deficiencies: difficulty incorporating trophic interactions (Davis *et al.* 1998), and the use of aggregate weather data that miss important short-term weather effects (see Lozier *et al.* 2009), implicit ecological and mathematical assumptions having no mechanistic basis (Soberón & Nakamura 2009) that make the results and transferability (validation) are often conjectural with a predictive power potentially lower than simple spatial interpolation (Bahn & McGill 2007). Further, some caution that *ENM* predictions of species responses to climate change based on projecting altered environmental conditions may be unsound, as climate change may influence the abundance of species and the direction of selection that may also disrupt trophic interactions (van der Putten *et al.* 2010, Wardle *et al.* 2011). Despite shortcomings, *ENMs* have been used widely to assess the potential distribution of invasive species under climate change (Jeschke and Strayer 2008). Thuiller *et al.* (2005) suggests that *ENMs* provide unbiased first-steps for screening the potential range of invasive plants in new areas, and we add, *ENMs* may also be a useful for initial evaluation of arthropods and insects as well (e.g., Lozier and Mills 2011).

3.2 Physiologically based demographic models (PBDMs).

Instead of using distribution records from the native range of an invasive species as the basis for estimating the ecological niche (see above), *PBDMs* explicitly model the mechanistic weather driven biology of the species and of relevant species in its food chain or web (i.e. the system), and use the model to predict the phenology, dynamics and distribution of the species across geographic areas. The *PBDM* approach is holistic and assumes that the weather changes but not the biology of the species, except on a longer time scale. This physiological demographic approach has early roots in the work of de Wit and Goudriaan (1978), the underpinning modeling concepts are summarized by Gutierrez and Baumgärtner (1984, 2007), Gutierrez (1992, 1996) and Gutierrez *et al.* (2008b). In their most complete form, *PBDMs* capture the weather driven daily age-structured dry matter allocation resources. Although the allocation quantities and proportions may differ radically among species, allocation is first corrected for egestion, then respiration and conversion costs, and then allocated to reproduction if the organism is mature or growth if the organism is immature, and to reserves if there is a surplus. This allows the same model to be used to model all plant and animal species despite very different apparent biology and the widely differing allocation fractions. *PBDMs* may have age, mass and other attributes, and embed the biology of resource acquisition and the weather-driven biology of aging, reproduction, survivorship and dormancy and other factors as appropriate. The *PBDMs* may vary in complexity but must include the developmental rate of the organism (Brière *et al.* 1999), resource acquisition rates (e.g., photosynthesis, water and nitrogen acquisition by plants, and resource acquisition by higher trophic levels; Gutierrez 1992, 1996; Gutierrez and Baumgärtner 1984, 2007), temperature dependent rates of mortality, age specific fecundity, and dormancy if appropriate (see Gutierrez and Ponti in press b). The model parameters may be estimated from dry matter allocation studies and from age specific life table studies conducted across gradients of ecological factors with temperature being the dominant one. The models may include considerable physiology driven by solar radiation, temperature, and soil water and nutrients. *PBDMs* are in essence time varying life tables (*sensu* Gilbert *et al.* 1976), the parameters of which have physiological nuance and may vary over time with weather and other factors. Because *PBDMs* are weather driven, applications to climate change scenarios are a nature application.

4 Examples of PBDM

4.1 A plant and an insect

Models for plants consist of linked sub population dynamics models for the age-structured mass of leaves, stems and shoots, and roots, and of mass and number of healthy and infested fruit. The models for herbivores or their natural enemies may be age structured models of the different life stages and may also have attributes of mass, stage, sex, dormancy and other factors as required, but for many situations the mass dynamics may be ignored. A *PBDM* for the per capita mass and number dynamics of cotton and the mass dynamics of cotton and a ladybird beetle are illustrated in Fig. 1a, b respectively (see other examples in Gutierrez *et al.* 1987). Each figure illustrates the daily dry matter allocation to respiration, egestion, growth and reproduction, and together the figures show the level of biological detail provided by *PBDMs*. Note that the figure legends for the different components of dry matter allocation are the same for both species.

PBDMs may be used to model individual growth and development (e.g., Fig. 1 above), at the population level and in a tri-trophic context, in a meta- population context if the rules of movement are known (e.g., say between plants or locations; Gutierrez *et al.* 1999), at a regional

or larger level using a geographic information system (GIS) kriging to smooth data between locations (see below). More complete details for developing PBDMs are presented in chapter 17.

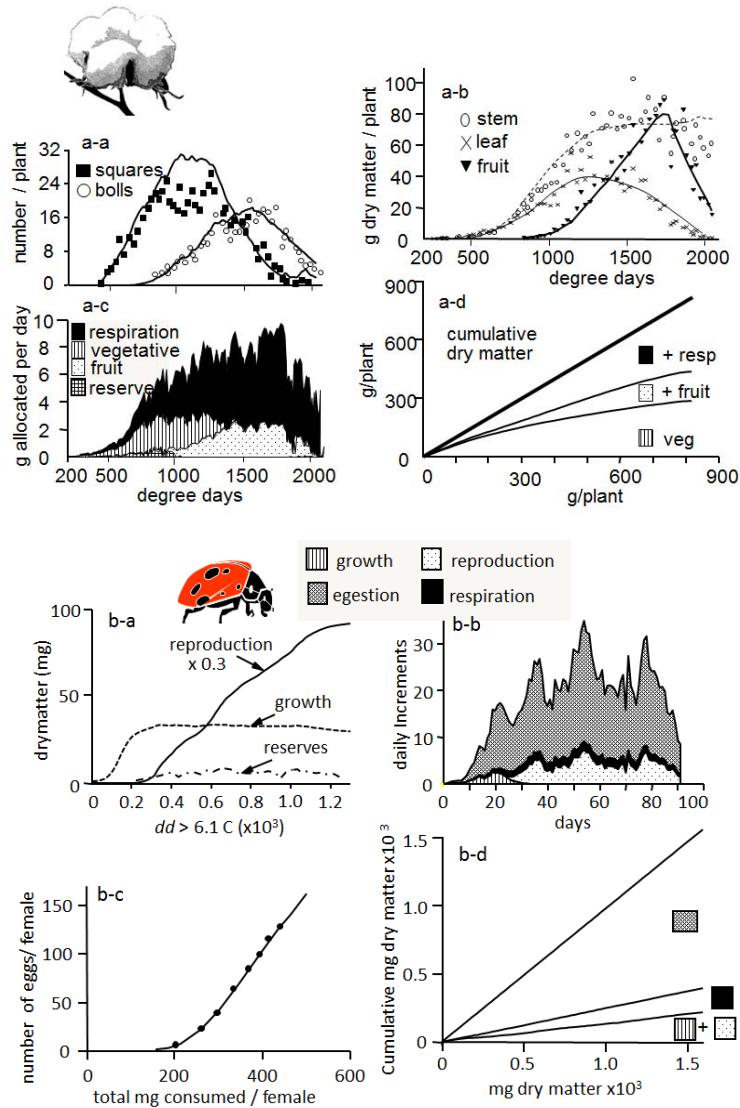


Figure 1. PBDM : (a) cotton (*Gossypium hirsutum*)(weather data, (a-a)number of fruit, (a-b) drymatter, (a-c) daily allocation of drymatter and (a-d) cummulative allocation of drymatter, and (b) a ladybeetle (*Hippodamia convergens*) (b-a) drymatter, b-b) daily drymatter allcation, (b-c) eggs per day and (b-d) cummulative allocation of dry matter (see Gutierrez *et al.* 1987 for details and other examples). Symbols are data and lines are simulation results.

5. Regional analysis of four invasive insect species with global warming

Seven invasive pests were reviewed by Gutierrez and Ponti (in press a, b) with the goal of evaluating the ongoing eradication/containment efforts against them. Here, the distribution and abundance of four of these invasive insects are reviewed under observed and +2°C scenarios to examine the effects of weather on their distribution and relative abundance: the tropical new world screwworm (*Cochliomyia hominivorax* (Coquerel)), pink bollworm (*Pectinophora gossypiella* (Saunders)) on cotton (*Gossypium hirsutum* L), Mediterranean fruit fly (*Ceratitis*

capitata (Wiedemann) (i.e., medfly)) on a fruit tree hosts, and olive fly (*Bactrocera oleae* (Rossi)) on olive (*Olea europaea* L). The predicted abundance of each species is presented in four range groups that should be viewed only as indices of relative favorability in response to observed weather and +2°C climate warming on their distribution.

5.1 Screwworm

The native tropical and subtropical new world screwworm causes myiasis in many vertebrate species including humans. Data to develop a model for screwworm were sparse in the literature despite more than \$750 million dollars spent during a 45+ year effort to eradicate the fly in the southern USA and Mexico using the sterile insect technique (SIT). The current eradication program is designed to keep the fly south of the eradication barrier at the Darien Gap in southern Panama (Krafsur *et al.* 1986).

Gutierrez and Ponti (in press b) sought to estimate the climatic factors limiting the fly's potential distribution and abundance. The fly has high lower and upper thermal thresholds making it susceptible to moderately cold temperatures. The field data suggests that cold temperatures are limiting in the northern reaches of its recorded distribution, with moisture being a further limiting factor in arid regions (see Parman 1945; Rahn and Barger 1973, Krafsur 1978). The 450mm isocline for annual rainfall separates arid regions from more humid subtropical and tropical areas, and was used to develop an index to scale favorability (Gutierrez and Ponti in press a).

Including in the PBDM only the daily effects of temperature on screwworm development, reproduction and survival, a wide distribution for screwworm is predicted (not shown). If we assume screwworm favorability decreases with decreasing annual rainfall ($0 \leq Ix_{rain} = \text{rainfall mm}/450\text{mm} \leq 1$), the PBDM yields the observed area of permanent distribution of average over-winter survival posited from field observations (Bushland 1985). The model fails to capture the favorable micro-climate of the lower Colorado River region created by river (Fig. 2a). The highest average densities of pupae y^{-1} are predicted in the southern tropical areas of Mexico. Areas with densities above the mid-range include south Texas and south Florida, suggesting that these areas may be suitable for permanent year-around survival of screwworm. Densities in the deserts areas of Arizona, California and northern highland Mexico are in the lower quartile of the range, and are likely unsuitable for permanent screwworm persistence. The results supports field observations that current cold temperatures limit winter survival northward and at higher elevations (central Mexico), while low rainfall and cold temperatures greatly limit the fly's distribution in the desert areas of the southwest USA and large areas of Mexico. Invasions of the fly into areas of Texas and elsewhere in the western USA occur during temporally favorable periods of weather, with prevailing winds aided by the fly's high vagility increasing the invasive potential (see Hightower *et al.* 1965, Mayer & Atzeni 1993).

Climate warming of +2°C is predicted to increase the area of permanent favorability for the fly northward, especially into the wetter areas of the SE USA (fig. 2b). The highly destructive, stenophagous pink bollworm (PBW) was first discovered in Florida in 1932 on tree cotton, and spread to commercial cotton in other areas of the USA and Mexico, especially into desert cotton in Arizona and southern California. Dispersal of the pest is aided by summer monsoon winds that annually transport adult migrants long distances from the desert valleys of southern California northward into the southern reaches of the Central Valley and elsewhere (Stern and Sevacherian 1978). The USDA and the California Department of Agriculture (CDFA) began an eradication program against PBW in 1968 in Arizona and California (Staten *et al.* 1992) using sterile insect technology (SIT), but eradication proved elusive (Chu *et al.* 1996) and the program was redirected with the new goal of preventing the establishment of PBW in the Central Valley. In 1997, genetically modified cotton expressing genes from the bacterium *Bacillus thuringiensis*

to produce an endotoxin (*Cry1Ac* β -endotoxin) was introduced across much of the cotton belt. *Bt* cotton is highly effective against PBW and greatly reduces its density in desert cotton (e.g., Tabashnik *et al.* 2010), and this was thought favorable for renewal of eradication efforts. More than \$450 million have been spent on the ongoing PBW eradication program now piggybacked on the *Bt* cotton technology.

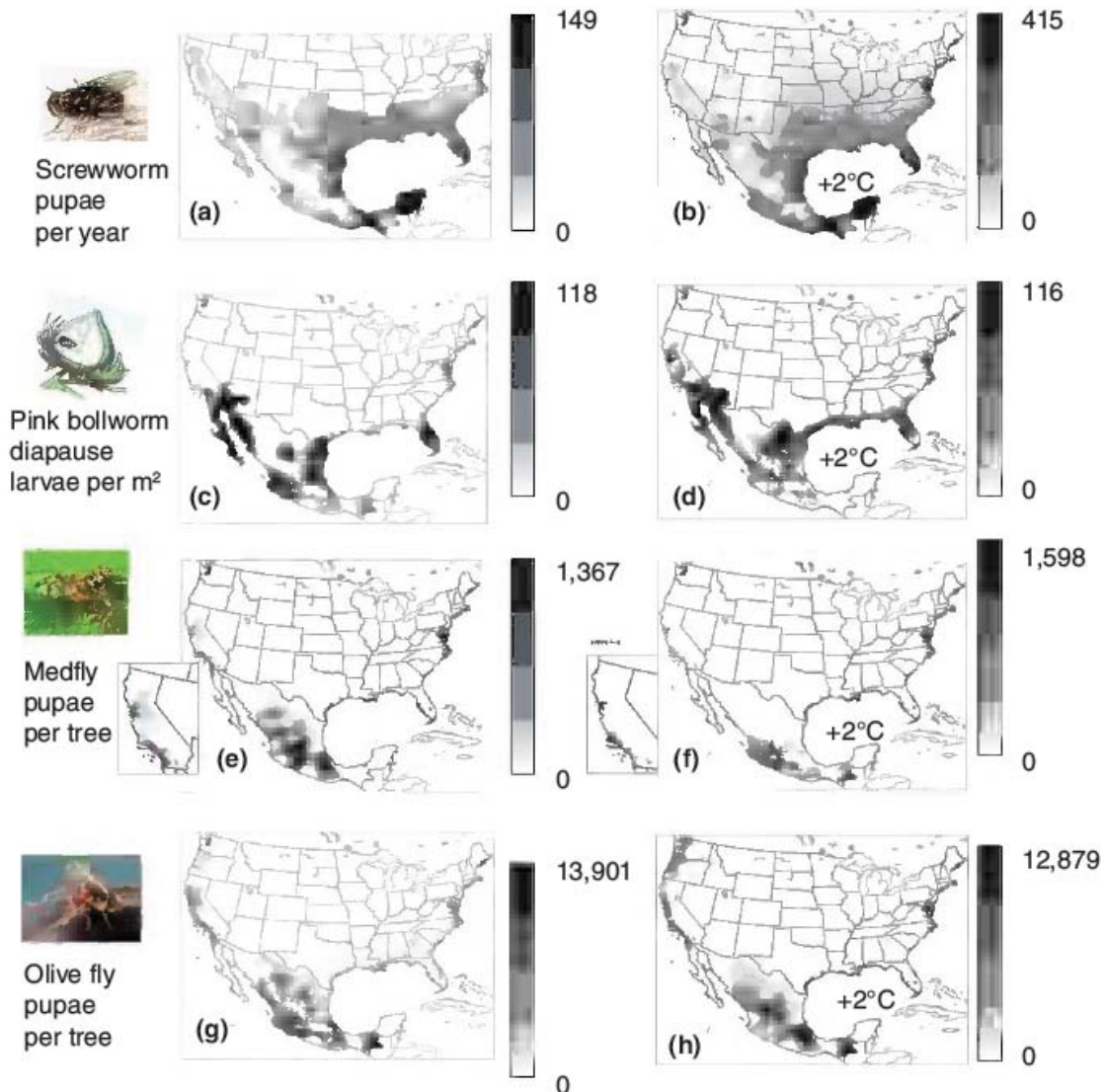


Figure 2. Distribution and abundance (cumulative y^{-1}) of four invasive species in four equally space density ranges below 3000m using observed 1983-2003 weather data (a, c, e, g) and +2°C (b, d, f, h): (a, b) screwworm pupae y^{-1} , (c, d). diapause pink bollworm larvae $plant^{-1}y^{-1}$, (e, f). medfly pupae y^{-1} and (g, h) olive fly pupae y^{-1} in the continental USA and Mexico (see Gutierrez and Ponti 2013 for greater detail). Note the insets for California in e, f

5.2 Pink bollworm

A *PBDM* system for analyzing cotton-pink bollworm was developed by Gutierrez *et al.* (1977) and refined by Stone and Gutierrez (1986) and Gutierrez *et al.* (2006c). This system was used to examine the potential distribution of pink bollworm in the USA and Mexico. Abundant biological data were available to parameterize nearly all aspects of the system model. Key elements of this biology are that diapause is initiated in late summer in response to decreasing photoperiod and

temperature (Gutierrez *et al.* 1981), and the diapause larval stage is cold-intolerant (Gutierrez *et al.* 1977, 2006a; see data in Venette *et al.* 2000).

Using total diapause larvae plant⁻¹ in the absence of control measures as a metric of favorability, the model predicts that highest populations (and survival) occur in the southern desert regions of Arizona, California and northwestern Mexico and Baja California where prior to the advent of Bt cotton, high summer populations and large numbers of fall diapause larvae were common (Gutierrez and Ponti *in press b*). We note that not all areas with temperatures favorable for pink bollworm have sufficient rainfall or irrigation for cotton production (e.g. lower Baja California). In contrast, the model predicts that survival in the Central Valley of California is exceedingly low (see Gutierrez *et al.* 2006a, Fig. 2c). Furthermore, although pink bollworm has been recorded from southern New Mexico and West Texas, average winter survival is predicted low and annually quite variable due to freezing winter temperatures common in the area. Pink bollworm in much of the southeastern USA is also limited by winter temperatures, and only southern Texas and central and south Florida are predicted favorable during the winter period. Central Mexico is moderately favorable, while the Yucatan is unfavorable due to the interaction of high temperatures and short photoperiod that adversely affects diapause development.

Of special interest to this study is that climate warming is projected to increase the distribution of the pest into the Central Valley (see Gutierrez *et al.* 2006a), along the gulf coast and northern Florida and eastern Central Mexico (fig. 2d).

5.3 Medfly

The polyphagous Mediterranean fruit fly (medfly) is a tropical species of East African origins (Balachowski 1950) that is intolerant of moderately low and high temperatures (see Gutierrez and Ponti 2011). The fly is established in sub Saharan Africa, the Mediterranean Basin, Argentina, Western Australia, Hawaii, Mexico and Central America, and possibly southern California (Carey 1991; Sutherst *et al.* 2007). Low numbers of adult medfly have been detected periodically in the Los Angeles Basin and elsewhere in California since 1975 (Carey 1991, 1996).

An intensive area-wide insecticide spray program to eradicate the fly was begun after it was first detected in southern California in 1975. The fly was not detected again until 1980 (Myers *et al.* 2000) when an intensive detection and eradication program based on protein bait and insecticide sprays was initiated. An ongoing SIT program was begun in 1994 costing more than \$270 million.

The medfly system model developed by Gutierrez and Ponti (2011) was used to examine the potential distribution of the fly in Arizona-California and later for North America to assess where the fly can establish and spread (Gutierrez and Ponti *in press b*). As observed, tropical southwestern Mexico and areas bordering Guatemala are highly favorable (Fig. 2e), while vast areas of northern Mexico are largely unfavorable. Compared to tropical Mexico, predicted fly populations in near coastal southern California (see insets) is about a third, with Florida predicted still less favorable, while the remaining areas of the USA are unfavorable.

Climate warming is predicted to decrease the currently limited range of the fly in California (Gutierrez and Ponti 2011), and in Mexico (fig. 2f).

5.4 Olive fly

Drought tolerant olive is of African origins, and has been planted worldwide. Olive is widely planted in coastal California, the Central Valley and southern desert areas of California, and some cultivation occurs in central Arizona and other areas of the USA (e.g., Texas, Florida). Olive

fly was first detected in the Los Angeles Basin of California in 1998 and quickly spread throughout the state where it is well established. Olive fly has not established in other olive areas of the USA. Eradication using SIT was attempted and failed in the Mediterranean Basin (Estes *et al.* 2011), but was not attempted in California.

A system model for olive and olive fly developed by Gutierrez *et al.* (2009) was used to predict successfully the distribution of olive fly in California (see field survey data Wang *et al.* 2009) and in Italy including its distribution in the microclimates along the northern lakes. The model was also used in a fine scale analysis of the fly's distribution and abundance in Sardinia (see Ponti *et al.* 2009), and on a 30 km grid across much of the Mediterranean Basin (Ponti *et al.* in press b, see below). Of special note is that olive has wider thermal limits than the fly.

At the scale of the US and Mexico, the model predicts a wide potential distribution for olive (see Gutierrez and Ponti in press b), while the potential distribution of olive fly is considerably smaller (Fig. 2g). In the USA, highest fly densities are predicted in coastal south and central California with penetration into the northern and central reaches of the Central Valley. The fly is limited by high temperatures in the southern Central valley of California, and the desert areas of the western USA and Mexico. Despite olive production in central Florida, olive fly densities are predicted prospectively to be half those of coastal-southern California, while areas of coastal Texas and Louisiana are predicted marginal. The areas of highest favorability for the fly in North America are south and central Mexico.

Climate warming of +2°C in California would restrict the distribution and abundance in the Central Valley, but increase it northward along the coast in California (see Gutierrez *et al.* 2009) into Oregon and into the higher elevations of Central Mexico (Fig. 2h).

5.5. Olive fly and climate change in the Mediterranean Basin

Daily weather data for climate warming scenarios are increasingly available, but each has its own set of assumptions. In this analysis of olive and olive fly in Mediterranean Basin, weather data from the ERA40 reanalysis of meteorological observations for years 1958-2000 (<http://www.ecmwf.int/research/era/>) were downscaled to a 30km grid using the PROTHEUS regional climate model, and used as observed data to drive the model (see Ponti *et al.* 2009b). A +2°C threshold (European Commission 2007; Zickfeld *et al.* 2009) is widely used to assess risks associated with dangerous levels of global warming and as a policy reference (Lowe *et al.* 2009; Rogelj *et al.* 2010). For heuristic purposes, a climate warming scenario that increases daily temperatures +2°C with all other weather variables remaining unchanged is used to assess the effects of increased temperature on olive and olive fly dynamics. No reliable trend for rainfall in the region is predicted, and hence the effects of rainfall are ignored. Projections of future weather from a climate model could also be used (see Ponti *et al.* in press b), but we use this simpler approach to illustrate the process and relative changes caused by climate warming.

Under present climate, mild coastal areas across the Mediterranean Basin are of high favorability for olive fly, whereas lower favorability occurs at higher inland elevations where low winter temperatures are unfavorable (e.g. areas of Europe), and areas of Morocco and the Middle East where high summer temperatures are close to the upper thermal limits of the fly decrease reproduction, induce reproductive dormancy and increase mortality (Fig. 3a).

With +2°C climate warming, olive fly abundance decreases in many of hot areas that previously were favorable under present climate (areas of Spain, coastal North Africa and Palestine/Israel) (Fig. 3b), and increase in high altitude inland areas with warmer temperatures (Central Spain and Italy) (Fig. 3b). Fruit infestation levels decline in hot areas as further warming makes temperatures unfavorable for the fly (Fig. 3c), whereas levels may increase in milder inland areas, especially at high altitudes that become more favorable for both olive (not shown) and the fly (Fig. 3c). Changes in olive yield and phenology and fly abundance can

increase or decrease fruit attack rates that affect fruit quality as well as changes in control costs. Combining all of these factors in a bioeconomic analysis would enable estimations of the economic impact of climate change (see chapter 17).

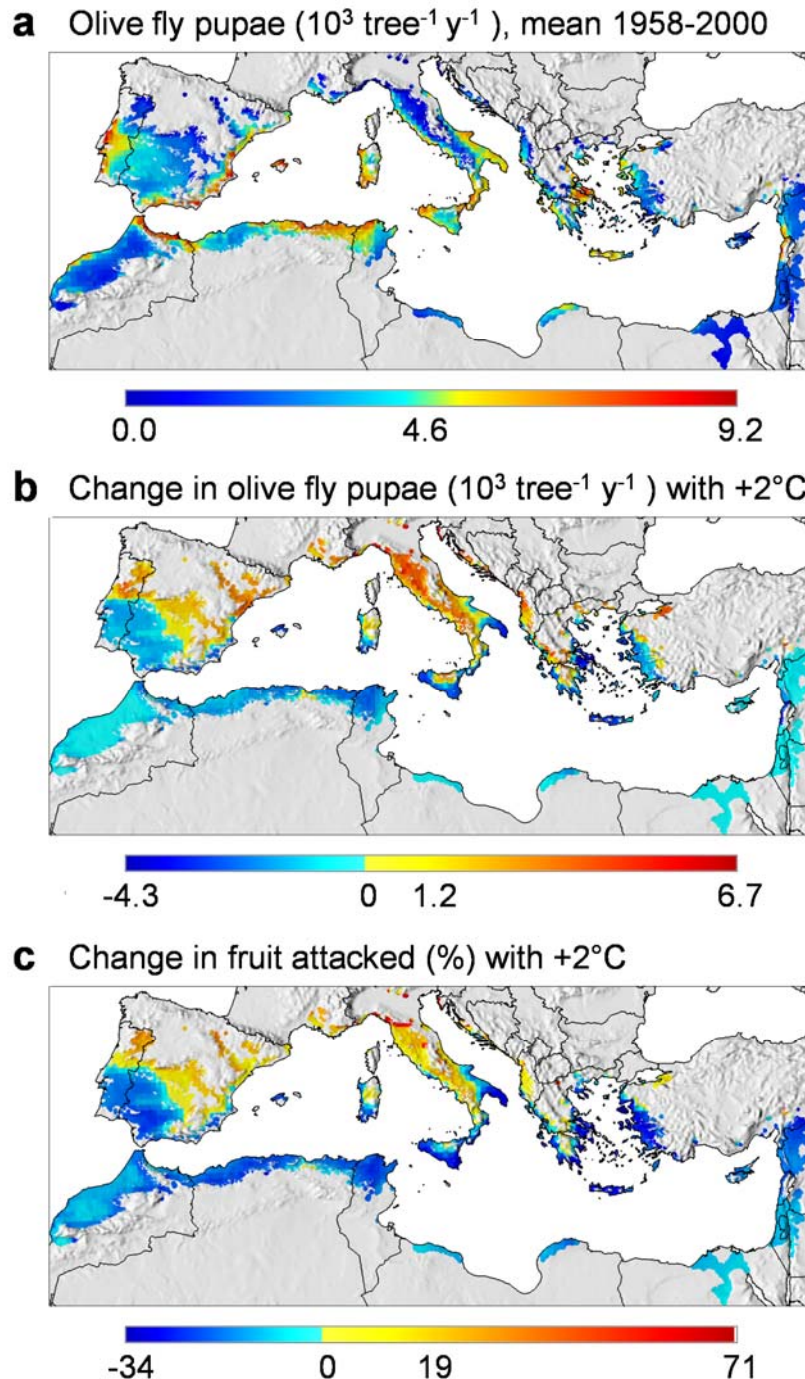


Figure 3. Simulated dynamics and economic consequences of olive fly (*Bactrocera oleae*) as influenced by bottom-up effects of olive growth and development as driven by present climate (years 1958-2000) and a +2°C warming scenario: cumulative number of pupae ($10^3 \text{ tree}^{-1} \text{ year}^{-1}$) under present climate (a), and changes with +2°C climate warming in pupal number (b) and in percent olive fruit attacked by the olive fly (c).

6. Summary

Climate change is expected to change the geographic distribution of many species, increase invasion of new areas by exotic species, and in some cases lead to extinction of some species and whole ecosystems. This chapter reviews some of the links between species invasions and climate change. Invasive species collectively cause in excess of \$140 billion in losses annually in the United States (Pimentel *et al.* 2000) and a trillion worldwide (Oerke and Dehne 2004). The effects of climate change on insect pest populations can be direct, through impacts on their physiology/ behavior, or indirectly through biotic interactions (i.e., bottom-up and top-down effects; Bale *et al.* 2002). Hellmann *et al.* (2008) identified five potential areas affecting insect invasions with respect to anthropogenic climate and global change: (1) mechanisms of transport and introduction, (2) enhanced establishment, (3) changes in the distribution of existing invasive species, (4) the impact of established invasive species, and (5) changes in efficacy of management strategies.

A critical first step to assess the degree of species invasiveness is to accurately predict changes in its population in space and time, but how to do this has been a difficult recurring problem (Gallien 2010). Commonly used methods to predict the geographic distribution of species are classed as ecological niche models (*ENMs*) that use occurrence records and aggregate weather data to characterize the ecological niche space of species. *ENMs* make implicit mathematical and biological assumptions not linked to biological data, and have limitations when used to predict the range of species and the effects of climate change. More holistic physiologically based demographic models (*PBDMs*) are being developed that explicitly model the biological and physiological responses of species to weather and species they interact with. *PBDMs* are independent of distribution records and offer a larger suite of insights concerning the potential distribution of the species under current and future climate change scenarios. Four invasive insect pests were reviewed under observed and +2°C weather scenarios across the USA and Mexico: the tropical new world screwworm, pink bollworm on cotton, Mediterranean fruit fly (i.e., medfly) on a fruit tree hosts, and olive fly on olive. The models predict fine scale distributions and relative abundance for these pests. +2°C climate change will increase the distribution of screwworm and pink bollworm, reduce the distribution medfly, and alter the distribution of olive fly. The model for olive fly was used to examine the distribution of the pest in the Mediterranean basin illustrating the changing patterns of infestation across the region, and the transferability of the model across space and time.

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