Eradication of Invasive Species: Why the Biology Matters

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ABSTRACT Published bi- and tri-trophic physiologically based demographic system models having similar sub components are used to assess prospectively the geographic distributions and relative abundance (a measure of invasiveness) of six invasive herbivorous insect species across the United States and Mexico. The plant hosts and insect species included in the study are: 1) cotton/pink bollworm, 2) a fruit tree host/Mediterranean fruit fly, 3) olive/olive fly, 4) a perennial host/light brown apple moth, 5) grapevine/glassy-winged sharpshooter and its two egg parasitoids, and 6) grapevine/European grapevine moth. All of these species are currently or have been targets for eradication. The goal of the analyses is to predict and explain prospectively the disparate distributions of the six species as a basis for examining eradication or containment efforts against them. The eradication of the new world screwworm is also reviewed in the discussion section because of its pivotal role in the development of the eradication paradigm. The models used are mechanistic descriptions of the weather driven biology of the species. Observed daily weather data (i.e., max–min temperatures, solar radiation) from 1,221 locations across the United States and Mexico for the period 1983–2003 were used to drive the models. Soil moisture and nutrition were assumed nonlimiting. The simulation results were mapped using GRASS GIS. The mathematical underpinnings of the modeling approach are reviewed in the appendix and in the supplemental materials.

KEY WORDS light brown apple moth, fruit flies, pink bollworm, glassy winged sharpshooter, European grapevine moth

We're in the middle of an eradication program and can't afford the luxury of research.
> —A "high USDA official" quoted by Paul Ehrlich (see Burk and Calkins 1983).

How would you make recommendations for control of an invasive species in the absence of information?
> —Question to A.P. Gutierrez from an invasive species scientist, USDA/APHIS/PPQ, Raleigh, NC.

Invasive species may be of any taxa, and collectively are estimated to cause in excess of $140 billion in losses annually in the United States (Pimentel et al. 2005) and a trillion worldwide (Oerke and Dehne 2004). Eradication of an invasive species may be desirable but elusive, and need not be attempted in some cases (see Myers et al. 1998, 2000). The sterile insect technique (SIT) (Knipling 1955), and other methods including pesticides, pheromones, cultural practices, quarantine, and combinations including applications of biotechnology (Robinson 2002) have been used in eradication or containment efforts. However, despite years of effort and expenditures of hundreds of millions of dollars, many invasive species problems remain unresolved.

In this article we examine prospectively the effects of weather on the distribution and relative abundance (invasiveness) of six invasive herbivorous insect species across the United States and Mexico, and use the results to examine the eradication or containment efforts against them. We use published weather-driven, physiologically based demographic models (PBDMs) developed by us and our colleagues in this effort.

The host/insect systems in our study are: 1) cotton (*Gossypium hirsutum* L.)/pink bollworm (*Pectinophora gossypiella* (Saunders)) (Gutierrez et al. 2006b); 2) a fruit tree host/Mediterranean fruit fly (medfly, *Ceratitis capitata* (Wiedemann)) (Gutierrez and Ponti 2011); 3) olive (*Olea europaea* L.)/olive fly (*Bactrocera oleae* (Rossi)) (Gutierrez et al. 2006c, 2009; Ponti et al. 2009a, b); 4) grapevine (*Vitis vinifera* L.)/glassy-winged sharpshooter (*Homalodisca vitripennis* (Germar))/two egg parasitoids (Wermelinger et al. 1991, Gutierrez et al. 2011); 5) a perennial host plant/light brown apple moth (*Epiphyas postvittana* (Walker)) (Gutierrez et al. 2010a); 6) grapevine/European grapevine moth (*Lobesia botrana* (Denis and Schiffermüller))

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(Gutierrez et al. 2012). Because of the pivotal role the native new world screwworm (*Cochliomyia hominivorax* (Coquerel)) played in the development of the eradication paradigm, its eradication in the United States, Mexico, and Libya is reviewed in the discussion section (Gutierrez and Ponti in press). The extensive literature and the basic mathematical structure underpinning the models are outlined in the cited articles, while the general form of the physiologically based demographic models (PBDMs) common to all of the species is reviewed in the Appendix and the Supplemental Materials.

Central to the analysis of the distribution and abundance of heterotherm species is the influences of weather and climate (e.g., Andrewartha and Birch 1954). Climate is the long-run pattern of meteorological factors (e.g., temperatures, rainfall, etc.) in a given location or larger region, while the term weather refers to short-run measures of these factors. The biology of heterotherm species evolves in response to climate, interacting species, and other factors in the native range that in total define its ecological niche (see van der Putten et al. 2010). This biology determines a species' temporal and spatial dynamics and geographic range, and the potential areas it may invade. Weather (e.g., daily) affects heterotherm physiology, behavior, interactions with other species, and hence the dynamics of the species in current time and place.

Modeling the Distribution and Abundance of Invasive Species

Several methods have been used to assess the geographic distribution of heterotherm species. For perspective, we contrast the commonly used ecological niche modeling (ENM) approach(s) and the PBDM approach used here. Each approach has strengths and weaknesses.

ENM Approach. The ENM may be statistical, physiological indices, or based on information theory (see Elith and Leathwick 2009). ENMs are relatively easy to implement and seek to characterize climatically the geographic range of a species based on aggregate weather data (and other factors) from areas of the recorded distribution (Beaumont et al. 2009). ENMs are used to predict the potential native range of the species and prospectively its range in new areas. However, ENMs have implicit ecological and mathematical assumptions that lack mechanistic biological underpinnings (Soberón and Nakamura 2009), and as the Fourth Assessment Report of the Intergovernmental Panel on Climate Change Working group 2 (Fischlin et al. 2007) concluded, ENMs are unable to account for species interactions and population processes. These deficiencies make them problematic when extended to climate change scenarios. We note that the physiological index ENM (e.g., CLIMEX) has elements in common with the PBDM approach outlined below (see Gutierrez et al. 1974, Sutherst and Maywald 1985, Sutherst et al. 2007).

PBDM Approach. Applications of the PBDM and other demographic approaches were reviewed by Barlow (1999) and Hawkins and Cornell (1999) (see

Appendix). PBDMs capture mechanistically the biology of species in response to weather and trophic interactions independent of species distribution data. Tri-trophic PBDM systems may include bottom-up effects on phenology, growth and development of whole plants and plant subunits (e.g., fruits, leaves, etc.); the relevant biology and dynamics of herbivorous species feeding on them; and as required the top-down action of natural enemies (e.g., Gutierrez and Baumgärtner 1984, Gutierrez et al. 1994). Consumer species affect the dynamics of the resource species and vice versa. The tri-trophic grapevine/glassy-winged sharpshooter/parasitoid system model provides a good overview of the PBDM approach (Gutierrez et al. 2011).

With variations, the PBDM approach to modeling plant growth and development is well established in the literature (see Marcelis and Heuvelink 2007, Rodríguez et al. 2011). PBDMs for plants consist of age and mass structured subunit population dynamics models linked via photosynthate availability that governs growth and development of extant subunits and the production of new ones. Photosynthesis is estimated using a functional response model (predator form) driven by current age structured assimilation demands, leaf area index, light, temperature, and other factors (see Gutierrez et al. 2005, 2006b). We assumed nonlimiting water and nutrients in our analyses because data on plant species root depth, soil moisture holding capacity, and soil fertility on a continental scale were unavailable. This may lead to over prediction of plant distribution in arid areas (see Hickler et al. 2009). A tri-trophic study of the noxious yellow starthistle (*Centaurea solstitialis* L.) in California included soil moisture and explained the failed biological control of the weed (Gutierrez et al. 2005).

PBDMs for the insect species are also age-structured but may have attributes of stage, mass, sex, dormancy, behavior, and other factors as necessary. The data required to formulate the models for each insect species are outlined in the Appendix (Figs. A1 and A2). The herbivore models are driven primarily by temperature and the demand for and supply of preferred plant subunits. The acquisition biology of this and higher trophic levels is captured by the same functional response model used for plant photosynthesis, albeit with different units, and using either the predator or parasitoid forms as appropriate (see Appendix equations A3i and ii). Similarly, natural enemy models are driven by temperature and their demand for and supply of preferred host or prey stages.

Weather, Simulation, and GIS Analyses

Weather. Daily weather data (i.e., maximum and minimum temperatures, solar radiation $(cal/cm^2/d)$) from 1,221 locations across the continental United States and Mexico for the period 1 January 1983 through 31 December 2003 were used to run the models continuously across years. Weather data for Hawaii were available from very few locations. The weather data were obtained from the Research Data Archive

(RDA), Computational and Information Systems Laboratory (CISL), National Center for Atmospheric Research (NCAR), Boulder, CO.

Simulation. The species are assumed present at all locations with weather driving the dynamics models and determining the relative favorability of each location for them. Initial conditions differed among the systems, but were the same for all locations within a system study (e.g., olive/olive fly). We do not attempt to model the geographic invasion of the species as this is an impossible task. Numerous life-history variables are computed daily for each species in each system, but total pupae per year was used as a measure of favorability for the holometabolus medfly, olive fly, apple moth, and grapevine moth; total diapause larvae plant per year was used for pink bollworm, and total new adults per year was used for the hemimetabolous glassy-winged sharpshooter. These summary variables should be viewed as indices of favorability.

The output variables were geo-referenced and written by year to batch files. Means, SDs and coefficients of variation were computed for each variable across years at each location. The system models were assumed equilibrating to local weather during the first year (1983), and hence these data were not used in calculating the summary statistics.

GIS. Except in Hawaii, where a 1 km grid was used, the simulation data were mapped using inverse distance weighting on a 3 km raster grid using the GIS software GRASS (Geographic Resources Analysis Support System, GRASS Development Team 2011, http://grass.osgeo.org). The distribution patterns in the maps reflect average local site favorability and the geographic distribution and distance between locations. Red on the color bar indicates high favorability and clear indicate very low favorability. The dots in the maps are the locations of the weather station used.

Integration of the Biology and Model Results

The scope of the study is large, and hence a brief review of the biology, invasion history, and eradication or containment efforts for each of the six invasive species is given as background for evaluating their prospective geographic distribution and abundance. The species are discussed in chronological order of their invasion of California.

Pink Bollworm. The stenophagous pink bollworm is a tropical species of Indian or more likely Papua-New Guinea–North Australian origins (van den Bosch and Messenger 1973, see Grefenstette et al. 2009). It is widely distributed in cotton growing areas worldwide where it also attacks other species of Malvaceae (e.g., okra and hollyhock). Pink bollworm was first discovered in Florida in 1932 on tree cotton, and spread to commercial cotton in the United States and Mexico. The moth invaded the desert cotton areas of Arizona and southern California in the late 1960s where it became the key pest. Dispersal of the pest in California is aided by southwesterly monsoon winds that annually carry adult moths from the southern desert valleys

northward into the Central Valley and elsewhere (Stern and Sevacherian 1978).

In 1968, the U.S. Department of Agriculture (USDA) and the California Department of Agriculture (CDFA) began an eradication program in Arizona and California using the sterile insect technique (SIT) (Staten et al. 1992), but when eradication proved elusive (Chu et al. 1996), the program was redirected with the goal of preventing the establishment of pink bollworm in Central Valley cotton. In 1997, genetically modified cotton expressing the protoxin of the bacterium *Bacillus thuringiensis* (Bt) was introduced across much of the U.S. cotton belt, but not in the Central Valley of California (Godfrey 2004; Gutierrez et al. 2006a, b). Bt cotton is highly effective against pink bollworm reducing its populations to very low levels (e.g., Tabashnik et al. 2010), and this created conditions thought favorable for the renewal of eradication efforts.

In 2001 to 2002, a three-phase SIT eradication program piggybacked on the Bt cotton technology was initiated in the United States and Mexico (Grefenstette et al. 2009; see Fig. 1a). Phase 1 targeted the El Paso/Trans Pecos region of west Texas, south–central New Mexico, and northern Chihuahua, Mexico. Phase 2 was begun in Arizona and New Mexico in 2006, and sub phase 3a–b was begun in 2007–2008 along the Colorado River and in the desert valleys of Arizona, California, and Mexico (http://www.aphis.usda.gov/plant_health/plant_pest_info/cotton_pests). The Central Valley is considered an area of pink bollworm suppression and control because the USDA claimed its SIT program has prevented the moth's establishment there (Staten et al. 1992).

Based on abundant data, PBDMs for cotton and pink bollworm used in this study were developed by Gutierrez et al. (1977), refined by Stone and Gutierrez (1986) with the effects of Bt cotton on the major cotton pests in California added by Gutierrez and Ponsard (2006) and Gutierrez et al. (2006a). Critical elements of pink bollworm biology include tight links to the phenology and dynamics of cotton fruiting, diapause initiation in late summer in response to decreasing photoperiod, and temperature (Gutierrez et al. 1981), and cold-intolerance of diapause larvae (Gutierrez et al. 1977, 2006b; see data in Venette et al. 2000).

Pink Bollworm Distribution and Relative Abundance. Three measures of favorability for pink bollworm were estimated: normalized average winter survival of diapause larvae (Fig. 1b), average number of diapause larvae/plant/year (Fig. 1c), and average cumulative larvae/plant/year (i.e., larval days, Fig. 1d). Not all areas with temperatures favorable for pink bollworm have sufficient rainfall and/or irrigation for cotton production (i.e., roughly the desert areas outside the shaded zones in Fig. 1a).

Winter survival is predicted to be highest in the southern desert regions of Arizona, California, and northwestern Mexico (Fig. 1b) where before the introduction of Bt cotton, high densities of diapause larvae and summer larval populations were common (Fig. 1c and d, respectively). In sharp contrast, very
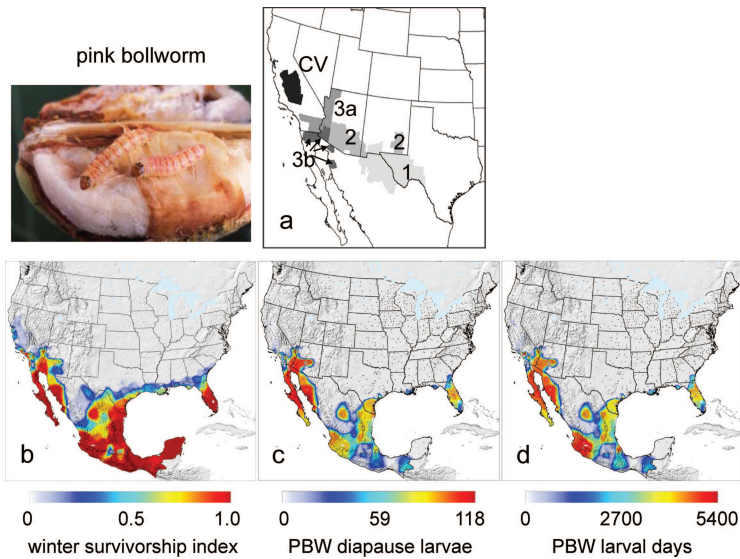
Fig. 1. Prospective distribution and abundance of the pink bollworm in the United States and Mexico below 2,000 m during 1984–2003 using the model of Gutierrez et al. (2006b): (a) phases of the USDA eradication program (phases 1–3b, see text) and the Central Valley (CV) exclusion zone; (b) the normalized average winter survival of diapause larvae; (c) average diapause larvae/plant/year; and (d) cummulative daily counts of larvae/plant/year. Note that shaded areas in Fig. 1a are roughly the distribution of commercial cotton in the south–west United States and northern Mexico. (Image reference: http://www.oxitec.com/moth-gallery/k10075–6-ars-pink-bollworms/).

low winter survival is predicted in the Central Valley (CV) of California (see Gutierrez et al. 2006a–c), and over much of the cotton belt in the south–east United States and the northern half of Texas, southern New Mexico, and north–central Mexico (Fig. 1b). High winter survival is predicted in the Yucatan Peninsula (Fig. 1b), but a combination of high temperatures and photoperiod in the region adversely affect diapause induction (see Gutierrez et al. 1981), and hence population development (Fig. 1c and d).

The predictions of our model contrast sharply with the findings of Venette et al. (2000) that abiotic factors do not preclude pink bollworm's establishment over much of the cotton belt, and that its absence is the result of federal monitoring, quarantine, and local eradication programs. The predictions of the model also conflict with the claim that the ongoing SIT eradication or suppression program has kept pink bollworm from establishing in the Central Valley of California (Staten et al. 1992) under current climate, but this is expected to change with climate warming (Gutierrez et al. 2006a–c). We note that piggybacking the SIT program on the Bt cotton technology in areas where PBW is able to persist increases the likelihood of success for the ongoing eradication program.

Mediterranean Fruit Fly. The polyphagous Mediterranean fruit fly (medfly) is a tropical species of East African origins (Balachowski 1950) that is established in sub Saharan Africa, the Mediterranean Basin (e.g., Italy), Argentina, Western Australia, Hawaii, Mexico, and Central America. The fly was first detected in southern California in 1975 (Carey 1991) and an intensive area-wide eradication program based on insecticides was initiated. The fly was not detected again in southern California until 1980 (Myers et al. 2000) when a detection/eradication program based on protein-bait and insecticides was begun. An ongoing SIT program against medfly was begun in 1994 that currently extends through Mexico and Guatemala.

Low numbers of adult medfly have been detected periodically in the Los Angeles Basin that Meixner et al. (2002), using microsatellite and mitochondrial DNA analyses, determined were new invasions. The fly was also discovered during 1975, 1980, and 1981 in Santa Clara County south of San Francisco Bay, and has occasionally been found in inland locations in the state (J.R. Carey http://entomology.ucdavis.edu/news/califmedfliescities. html, see Gutierrez and Ponti 2011). We note that no ongoing measureable populations of the fly have been found in California.

Key features of medfly's biology are its narrow thermal limits and reproductive quiescence in females when fruit are unavailable. To analyze prospectively the potential distribution of the fly in tropical areas such as Florida, Hawaii, and Mexico, the model developed by Gutierrez and Ponti (2011) for Arizona–California and Italy was modified so that fruit hosts would be available nearly all year-around. This change enabled separation of the limiting effects of temperature on fly dynamics from host availability.

Medfly Distribution and Abundance. The model predicts that only the coastal plain of southern California and Hawaii are potentially favorable for medfly (Fig. 2a and c), with Florida being less favorable, and other areas of the United States being unfavorable (Fig. 2b). As observed, tropical southern Mexico and areas bordering Guatemala are highly favorable for the fly, while the vast desert-highlands areas of north–
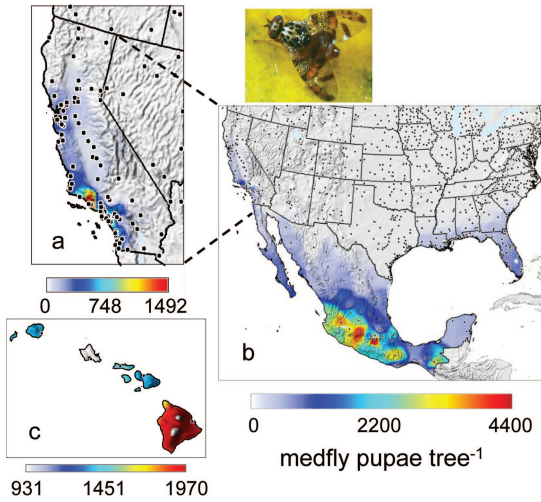
Fig. 2. Prospective distribution and abundance of medfly (pupae/plant/year) below 2,000 m during 1984–2003 using the modified Gutierrez and Ponti (2011) model: (a) California, (b) continental United States and Mexico, and (c) Hawaii. Note that the scales used for Fig. 2a–b and c differ. (Image reference: http://www.freshfromflorida.com/pi/medfly/index.html).

ern Mexico are unfavorable and may serve as a barrier to overland infestation of the United States. Predicted population levels in southern California and Hawaii are about a third those in southern Mexico, while levels in Florida are about a fourth. We note that the same model predicted the observed wide distribution of the fly in Italy (Gutierrez and Ponti 2011).

The limited distribution of medfly in California (and the United States), and more important, its failure to establish and spread after multiple introductions (Meixner et al. 2002) suggest that medfly is not a serious threat to California (or United States) under current climate. Our results questions claims of establishment (Carey 1991, 1996) and hence of eradication.

Olive Fly. Drought tolerant olive is of African origin, and has been planted worldwide in Mediterranean climates. Earliest plantings in California were introduced from Mexico during the Spanish colonial period. Olive is widely grown in the Central Valley and in southern desert areas of California with some cultivation in central Arizona and other areas of the United States (e.g., Texas and Florida). The host specific olive fly was first detected in the Los Angeles Basin in 1998, and quickly spread to the major olive growing areas of the state.

The extensive European literature was used to develop the PBDMs for olive and olive fly (see Gutierrez et al. 2009). Olive requires moderate chilling to produce fruit, but this may not occur in some tropical areas limiting olive production and the distribution of the fly. In addition, the thermal limits of olive are considerably broader than those of the fly. Moderate cold and hot temperatures reduce adult fly survival and reproduction, and females become reproductively quiescent when fruit are unavailable and/or temperatures are high.

Olive Fly Distribution and Abundance. The model predicts a wide geographic distribution for olive in the United States and Mexico (Fig. 3a), while the distribution of olive fly is considerably smaller (Fig. 3b).
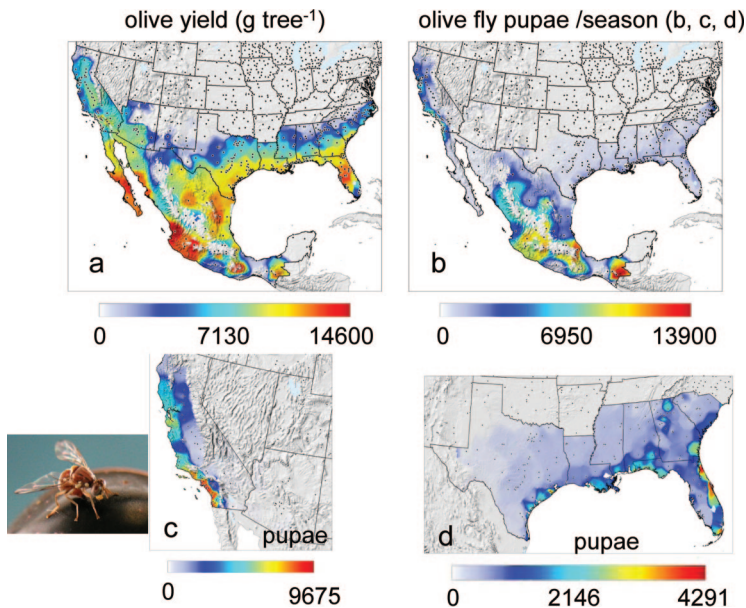

Fig. 3. Prospective distribution and abundance of olive yield and olive fly pupae below 2,000 m during 1984–2003 using the Gutierrez et al. (2009) model: (a) prospective distribution of olive yield (grams/tree/year), and (b) cumulative olive fly pupae/tree/year in the United States and Mexico, and using enlarged maps and different scales for (c) Arizona and California and (d) the south–east United States. (Image reference: Marshall W. Johnson, nature.berkeley.edu).
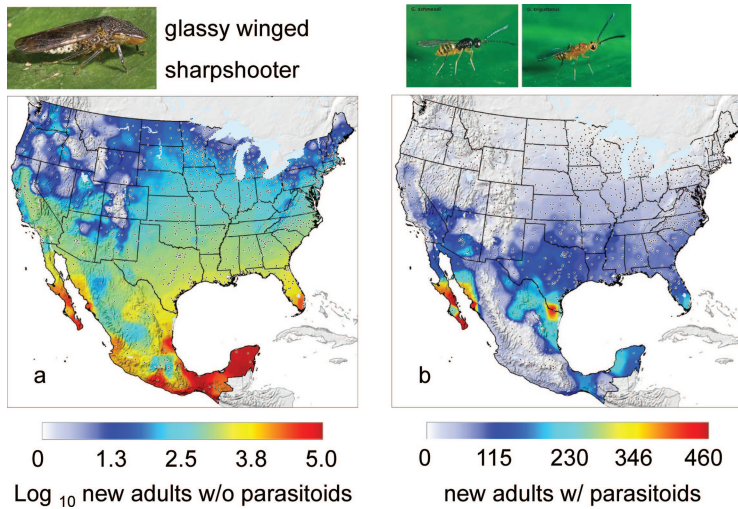
Fig. 4. Prospective distribution and abundance of glassy winged sharpshooter below 2,000 m during 1984–2003 using the Gutierrez et al. (2011) model: (a) average $\log_{10}$ cumulative new adults/vine/year in the absence of natural enemies, and (b) average cumulative new adult glassy-winged sharpshooter/grapevine/year (arithmetic scale) after the action of the parasitoids *G. ashmeadi* and *G. triguttatus.* (Image references: http://www.acgov.org/ cda/awm/agprograms/pestexclusion/ sharpshooter.htm and http://biocontrol.ucr.edu/irvin/ California_agriculture.pdf).

The fly is reported only from California where highest densities are predicted in coastal south and central California with penetration into the northern half of the Central Valley (Fig. 3c). The fly is limited in the southern reaches of the Central Valley and desert valleys of California and Arizona by high summer temperatures (Gutierrez et al. 2009, see also Wang et al. 2009, Johnson et al. 2011). Olive fly densities in central Florida are predicted to be half those of southern California, while areas of coastal Texas and Louisiana are predicted marginal (Fig. 3c vs. 3d). The areas of highest favorability for the fly are predicted to be south and central Mexico, but no infestations are reported there.

The model predicted the distribution of olive and olive fly in California (see Wang et al. 2009) and Italy including the microclimates along the northern Italian lakes (Gutierrez et al. 2009). The model was tested against field data from Sardinia (Ponti et al. 2009a), and was used to map the prospective distribution of the fly in the Mediterranean Basin (Ponti et al. 2009b).

SIT eradication of the fly was attempted in the Mediterranean Basin but failed (Estes et al. 2011). Eradication was not attempted in California where the fly has reached the limits of its climatic/geographic distribution.

Glassy-Winged Sharpshooter. Glassy-winged sharpshooter is a polyphagous subtropical species native to Texas, the south–east United States and Mexico (Triapitsyn and Phillips 2000) that in 1989 extended its range into California (Sorensen and Gill 1996). The sharpshooter feeds on nutrient-poor xylem (Mizell et al. 2008) of numerous host plants (Lauzière and Sétamou 2009). It vectors the pathogenic bacterium, *Xylella fastidiosa* (Wells et al. 1987) that causes Pierce's disease in grape and scorch-like diseases in

other plants (e.g., oleanders and almonds) (Purcell 1997). The sharpshooter lacks a dormant stage and over-winters as reproductively dormant adults (Turner and Pollard 1959) with citrus being a major over-wintering host (Hummel et al. 2006).

High populations were initially found in southern California where two or more generations occur per year (Blua et al. 2001). An area-wide control program based on insecticides and quarantine measures was used with modest success to limit its spread (California Department of Food and Agriculture [CDFA] 2003). Biological control by egg parasitoids (*Gonatocerus ashmeadi* Girault (GA) and *G. triguttatus* Girault (GT)) (Hymenoptera: Mymaridae) greatly reduced sharpshooter densities in California (Pilkington et al. 2005, Gutierrez et al. 2011).

Glassy-Winged Sharpshooter Distribution and Abundance. PBDMs for glassy-winged sharpshooter and its parasitoids (Gutierrez et al. 2011) were linked to a model for grapevine (*Vitis vinifera* L.) (Wermelinger et al. 1991). In the absence of parasitism, the model predicts prospectively a wide geographic distribution and high abundance of the sharpshooter in the United States and Mexico (Fig. 4a). Cold limits the sharpshooter northwardly in the United States and in the central highlands of Mexico. Highest favorability is predicted in subtropical areas of the United States, and especially in tropical areas of Mexico.

Including the action of the egg parasitoids in the model changes the distribution and abundance of the sharpshooter dramatically to roughly its recorded native range (see Triapitsyn and Phillips 2000; Fig. 4a vs. 4b). The predicted distribution and reduced abundance in California accord with current field observations (see Gutierrez et al. 2011). With parasitism, very low densities are predicted in cold areas of Ar-
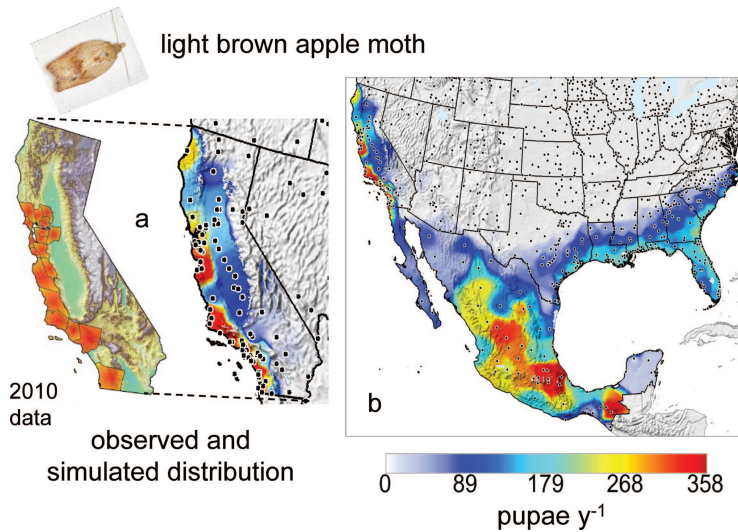
Fig. 5. Prospective distribution and abundance of the light brown apple moth (larval-days) below 2,000 m during 1984–2003 using the Gutierrez et al. (2010a) model: (a) observed (USDA–APHIS-PPQ) and predicted distributions in California, and (b) the prospective distribution and abundance (i.e., larval-days) across the United States and Mexico. (Image reference: http://ucanr.edu/blogs/bugsquad/blogfiles/964.jpg).

izona and New Mexico, and at higher elevations in central and southern Mexico. Mid-range populations are predicted in south Florida, the Yucatan, and the tropical areas of western and eastern Mexico. Highest densities are predicted in south Texas and areas of western Mexico and Baja California. The change in apparent distribution with parasitism supports conjecture by Davis et al. (1998) and van der Putten et al. (2010) that higher trophic levels may need to be included in analyses to estimate the geographic distribution of invasive species.

Light Brown Apple Moth. The polyphagous, temperate-climate light brown apple moth is indigenous to Australia where it is recorded from a wide range of crops, ornamentals, herbaceous weeds, and pome fruit and grape (see Geier and Briese 1981). The moth was detected in California in 2007, and has since been found in 15 coastal and near coastal counties (Fig. 5a; Gutierrez et al. 2010a). Its wide distribution in California when found suggests that it had been present for several years before detection.

The PBDM for apple moth was developed using mostly Australian data (e.g., Danthanarayana 1975, 1976a–c), and was linked to a model for a generic perennial host plant (Gutierrez et al. 2010a). The PBDM system was used to analyze prospectively the moth's distribution in Arizona and California, and here to assess the distribution across the United States and Mexico. Salient features of the apple moth's biology include narrow thermal limits for development, lack of a dormant stage, and low host plant availability during hot-dry summers in nonirrigated areas.

Light Brown Apple Moth Distribution and Abundance. Fowler et al. (2009) predicted a wide distribution for the apple moth that included all areas of the United States having sufficient thermal units for the completion of three generations, and where winter temperatures did not fall below −16°C. In response to this perceived threat, the USDA quarantined the affected counties in California, and Hawaii (Federal Quarantine Order of 2 May 2007). In late 2007, an eradication program was initiated in California using pheromones and insecticides that engendered considerable public protest concerning claimed public health and ecological risks. This led to numerous public meetings including California State Senate hearings, and to an NAS Panel review in 2009 that concluded the USDA's projections of the moth's "... potential geographic distribution in the United States are problematic and in some cases not based on sound, rigorous science" (http://www.nap.edu/catalog/12762.html). The eradication program was switched to a SIT program, and later to a containment effort with strong enforcement.

Our model predicts the apple moth's distribution in California is restricted to near-coastal and inland areas moderated by ocean breezes (i.e., the Davis–Sacramento area), with the Central Valley of California being considerably less favorable (Gutierrez et al. 2010a; Fig. 5). The fine scale predictions of our model for California are in accord with the 2010 county level distribution records (http://www.nappfast.org/powerpointpres/08_Fowler_Pathway_Analysis.pdf); see Fig. 5a).

Prospectively on a continental scale, coastal and near-coastal areas of the Gulf States, eastern Florida, southern and eastern Georgia, and the coastal parts of the Carolinas are predicted moderately favorable. Large areas of Mexico are predicted to be highly favorable. Lozier and Mills (2011) used the ENM *MaxEnt* algorithm (Phillips and Dudík 2008) and predicted a similar distribution for the apple moth in the United
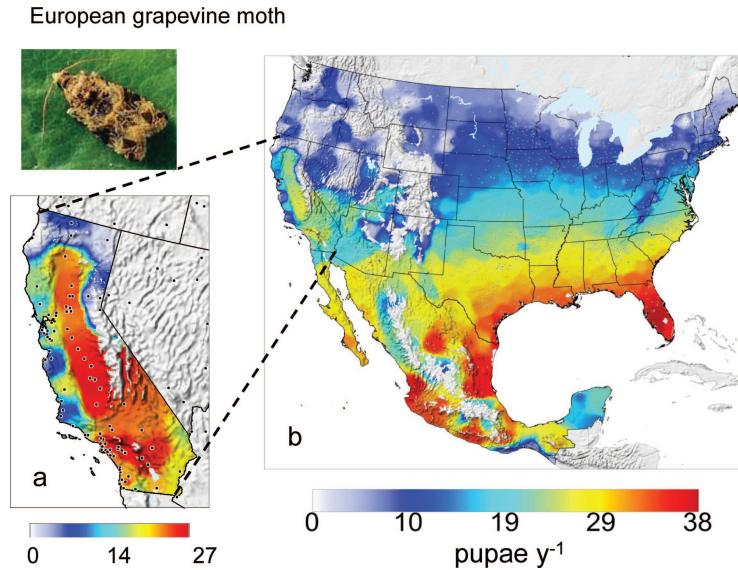
Fig. 6. Prospective distribution and abundance of the European grapevine moth (pupae/vine/year) below 2,000 m during 1984–2003 using the Gutierrez et al. (2012) model: (a) California and (b) the United States and Mexico (note the different scales for a and b). (Image reference: http://www.co.lake.ca.us/Government/Directory/Ag/Agprograms/EGVM.htm).

States and Mexico. He et al. (2012) used the CLIMEX algorithm to map the potential global distribution of the moth, but the coarse grain of the maps makes comparison difficult.

European Grapevine Moth. The polyphagous, temperate-climate European grapevine moth is the most important pest of grape in the Mediterranean Basin (Savopoulou–Soultani et al. 1990). The moth larvae feed on the inflorescence and fruit of plants in >27 plant families over a geographic area that spans central Europe, the Mediterranean Basin, southern Russia, Japan, the Middle East, Near East, and northern and western Africa (Venette et al. 2003). Based on vegetation type and area, Venette et al. (2003) estimated that ≈29% of the continental United States would be favorable for the moth.

The grapevine moth was discovered in northern California in 2009, and by the end of the 2010 season had been detected in nine north central counties (Varela et al. 2010). An ongoing eradication program using quarantine, insecticide, and pheromone for detection and mating disruption was initiated in 2010. High numbers of adult moths were trapped in Napa County in 2010, but very low numbers were trapped during the unseasonably cold-rainy spring–summer of 2011 when the eradication program was also fully active (USDA APHIS-PPQ data reported in Varela et al. 2011). Very few adults were captured during 2011 and 2012 in other infested areas.

Extensive European data were used to develop the model for grapevine moth (Gutierrez et al. 2012) that was linked to a model for grapevine growth and development (Wermelinger et al. 1991). The moth has a wide tolerance to temperature, and depending on temperature produces 2–5 generations per year across its Palearctic range and in California (Gutierrez et al.

2012). Larvae are stimulated to enter diapause in late summer in response to decreasing daylength, but continue development until maturity when they pupate in sheltered places on the vine bark.

European Grapevine Moth Distribution and Abundance. The model predicts prospectively that the moth could infest all of the major agricultural areas of the state (Fig. 6a) and wide areas of the United States and Mexico (Fig. 6b). This prediction is in accord with the range in the United States posited by Fowler and Lakin (2002). Highest favorability is predicted for subtropical and tropical areas of the United States and parts of Mexico. The Yucatan Peninsula and the State of Chiapas are only moderately favorable.

Discussion

Liebhold and Tobin (2008) reviewed the ecology of insect invasions and management, and proposed that strategies to eradicate newly established populations should in theory focus on suppressing populations below Allee thresholds where extinction proceeds without further intervention (see Stephens et al. 1999). On a more practical level, the factors determining the potential geographic range and invasiveness of exotic species must be known to assess their invasive potential, and to help guide development of strategies for eradication, or management should eradication fail (e.g., Gutierrez et al. 2012). Nonetheless, how to make these assessments is an open question.

ENM approaches based on species distribution data have been widely used for unbiased screening of the potential range of invasive species (e.g., Thuiller et al. 2005, Lozier et al. 2009). Important limitations of ENMs were outlined in the text, and their bases contrasted to the mechanistic, weather-driven, PBDMs used

Table 1.   Type and adequacy of data used to develop PBDMs for seven invasive species in North America

	Pink bollworm	Medfly	Olive fly	Apple moth	Grapevine moth	Glassy-winged sharpshooter	Screwworm
Climate type	Tropical	Tropical	Subtropical	Temperate	Temperate	Subtropical	Tropical
Origins	Exotic	Exotic	Exotic	Exotic	Exotic	Native	Native
Host specificity	Steno[a]	Poly	Specfic	Poly	Poly	Poly	Poly
Host model[b]	+	—	+	—	+	+	O
Functional response	+	+	+	+	+	+	O
Developmental rate	+	+	+	+	+	+	—
Fecundity	+	+	+	+	+	+	—
Mortality (T)	+	+	+	+	+	+	—
Mortality (biotic)	—	O	O	—	—	+	O
Dormancy	Strong	Transient	Transient	None	Strong	None	None
$ cost $\times 10^{6c}$	>300[d]	>450[e]	Unknown[f]	25–50	>25	<5	>750
Eradication success[g]	U	U	A	A	U	B	P

[a] Poly, polyphagous; steno, stenophagous; specific, host specific.
[b] Symbol +, sufficient data; —, marginal data; O, insufficient data.
[c] Conservative estimates made from the literature.
[d] 156 million for the current ongoing eradication efforts + prior costs.
[e] 14 million per year since 1980 + emergency spray program costs.
[f] Eradication costs in the Mediterranean Basin unknown.
[g] U, unknown; A, abandoned; B, effective biological control; P, probable.

here to predict the distribution, dynamics, and invasiveness of six invasive species. To develop PBDMs requires sound biological and ecological data that may not be available or be of marginal quality (Fig. A2). The adequacy of the data in the literature used to formulate our models is summarized in Table 1 as sufficient (symbol +), marginal (—), and insufficient (O) with nominal values of 1, 0.5, and 0, respectively. A plot of estimated costs of the eradication or containment efforts ($\times 10^6$) gleaned from the literature on the sum of the nominal values (V) yields an inverse relationship (costs = $-85.7V + 1045.3$; $R^2 = 0.83$; df = 6); see Supp. Fig. 1 [available online only]).

Eradication Programs. Controversy, for various reasons, has been associated with eradication programs. Two major reasons have been the lack of adequate scientific documentation and analysis, and the high costs.

Screwworm. The eradication of the native tropical new world screwworm in North America during the 1960s and 1970s is the hallmark of the eradication paradigm (USDA 2012). That eradication occurred is beyond doubt, but what role did weather play? Despite costs of more than $750 million since the inception of the program (Myers et al. 1998), data to develop a sound PBDM to assess the relative contribution of weather, chemical control, and SIT in the eradication effort remain sparse (see Table 1; Supp. Fig. 1 [available online only]). Novy (1991) reported that periods of rain and warm temperatures in arid areas of the United States and Mexico enabled the fly to build rapidly and to disrupt eradication efforts until normal weather patterns returned. Readshaw (1986, 1989) argued that cold weather rather than the SIT program was responsible for the decline of screwworm. A PBDM based on the limited available data (Gutierrez and Ponti in press) supports observations by Bushland (1985) that low nonfreezing temperatures and/or low rainfall limit screwworm winter persistence in the United States to south Texas and south Florida. The PBDM analysis also suggests that eradica-

tion in Texas during the 1960–1970s (see Krafsur et al. 1986) and in Libya during the early 1990s (see Vargas–Terán et al. 2005) was greatly aided by periods of dry cold weather that greatly reduced fly populations.

Pink Bollworm. The ongoing $300 million SIT eradication program against pink bollworm (see Grefenstette et al. 2009) appears to have a good chance of success, but claims that the program prevented the establishment of the moth in the Central Valley of California (Staten et al. 1992) conflicts with biological data and modeling that predict that low winter temperatures are the limiting factor (see text; Gutierrez et al. 2006b).

Medfly. An eradication/detection program against the medfly is ongoing in California, and in Mexico and Guatemala where medfly is a serious pest. The total costs of the eradication program have been more than $450 million. Despite multiple introductions in California (Meixner et al. 2002), and claims that the fly is established at densities below detection levels (Carey 1991, 1996), no permanent populations have been found. The model predicts that persistence of the fly is likely only in the coastal plain of southern California (Gutierrez and Ponti 2011), and suggests the threat to California agriculture (and the United States) was greatly over-estimated.

Olive Fly. In contrast to medfly, the olive fly established and quickly spread to its climatic limits within California (Gutierrez et al. 2009). SIT eradication of the olive fly was attempted in the Mediterranean Basin where it failed (Estes et al. 2011). Eradication was not attempted in California.

Glassy-Winged Sharpshooter. Invasion of California by glassy-winged sharpshooter was an extension of its native range from Texas, the south–east United States and northern Mexico. Eradication of this pest in California proved infeasible as it quickly spread aided by the movement of nursery stocks. Effective biological control by egg parasitoids helped resolve the problem in California (Pilkington et al. 2005) and in French

Polynesia (see Gutierrez et al. 2011). In contrast to other eradication efforts, the costs of the program were relatively low.

Light Brown Apple Moth. A \$100 million eradication effort was proposed for light brown apple moth in California based on a predicted wide distribution and high economic damage (Fowler et al. 2009, see text). The eradication program was abandoned, and yet no outbreaks of the moth have been reported in California (Wang et al. 2012, N.J. Mills personal communication). The observed and predicted geographic range of the moth remains primarily near the coast (Gutierrez et al. 2010a).

European Grapevine Moth. The ongoing eradication program against European grapevine moth in California seeks to eradicate the moth while its distribution is relatively limited. If eradication fails, the range of the moth will be very large (Fig. 6). However, the European experience has shown that the pest is easily managed, albeit with associated increases in production costs and environmental damage (see Gutierrez et al. 2012).

The Biology Matters. While the PBDMs were able to predict prospectively the geographic range of the six invasive species in our study, no set of biological traits emerged that a priori would enable forecasting their invasiveness, much less their geographic ranges. The geographic patterns of prospective favorability of the species across North America are checkered. Focusing on California, subtropical and temperate species such as olive fly, glassy-winged sharpshooter, apple moth, and grapevine moth readily established but in different areas of the state, while the tropical pink bollworm established only in frost-free desert areas. Establishment of the tropical medfly appears tenuous in coastal southern California, and yet its observed establishment is predicted in Italy (see Gutierrez and Ponti 2011) and southern Mexico/Guatemala (this study).

Dormancy may enable species to survive adverse periods (see Nechols et al. 1999), but it occurs in only two of our six species: the pink bollworm and European grapevine moth. Dormant pink bollworm larvae are cold susceptible limiting the pest's northward range, while a combination of unfavorable high temperatures and daylength may affect diapause development (see Gutierrez et al. 1981) limiting its geographic range in tropical areas (e.g., the Yucatan). In contrast, dormant grapevine moth pupae are cold tolerant and have wide thermal limits that enable the pest to invade a wide variety of climatic regions. The tropical medfly and subtropical olive fly lack a true dormant stage but may enter reproductive quiescence when hosts densities are low, but only olive fly was able to establish widely in California because of its wider thermal limits.

A common thread across the invasive species studied is that decisions to initiate eradication or containment efforts were often not based on sound prospective analyses of the factors determining the potential distribution and invasiveness. Lorraine (1991) captured the essence of the problem in a study of the medfly eradication program in California, concluding that decision makers were unable to determine important areas of uncertainty, identify and interpret feedback (expert opinion), and respond adaptively to the evolving problem. Discussions with scientists in government agencies responsible for eradication programs suggests the agencies often lack the flexible administrative structure to allow their scientists the freedom to inform agency decision making. Our extensive experience with government agencies responsible for the eradication or containment programs strongly suggests a distrust of non-inhouse analyses. Furthermore, eradication or containment programs are often implemented using militaristic metaphors to describe the problem and control tactics; metaphors that often hinder the development of realistic management and conservation goals (Larson 2005).

In the absence of sound analyses of the dominant factors determining the distribution and abundance of invasive species, claims of eradication need (e.g., light brown apple moth in California; Gutierrez et al. 2010a) or of success (e.g., medfly in California, Gutierrez and Ponti 2011) may not hold up to scientific scrutiny, and at times may be exercises that appear to succeed (e.g., pink bollworm in the Central Valley of California; Gutierrez et al. 2006b, Grefenstette et al. 2009), or may succeed after sufficient investment of resources (e.g., screwworm; Krafsur et al. 1986, USDA 2012, Gutierrez and Ponti in press). We propose that the field of invasion biology has matured sufficiently so that realistic prospective analyses of exotic species, be they ENM or PBDM based, can be made in a timely manner and used to help develop science based eradication or containment policies and strategies. We favor the PBDM approach because the models serve as a dynamic library of the biology as it becomes available, and can be used to develop testable management scenarios (e.g., Gutierrez et al. 2012). As a final plea in a time of diminishing budgets, we are reminded of Sir Ernest Rutherford's (Nobel Laureate in Chemistry) admonition: "Gentlemen, we have run out of money. It is time to start thinking."

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Appendix: A Review of PBDM

Overview

Tritrophic population dynamics models, including the physiologically based demographic modeling approach (PBDM), were reviewed in Hawkins and Cornell (1999). Barlow (1999) proposed that PBDMs have large numbers of parameters and hence are difficult to develop, but this is not the case. All of the models in this study, except pink bollworm, were developed using data in the literature. However, in the absence of sufficient available data on a species, the model structure provides guidance as to the data to be collected, and this greatly shortens the process of model development (see below). Data to parameterize the submodels may be obtained in a variety of ways with the most direct one being laboratory age-specific life table studies at different temperatures and gradients of limiting factors as required. Such data enable capturing the effects of these factors on time varying vital rates in the field (e.g., daily) as driven by temperature, resource availability, and other factors. Observations on behavior may be critical and must be made.

Modeling is facilitated by the fact that the same dynamics model and submodels for analogous processes in the life histories are used across trophic levels (see below). The linkages between trophic levels encourages a modular structure permitting different combinations of interacting species to be implemented in a model run using Boolean variables (e.g., Gutierrez et al. 2006a–c, 2008a, b, 2010b; Gutierrez and Ponti 2011). The analyses may be viewed from the perspective of any species in the system. Population dynamics models developed in this manner may be viewed as time-varying life tables (sensu; Gilbert et al. 1976). The models were implemented in Borland Delphi Pascal.

The Dynamics Model

The time invariant and time-varying distributed-maturation time demographic models (see Vansickle 1977) were used to model the dynamics of all populations in case studies be they plant or insect (see Di Cola et al. 1999, pp. 523–524). The forcing variable is temperature (T), and time (t) is a day that from the perspective of the poikilotherm organisms is of variable length in physiological time units above its lower thermal threshold. The numerical solution for the time-varying model for the ith age class of a life stage with $i = 1, 2,\ldots, k$ age classes (see Fig. A1) is equation A1 (see Severini et al. 2005).

$$r_i(t + 1) = r_i(t) + \frac{\Delta x(t) \cdot k}{X(t)}\left\{r_{i-1}(t) - r_i(t) \cdot \right.$$

$$\left. \left(1 + \frac{X(t) + [\mu_i(t) - 1] \cdot X(t - 1)}{\Delta x(t) \cdot k}\right)\right\} \quad [A1]$$

The state variable $r_i(t)$ is density as a rate that may be in units of number or mass. Mean developmental time (X) in degree-days (dd) may vary on two consecutive days ($X(t), X(t-1)$) because of nutrition and other factors (e.g., fertilizer for a plant or fruit age in pink bollworm). If X is constant (i.e., $X(t) = X(t-1)$), the model becomes the time-invariant form of the model. $\Delta_x(t(T))$ is an increment of physiological age (x) (see below), and $\mu_i(t)$ is the proportional age specific net loss rate that includes the rich biology affecting age class deaths, growth, predation, net immigration, and other factors as required by the biology of each species or stage. Immigration was not included in our models. Births flow into the first age class ($k = 1$, see below), and some individuals exit as deaths at maximum age (from cohort k). The density of cohort i is $N_i(t) = r_i(t) \cdot X(T(t))/k$, and the total density in a life stage (or population) is $N(t) = \Sigma_{i=1}^{k} N_i(t)$, where $k = X^2/var$, and var is the variance of observed developmental times. One scheme for modeling the flow between ages and stages in the dynamics model is illustrated in Fig. A1a, but other schemes may also be developed. Fig. A1b shows the distribution of developmental times with different values of k.

Submodels

Subfigures in Fig. A2 lack numerical scales indicating that the shapes of the functions are similar across species, albeit with different units.

Developmental Rates and Time. The developmental rate is nonlinear with temperature ($R(t(T))$) (equation A2 ; Fig. A2a; Brière et al. 1999), but can also be influenced by other factors.

$$R(t(T)) = 1/days(T) = \frac{a(T(t) - T_L)}{1 + b^{T - T_U}}$$
[A2]

Variables a and b are fitted constants and T_L and T_U are the lower and upper temperature thresholds. A cohort initiated at some time t_0 completes development on average when $\int_{t_0}^{t} R(t(T))dt = 1$. Average developmental time in dd is computed in the linear range of favorable temperatures as $X = day(T) \cdot (T(t) - T_L))$. Daily increments of physiological time are computed as $\Delta x(t(T)) = R(t(T))X$.

Developmental times vary with temperature (equation A2) but it may also vary with nutrition (e.g., fruit age for pink bollworm) that increases developmental time compared with the minimum time from the base scalar value of 1. A scalar function such as that illustrated in Fig. A2b could be used to correct $X(t(T))$ in equation A1 for the effects of say nutrition or some other factor. In the time-varying form of the model, $X(t(T))$ may vary on daily or shorter time scales.

Growth and Reproduction

The Functional Response. All organisms are consumers, and the process of resource acquisition in the models is demand driven (Gutierrez 1992, 1996, Gutierrez and Baumgärtner 1984). The per capita resource acquisition rate S is computed using the ratio-dependent functional response model (equation A3) at resource (N) and consumer (C) densities, where D is the per capita consumer demand, and α is the proportion of the resource that may be discovered during Δt. The demand may be for photosynthate, water and nitrogen in plants, or prey biomass or hosts by higher trophic levels including the economic level (Regev et al. 1998). As appropriate for the biology, the per capita functional response model may be the parasitoid (equation A3i; Frazer and Gilbert, 1976) or predator (equation A3ii) forms of the model (see discussion in Gutierrez 1996, p. 81). The predator form of the model is related to Watt's model (Watt 1959).

$$S = N\left[1 - e^{\frac{-DC}{N}\left(1 - e^{\frac{-\alpha N}{DC}}\right)} \right] \text{ (parasitoid form)}$$
[A3i]

$$S = DC(1 - e^{-\frac{\alpha N}{DC}}) \text{ (predator form)}$$
[A3ii]

equations A3i and ii are type II models if α is constant, but type III if α is increasing on N (i.e., $\alpha(N)$). Here we focus on the parasitoid form, though similar arguments apply for the predator form.

To parameterize equation A3i, we assume for exposition purposes that an herbivore female lays one or more eggs per host (e.g., a parasitoid). If only one progeny survives per host, the supernumeraries are assumed to die. Further, assume that from life table studies females have a maximum average age-specific oviposition profile at optimum temperature t_{opt} (i.e., $f(x, T_{opt}) = $ eggs/female; at T_{opt} and age x) (Fig. A2c; equation A4; Bieri et al.1983).

$$f(x, T_{opt}) = \frac{ax}{b^x}$$
[A4]

The total eggs load (i.e., $D(t,T)$) of the adult female population ($C(x,t)$) with age structure (x_0 to x_{max}) is

$$D(t,T)C(t) = sr \cdot \phi_T(t(T)) \int_{x_0}^{x_{max}} f(x, T_{opt}) \cdot C(x,t)dx$$
[A5]

The variable sr is the sex ratio that may vary over time, and $\phi_T(t(T))$ scales for the effects of temperature (Fig. A2d).

Substituting $D(t,T)C(t)$ and host densities in equation A3i enables computation of the number of egg laid (S) in hosts, with the ratio $0<S/DC<1$ being the proportion of the demand satisfied. Other factors may affect the time-varying demand rate (Gutierrez 1992, 1996), and S/D may affect demographic variables such as developmental times, and emigration and survival rates. Adult and immature stages often have different resource requirements, and the model formulation must accommodate this as well. Similar logic could be developed for plants seeking light, water, or nutrients or predators seeking prey (e.g., Rodríguez et al. 2011).

Mortality

Temperature and other factors affect the daily mortality rate and enter equation A1 as components of $\mu(t(T))$. These effects vary widely across species but may be captured by similar functions (e.g., Fig. A2e).

Dormancy

A review of dormancy in insects is found in Nechols et al. (1999). In our study, dormancy (say winter diapause) occurs in the European grapevine moth in response to daylength (Fig. A2f; Gutierrez et al. 2012), or in pink bollworm in response to temperature and daylength (Fig. A2g; Gutierrez et al. 1981). Dormancy may be transient and induced by low host density and/or high temperatures (e.g., olive fly, medfly; see Gutierrez et al. 2009, 2011). In some species, dormancy may also be influenced by nutrition (e.g., pink bollworm, olive fly), and other factors that may be included in the model as identified. As a practical consideration, individuals entering dormancy may be transferred to a separate dy-

namics model formulated using equation A1, where development proceeds on a different time scale.

GIS Analysis

Figure A3 shows the flow of the analysis, including weather data acquisition, simulation runs, and GIS mapping of the data. The simulation data might also be summarized using multiple regression, and the marginal effects of each (or combinations of) independent variables on a dependent variable of interest assessed (e.g., total pupae/year; $\delta y/\delta x_i$). An extensive example of the use of marginal analysis is provided by Gutierrez et al. (2005).
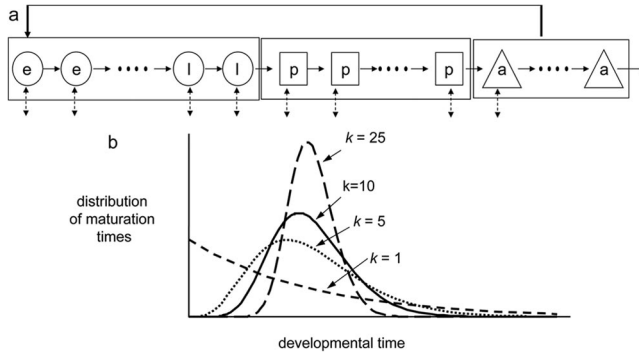

Fig. A1. Population dynamics: (a) an age structured model for the dynamics for the egg (symbol *e*), larval (*l*), pupal (*p*), and adult (*a*) stages with flows (aging) between age classes and stages, with the double arrows indicating net age specific mortality, and (b) the distribution of developmental times based on the number of age cohorts (k) in sub figure A1a (see Severini et al. 2005).
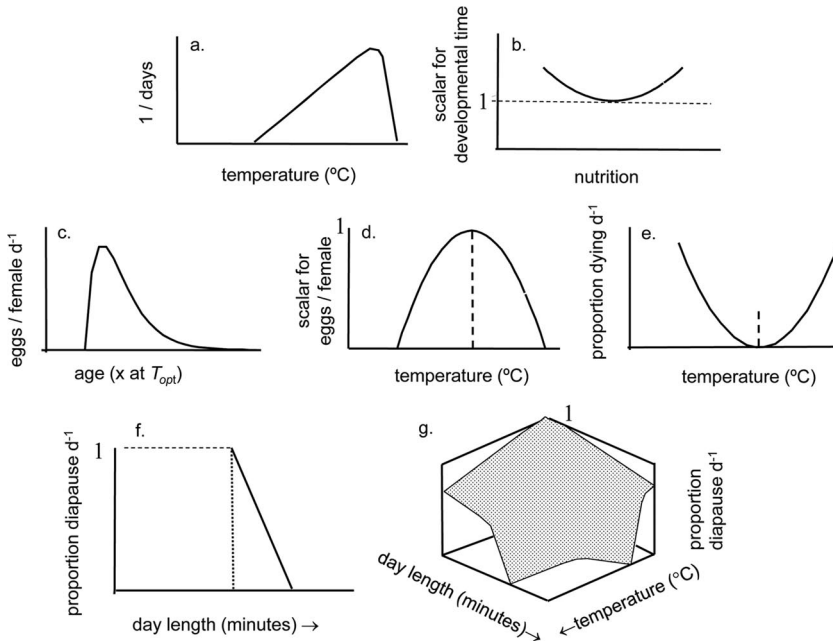

Fig. A2. Submodels of biological processes: (a) the rate of development on temperature (Brière et al. 1999), (b) a scalar for the effects of say nutrition on developmental time, (c) the per capita fecundity profile on female age (*x*) (Bieri et al. 1983) at the optimum temperature (see the vertical dashed line in 2d, e), (d) the effects of temperature on normalized fecundity, (e) the mortality rate per day on temperature, (f) the proportion diapause induction as a function of daylength (e.g., grapevine moth; Gutierrez et al. 2012), and (g) diapause as a function of daylength and temperature (e.g., pink bollworm; see Gutierrez et al. 1981). Subfigures without references apply to all species.
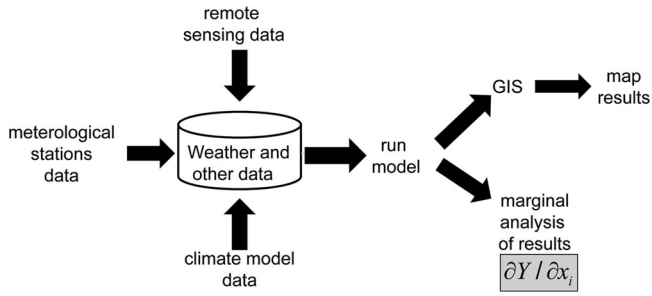
Fig. A3.   Flow of the analysis in the PBDM/GIS system (see Appendix text).