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Climate change effects on poikilotherm tritrophic interactions

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Abstract Species of plants and animals have characteristic climatic requirements for growth, survival and reproduction that limit their geographic distribution, abundance and interactions with other species. To analyze this complexity requires the development of models that include not only the effects of biotic factors on species dynamics and interactions, but also the effects of abiotic factors including weather. The need for such capacity has appreciably increased as we face the threat of global climate change. In this paper, bi- and tri-trophic physiologically based demographic models of alfalfa, cotton, grape, olive and the noxious weed yellow starthistle systems are used to explore some of the potential effects of climate change. A general model that applies to all species in all trophic levels (including the economic one) is used to simulate the effects of observed and projected weather on system dynamics. Observed daily weather and that of climate model scenarios were used as forcing variables in our studies. Geographic information system (*GRASS* GIS) is used to map the predicted effects on species across the varied ecological zones of California. The predictions of the geographic distribution and abundance of the various species examined accords well with field observations. Furthermore, the models predict how the geographic range and abundance of the some species would be affected by climate change. Among the findings are: (1) The geographic range of tree species such as olive that require chilling to break dormancy (i.e. vernalization) may be limited in some areas due to climate warming, but their range may expand in others. For example, olive phenology and yield will be affected in the southern part of California due to high temperature, but may expand in northern areas until limited by low winter temperatures.

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Pest distribution and abundance will also be affected. For example, climate warming would allow the cold intolerant pink bollworm in cotton to expand its range into formerly inhospitable heavy frost areas of the San Joaquin Valley, and damage rates will increase throughout its current range. The distribution and abundance of other cold intolerant pests such as olive fly, the Mediterranean fruit fly and others could be similarly affected. In addition, species dominance and existence in food webs could change (e.g. in alfalfa), and the biological control of invasive species might be adversely affected (e.g. vine mealybug in grape). The distribution and abundance of invasive weeds such as yellow starthistle will be altered, and its control by extant and new biological control agents will be difficult to predict because climate change will differentially affects each. (2) Marginal analysis of multiple regression models of the simulation data provides a useful way of analyzing the efficacy of biological control agents. Models could be useful as guides in future biological control efforts on extant and new exotic pest species. (3) Major deficiencies in our capacity to predict the effects of climate change on biological interactions were identified: (1) There is need to improve existing models to better forecast the effects of climate change on crop system components; (2) The current system for collecting daily weather data consists of a patchwork of station of varying reliability that often record different variables and in different units. Especially vexing, is the dearth of solar radiation data at many locations. This was an unexpected finding as solar energy is an important driving variable in biological systems.

1 Introduction

Most organisms, including humans, depend upon renewable resource species for their survival, and weather in the short run and climate in the long run are highly important determinants of the distributions and abundance of all species (e.g. Andrewartha and Birch 1954; Walther 2002). In natural and agro-ecosystems, weather determines much of the within season phenology and dynamics of species. In agriculture, weather affects crop yield and quality as well as the dynamics of pests and their regulation by natural enemies; regulation that largely goes unnoticed by humans (DeBach 1964). In the United States, pests cause annual losses in excess of \$137 billions y^{-1} (Pimentel et al. 2000), while losses in California are likely to be several billion. Pest outbreaks are currently assumed to be acts of GOD, but an increasing body of research is showing that they are highly predictable, but the outbreak patterns and intensity will be altered by climate change. Among the predicted changes in California's climate are increases in temperature due to increased levels of CO_2 and other green house gases (GHG), and changes in rainfall (http://meteora.ucsd.edu/cap/cccc_model.html).

The potential effects of climate change on renewable resource species was reviewed by Watson (2002), and a series of papers in Reddy and Hodges (2000) reviewed the potential effects in agriculture. Rogers and Randolph (2000) and Sutherst (2004) reviewed potential effects of climate change on some important vector-borne medical and veterinary diseases, and Coakley et al. (1999) reviewed potential effects on plant disease severity. Increases in atmospheric CO_2 have been shown to increase directly the severity of some invasive weeds (Ziska 2003), their tolerance to herbicides (Ziska et al. 1999), and to influence the susceptibility of some crops to attack by pests (e.g. Hamilton et al. 2005). The direct effects of increased levels of CO_2 were not included in our analysis.

The focus of this paper is on potential climate change effects (principally temperature and rainfall) on plant-insect interactions in four major agricultural crop systems in

California (alfalfa, cotton, grape, and olive), and an invasive weed (yellow starthistle) using models that explain how the interacting species respond to extant weather and to climate change scenarios on local and regional levels. A major focus is the effects of climate change on biological control agents and their efficacy. The climate envelope and physiologically based demographic modeling (PBDM) approaches are emphasized. Other methods have yielded important results (see Williams and Liebhold 2002), but a review of these and other approaches is beyond the scope of this paper.

2 Modeling weather effects on species dynamics

2.1 Climate envelope approach

In the 19th and 20th centuries, time series plots of daily, weekly or monthly temperature, rainfall, vapor–pressure deficit, and other variables were used to characterize climatic zones favorable for species. Davis et al. (1998) calls this the ‘climate envelope’ approaches wherein the current distribution of a species is mapped in climate-space (e.g. Fig. 1). This approach posits that if the position of the climate-space changes due to climate change, the distribution of the species would shift accordingly, but they caution, this might not be the case.

An important innovation to the climate envelope approach was to characterize the response of plant growth rates to abiotic variables including weather factors (Fitzpatrick and Nix 1968). For example, a normalized humped shaped growth rate index (values between 0 and 1) having lower and upper thresholds and an optimum can be used to characterize the growth rate of a species on temperature. Similar functions could be developed for other abiotic variables such as moisture (i.e., vapor pressure deficit), soil pH and nutrient content, and other factors. Any of these factors may limit the distribution and abundance of a species (von Liebig 1840), but the more common case is that many factors may be partially limiting. The combined limiting effects of all factors can be summarized mathematically as the product of their individual effects. For example, the overall favorableness for plant growth

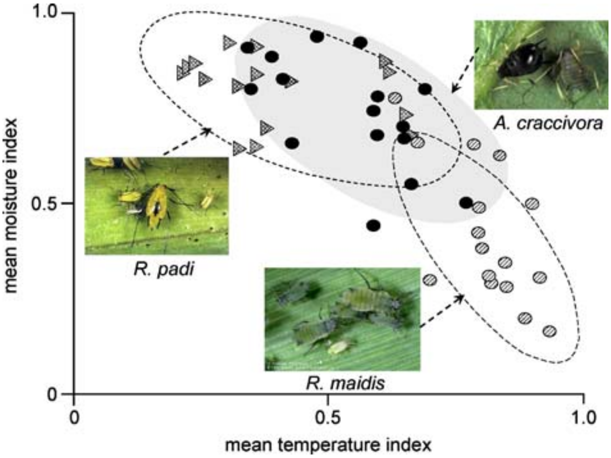

Fig. 1 Bi-variate normal fits to moisture and temperature indices of three exotic aphid pests (modified from Gutierrez et al. 1974)

(*GI*) at coordinate location *i,j* at time *t* due to temperature (*TI*), nitrogen (*NI*), soil water (*WI*), and other factors is the product of the individual factor indices (Fitzpatrick and Nix 1968).

$$0 < GI_{ij}(t) = TI_{ij}(t)xNI_{ij}(t)xWI_{ij}(t)\ldots < 1 \tag{1}$$

A location becomes increasingly marginal as any factor index declines to zero causing $GI_{ij}(t) \to 0$. The growth index approach is a modification of two old ideas, namely von Liebig's *Law of the Minimum* (1840) and Shelford's *Law of Tolerance* (1931).

The same approach could be used to characterize the response of insect species to factors that limit their distribution. An early application was a study of temperature effects on aphids directly and of soil moisture on the growth of their annual host plants in Australian pastures (Fig. 1; Gutierrez et al. 1974; Gutierrez and Yaninek 1983). Sutherst et al. (1991) used this approach to develop the GIS software CLIMEX.

Davis et al. (1998) criticized the use of the climate envelope approach for species where the interactions with interacting species are altered by climate change. They point out that current distribution of a species may also be the result of sources and sinks, wherein species appear to thrive in places where they persist only because individuals disperse there from elsewhere. The study of aphids in Australian pastures provides an example (Gutierrez et al. 1974). The physiologically based demographic modeling (PBDM) approach summarized below circumvents many of these limitations.

2.2 Physiologically Based Demographic Models (PBDM)

To understand how weather affects the dynamics of interacting plant and poikilotherm animal species, we must model how resource acquisition affects the growth, development, reproduction, behavior and polyphenism of species and their interactions as affected by weather in a manner that makes the *predictions independent of time and place* (Gutierrez et al. 1975; Gutierrez and Baumgärtner 1984; Gutierrez et al. 1984; Gutierrez 1992, 1996; Gutierrez et al. 2005). The model must capture both bottom-up effects of plants on herbivores and top-down effects of herbivory and predation. Identifying the common processes across trophic levels and determining how they impinge on the population dynamics of species simplifies the problem allowing the same functional (resource acquisition model) and numerical response (birth-death rates) models to be used to describe the dynamics of all species in tri-trophic systems. A very brief sketch of the mathematics of the resource acquisition and population dynamics models is given in the Appendix with full details given in the reference cited above.

Basic premises of the PBDM approach are that all organisms, including plants and animals including humans, are consumers (i.e., predators in a general sense), and that all have the same problems of resource acquisition and allocation in priority order to egestion, respiration (i.e., the Q_{10} rule), conversion costs, reproduction and growth (including reserves; Gutierrez and Baumgärtner 1984). The biology of resource (biomass) acquisition is captured by demand driven functional response models (see Appendix). The behavior and physiology of acquisition and assimilation to reproduction in adults and growth in immature stages falls under the ambit of the *metabolic pool model* (e.g. Petrusewicz and MacFayden 1970), and may be applied to all trophic levels including the economic one (Regev et al. 1998; Gutierrez and Regev 2005). The metabolic pool model is embedded in the population dynamics models used to simulate the age-mass and other attributes of structured populations.

Resource acquisition may be biomass fixed by plants or consumed by herbivores and carnivorous, or for parasitoids, it may be individual packets of energy represented by unitary hosts (e.g. individual herbivores in fruit). Energy (biomass) is the currency of interactions within and among species, and the success in meeting demands drives their population dynamics (Gutierrez and Wang 1977; Gutierrez and Baumgärtner 1984). Per capita consumer demand for resources may be a function of temperature, age, stage, sex and other factors, but because the search for resources is imperfect, the ratio of consumer resource acquisition (i.e. *supply*) to physiological *demand* is always less than unity. Other factors in addition to energy (biomass) may limit a species (e.g. Eq. 1) and are included in the model as supply/demand scalars for species vital rates from their maximum values. The within species mass and number dynamics are linked via aging rates, and age-specific birth, death, and net immigration rates. In poikilotherms, the aging rate of each species has a characteristic response to temperature, but this may be modified by nutrition and other factors.

The plant trophic level consists of a canopy of plants with populations of plant subunits that may be preferentially attacked by herbivores that in turn are attacked by carnivores. The plant model includes sub-models for the dynamics of leaves, stem and shoots, root and fruit, but the plant model also tracks the net balance of soil moisture (rainfall, evapo-transpiration, runoff, etc.) using the Penman equation based model (i.e. Ritchie 1972), and the net balance of nitrogen (i.e. uptake and input from available sources such as organic matter decomposition and fertilizer applications; Gutierrez et al. 1988; Wermelinger et al. 1991). Leaves search for light and roots search the soil for water and nutrients allowing the same functional response model to be used for the acquisition by both.

For species of arthropods, age structured models of mass and numbers are usually simulated, but other attributes may be included (e.g. morph, genotype, etc). Each species has age specific preferences for stages and ages of the resource species attacked.

Seasonality is an important aspect of the biology of many species. Dormancy occurs in plants and insects, and the ability to enter (or break dormancy) in response to photoperiod, temperature and moisture stimuli may determine whether a species survives in an area (Nechols et al. 1999). These factors are included in the models as required.

2.3 Weather variables

Among the variables used in the model are daily maximum–minimum temperatures, solar radiation, rainfall, daily runs of wind (km day^{-1}) and relative humidity. Complete weather data for the period 1 January 1995 to 31 December 2006 were available from 125 locations in California and 17 in Arizona, and were used in the biological simulation studies (Fig. 2).[1] Climate warming scenarios were made by increasing average daily temperatures across all sites and years.

Projections of temperature and rainfall for the period 1950–2100 from two state-of-the-art global climate models were used in limited studies at seven locations in California (Fig. 2, symbol O): (1) The low-sensitivity Parallel Climate Model (PCM) and (2) the medium-sensitivity Geophysical Fluids Dynamic Laboratory model (GFDL).[2] The climate models make different assumptions about the level of green house gas (GHG) emissions, and while each has two scenarios, only the scenarios that assume low levels of GHG were

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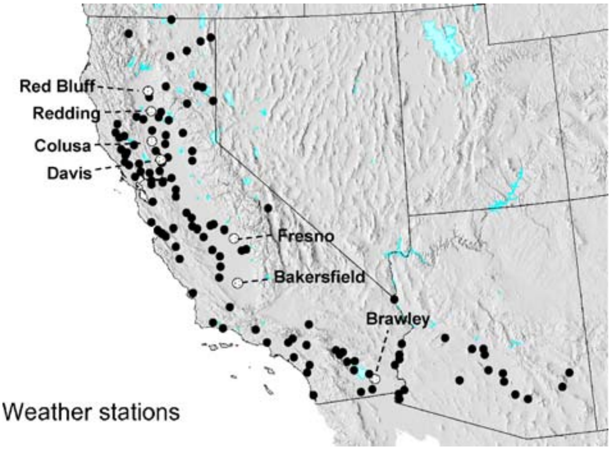
[1] UC/IPM, http://www.ipm.ucdavis.edu.

[2] The National Center for Atmospheric Research (NCAR) and the U.S. Department of Energy (DOE) groups, and the NOAA Geophysical Dynamics Laboratory, Princeton New Jersey.

Fig. 2 Weather stations (*filled circles*, *empty circles*) that had full weather data for the period 1995–2005. Climate model projections for seven locations were used in some studies (*empty circles*; see text for details)



used. The PCM scenario used has a sensitivity range of +1.7–3°C and the GFDL scenario has a range of +2.2–4°C, and yearly precipitation is expected to decline in both scenarios (GFDL>PCM; see Hayhoe et al. 2004; Maurer and Duffy 2005; Maurer 2007, and http://meteora.ucsd.edu/cap/cccc_model.html). The climate models do not predict daily solar radiation, and hence a linear regression of observed daily solar radiation on the difference of observed daily maximum and minimum temperatures at each location was used in the model.

2.4 GIS analysis

The predictions of the weather driven biological models across the varied landscapes of California were mapped using the geographic information system (GIS) software *GRASS* GIS.[3] Linear multiple regression models of the simulated data were also made. In some analyses, species presence–absence dummy variables (0, 1) were used as independent variables. Only independent variables having slopes significantly greater than zero were retained in the model ($p<0.05$; Neuenschwander et al. 1989). Marginal analysis (i.e. $\mathrm{d}y/\mathrm{d}x_i$) of the regression model was used to estimate the large effects of independent variables and their interactions on dependent variables of interest. The goal was to estimate the large effects of various factors on important ecological relationships, and not prediction as measured by explained variance (i.e. R^2; Gilbert et al. 1976).

3 The effects of climate change on selected crops and pest interactions

Analysis of complete ecosystems, even simple cropping systems, is impossible as there are simply too many species (e.g. Gilbert et al. 1976). For example, there are roughly 1500 species of arthropods in alfalfa, but fortunately most are under good natural or biological control and/or they are transients in the crop. Only a few species cause economic damage and hence we shall focus on some of these.

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[3] *GRASS* is an open source GIS software package originally developed by the United State Army Corp of Engineers. The version used is that maintained by the GRASS Development Team, 2006 (Geographic Resources Analysis Support System (GRASS) Software. ITC-irst, Trento, Italy: http://grass.itc.it)

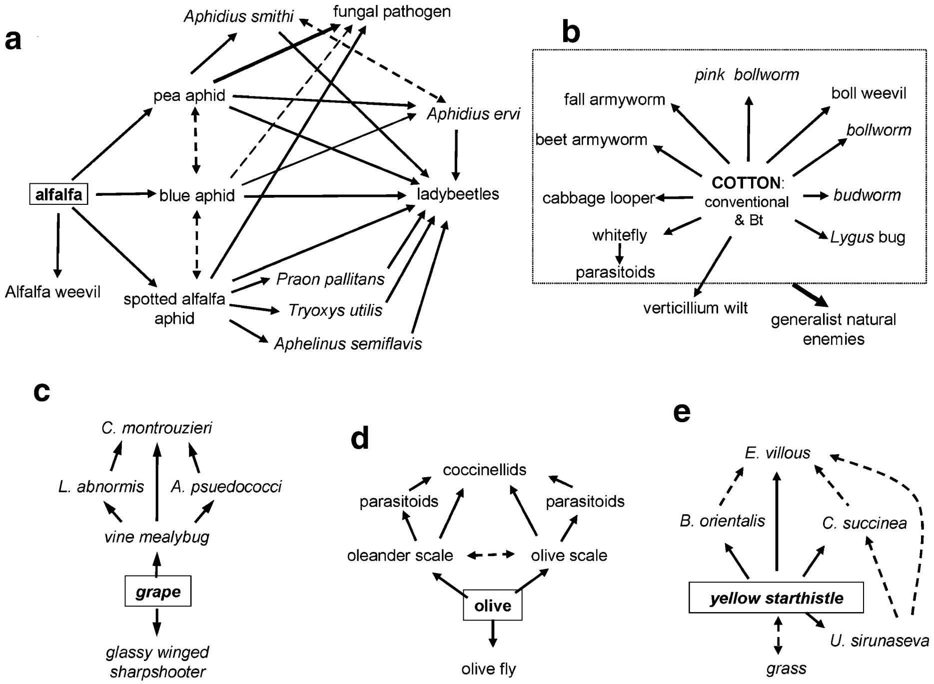

Fig. 3 Some agricultural system food webs that have been modeled subset of which are used to analyze the effects of climate warming on target pests. The *solid arrows* indicate the direction of energy flow while the *dashed arrows* indicate competition between species (modified from Gutierrez and Baumgärtner 2007). **a** alfalfa; **b** cotton; **c** grape; **d** olive; **e** yellow starthistle

Tritrophic interactions in several crop systems have been modeled (e.g. alfalfa, cotton, grape, olive and the noxious yellow starthistle; Fig. 3). The modular structure of the models allows any combination of the species and their interactions to be run over any number of years. However, only subsets of the interacting species are used to illustrate aspects of climate change on their biology, interactions, geographic distribution and abundance. The arrows in the figures indicate the direction of energy flow.

The following studies were conducted using observed and climate change scenarios: (1) Disease and natural enemy mediated competition between two aphid species in alfalfa; (2) The expansion of the geographic range of pink bollworm in cotton; (3) The biological control of grape vine mealybug by natural enemies; (4) Olive phenology and yield, and olive fly distribution and abundance; (5) The biological control of the weedy yellow starthistle. The complexity of the analysis is increased with each example, but the same level of biological complexity was been incorporated in each system.

3.1 Weather effects on species dominance in Alfalfa

Since the introduction of alfalfa (*Medicago sativa* L) to California more than 125 years ago, a series of exotic pests have been accidentally introduced (Fig. 3a), but most of them have been controlled by introduced natural enemies (i.e. biological control). However, climate change may change this situation by altering the interactions among species in this and in

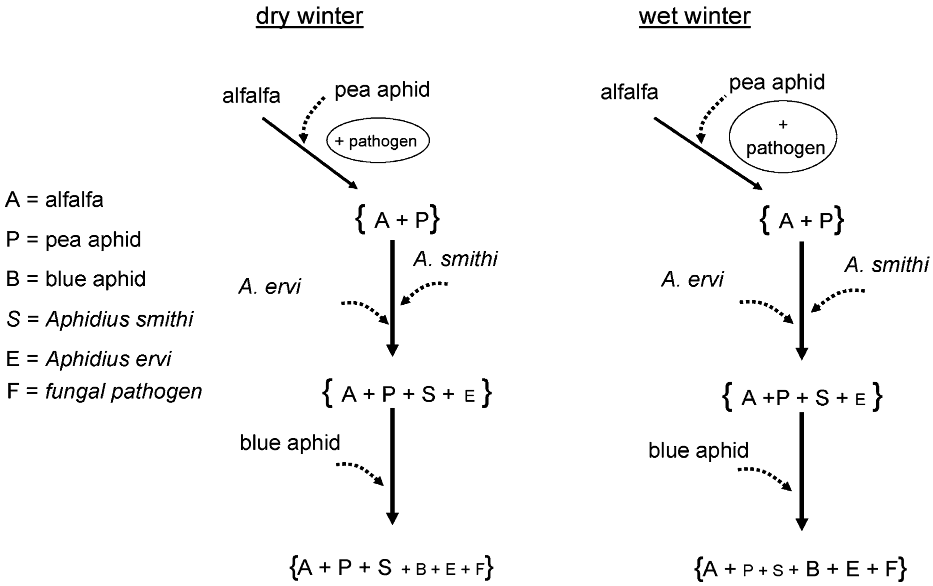

Fig. 4 Assembly diagrams (sequence of introduction) for pea and blue aphids and their natural enemies in California alfalfa and the dominance of different species under dry and wet winters (see text for an explanation). The *dashed arrows* indicate the time sequence of introduction, the *solid arrows* indicated the direction of time, and the *size of the symbols* indicate species dominance (cf. Schreiber and Gutierrez 1998; Gutierrez 2000)

other food webs. Here we use the exotic pea aphid (*Acyrthosiphon pisum*) and blue alfalfa aphid (*A. kondoi*) to illustrate how this might occur (Fig. 4).

Among the pests introduced to alfalfa (symbol A) are the pea aphid (symbol P) and blue alfalfa aphid (symbol B). In the absence of effective natural control, the aphids overwhelmed the capacity of native aphidophagous ladybird beetles (Coccinellidae) to control them. (The beetle is not included in the assembly diagram because its action does not regulate aphid populations.) Two parasitoids (*Aphidius smithi* (S) and *Aphidius ervi* (E)) and a fungal pathogen of the aphids, *Pandora neoaphidis* (*F*) were introduced resulting in good biological control. The sequence of introductions (the dashed arrows in Fig. 4) and species dominance were explored using assembly diagrams for dry and wet winter scenarios respectively (cf. Schreiber and Gutierrez 1998).

The parasitoid *Aphidius smithi* is specific to pea aphid and both aphids are attacked by *A. ervi* that prefers pea aphid. In addition, pea aphid is ten fold more susceptible to the fungal pathogen than is blue aphid (Pickering and Gutierrez 1991). During the normally wet Northern California winter, the pathogen causes catastrophic mortality to pea aphid, but during hot dry periods, the impact of the pathogen declines and pea aphid has a competitive advantage over blue aphid. During dry winters, pea aphid and its host specific parasitoid *A. smithi* would be dominant over blue aphid and *A. ervi*. Dominance is indicated by the larger letters. However, during wet winters favorable for the pathogen, the fungus suppresses pea aphid and hence *A. smithi* allowing the dominance of blue aphid and *A. ervi*. In addition, pea aphid has a higher thermal threshold than blue aphid, hence as temperatures in California increase and rainfall decreases as the climate models predict, then pea aphid would likely become more abundant than it currently is.

> *The important general point is that climate change will alter the balance between species not only in this, but also in many other natural and agricultural food webs leading to a myriad of new food webs and/or new geographic distributions. Some of the outcomes may be harmful to human welfare as renewable natural resources may be threatened directly by climate change and by increased herbivore damage in agricultural and natural ecosystems.*

3.2 Expansion of pest geographic range due to climate warming - cotton/pink bollworm

Cotton is grown as an irrigated annual crop in California, principally in the southern half of the great Central Valley (i.e., the San Joaquin Valley), in the desert Valleys of Southern California, and in Southern Arizona. Cotton is attacked by several insect pests, and ten of the common ones have been included in the model (Fig. 3b). Of these, only the pink bollworm (*Pectinophora gossypiella*, PBW) is a primary pest, and only in the southern desert valleys of California (e.g., the Imperial and Coachella valleys), along the Colorado River and in south central Arizona (Gutierrez et al. 1977). Annually, late summer migrants are blown northward into the lower San Joaquin Valley, but winter frosts are thought to prevent its establishment there (Gutierrez et al. 1977). In contrast, Venette et al. (2000) analyzed the potential geographic range of PBW in the Southeastern United States using CLIMEX (Sutherst et al. 1991). They concluded that weather did not preclude the establishment of PBW over much of region and that failure to expand its range was due to quarantine and other measures.

To examine these issues, weather data for the period 1995 to 2005 and the cotton/ pink bollworm modules of the cotton system were used to simulate the distribution and

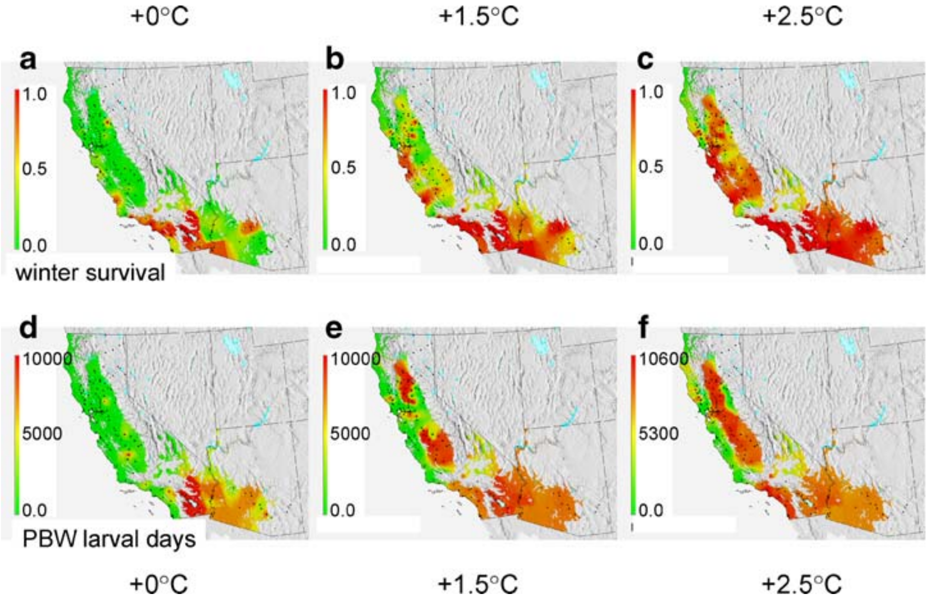

Fig. 5 Cotton/pink bollworm: predicting areas of favorableness below 1,000 m of elevation. The effects on average proportion winter survival of diapause larvae (**a**–**c**) and average total seasonal PBW larval densities (i.e., larval days, **d**–**f**). Results using observed weather (+0°C, **a**, **d**) and with increases of +1.5°C (**b**, **e**) and +2.5°C (**c**, **f**) in average daily temperature respectively (modified from Gutierrez et al. 2006)

abundance of PBW in Arizona and California (Gutierrez et al. 2006). Four climate warming scenarios that increased observed average daily temperature 1.0, 1.5, 2.0 and 2.5°C were used, but only the results for the 1.5 and 2.5°C scenarios are shown (Fig. 5). In all studies, the same initial PBW density was assumed at all locations during the first season, but thereafter the simulated numbers of surviving over-wintering diapause larvae produced at each site during September–October were used as starting conditions the following spring. The 1995 simulation data were not used in the analysis. The goal of the study was to estimate the geographic limits set by weather, and hence the average proportion of winter survival and the average cumulative larval days per year for the period 1996–2005 were used as metrics of local persistence at each location below 1,000 m (Fig. 5).

The predicted geographic distribution of pink bollworm using observed weather is in good agreement with its current distribution (+0°C, Fig. 5a,d). However, when average daily temperatures are increased +1.5 and +2.5°C, winter survival of diapause larvae is predicted to increase greatly in southern California and Arizona and also in the Great Central Valley (Fig. 5b,c) resulting in increased summer populations of PBW (Fig. 5e,f).

> *The key point is that climate warming would increase the geographic range of this and likely other cold limited species (e.g. Mediterranean fruit fly).*

3.3 Geographic distribution and abundance—grape/vine mealybug/natural enemies

European grape vine (*Vitis vinifera*) is widely grown in California, and climate change will affect not only grape yield but its pests. A recently introduced invasive pest of grape, the vine mealybug (*Planococcus ficus*, VMB), has spread throughout much of California despite extensive quarantine and biological control efforts that to date have proven ineffective (Gutierrez et al. 2007).

Among the natural enemies introduced to control VMB (and other mealybugs) are the beetle predator *Cryptolaemus montrouzieri* (Coccinellidae) and two parasitoids (*Anagyrus pseudococci* and *Leptomastidae abnormis* (Hymenoptera: Encyrtidae) (Bartlett 1974; Noyes and Hayat 1994; Daane et al. 2003; Fig. 3c). Control of VMB is complicated by the presence of a spatial refuge under the vine's bark and in the root zone. This refuge shields a large proportion of the VMB population from attack by natural enemies, and in addition increases VMB winter survival (Gutierrez et al. 2007).

The PBDM was developed and used to examine the efficacy of the ongoing VMB biological control efforts and on the distribution and abundance of the interacting species as modified by weather and projected climate-warming scenarios (Fig. 6). The simulation predicts the daily densities of each species life stage, but only the cumulative daily densities of some stages over the season (i.e. species days) are used as measures of abundance. The results using observed weather (Fig. 6) are contrasted with climate-warming scenarios that increase daily temperature +2° and +3°C (Fig. 7; see Gutierrez et al. 2007).

Using observed weather, the average distribution and abundance of the mealybug (Fig. 6a) and its natural enemies are patchy across the different grape growing regions of California (Fig. 6b–d). The coccinellid predator *C. montrouzieri* is predicted to be most abundant in the south where grape culture is sparse and along the near coastal areas of Central California (6b). The distribution of the parasitoid *A. pseudococci* is quite similar to that of the mealybug (Fig. 6a vs c), while the parasitoid *L. abnormis* is most abundant in the hotter desert regions of southern California (6d). The predicted distribution and abundance of the mealybug accords well with data from field studies at Parlier (·) in the mid Central Valley and at Mecca (Δ) in the south of California (Daane et al. 2003).

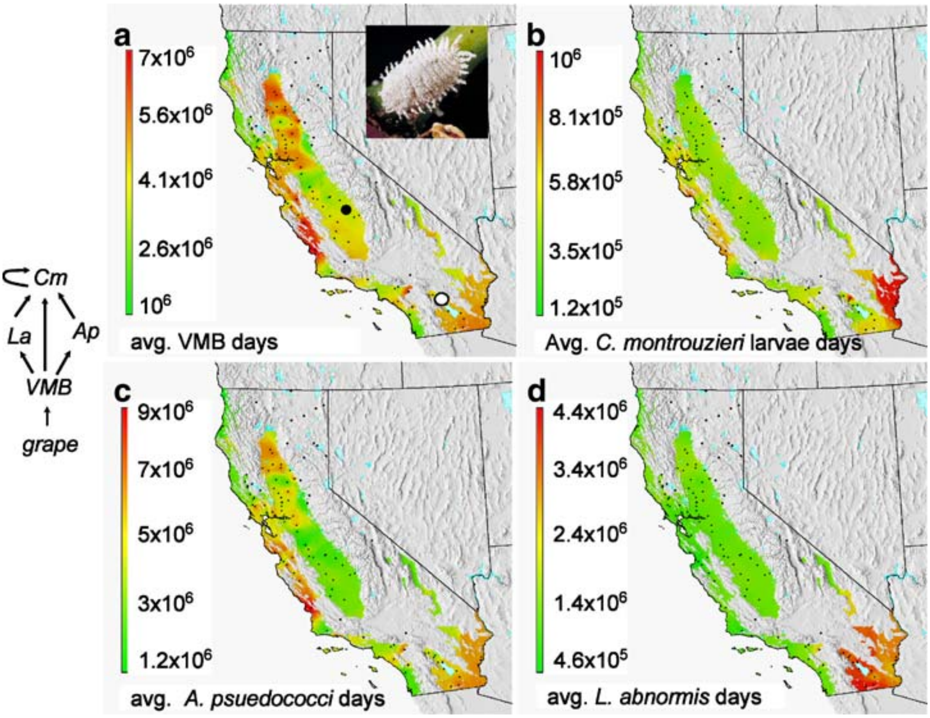

Fig. 6 Predicted areas of average favorableness below 750 m of elevation for **a** vine mealybug, **b** larvae and adults of the coccinellid predator *C. montrouzieri*, **c** immature stages of the parasitoids *A. pseudococci* and **d** *L. abnormis*). Parlier in the mid Central Valley is indicated by the symbol (*filled circle*) and Mecca in Southern California by (*empty circle*) in (**a**) (cf. Gutierrez et al. 2007). The density scale indicates the cumulative daily values for the season for each species (i.e. species days)

Climate warming will affect not only grape yield (and quality), but also the densities of mealybug and its natural enemies over their entire geographic range. We present only the results for the mealybug (Fig. 7). With increases of 2 and 3°C in average daily temperatures, the geographic distribution of the mealybug across California remains relatively unchanged, but the areas favorable for its development shift increasingly northward with population levels generally increasing everywhere due to increasing failure of biological control (Fig. 7a vs b,c).

> *The major conclusion is that increasing climate warming will affects not only the distribution and abundance of the mealybug, but those of its natural enemies as well (see Gutierrez et al. 2007). Similar effects will occur in other biological systems (olive; Gutierrez and Pizzamiglio 2007). Including the interactions between species as altered by their differing responses to weather (and climate change) addresses the criticisms of the 'climate envelope' approach (Davis et al. 1998).*

3.4 Crop phenology and distribution—Olive/Olive fly

Olive (*Olea europaea* L) is a drought tolerant long-lived plant whose northward distribution is limited by low winter temperature and by extreme high temperatures in more southern areas. Denney et al. (1985) proposed a damage index model for assessing the effects of low

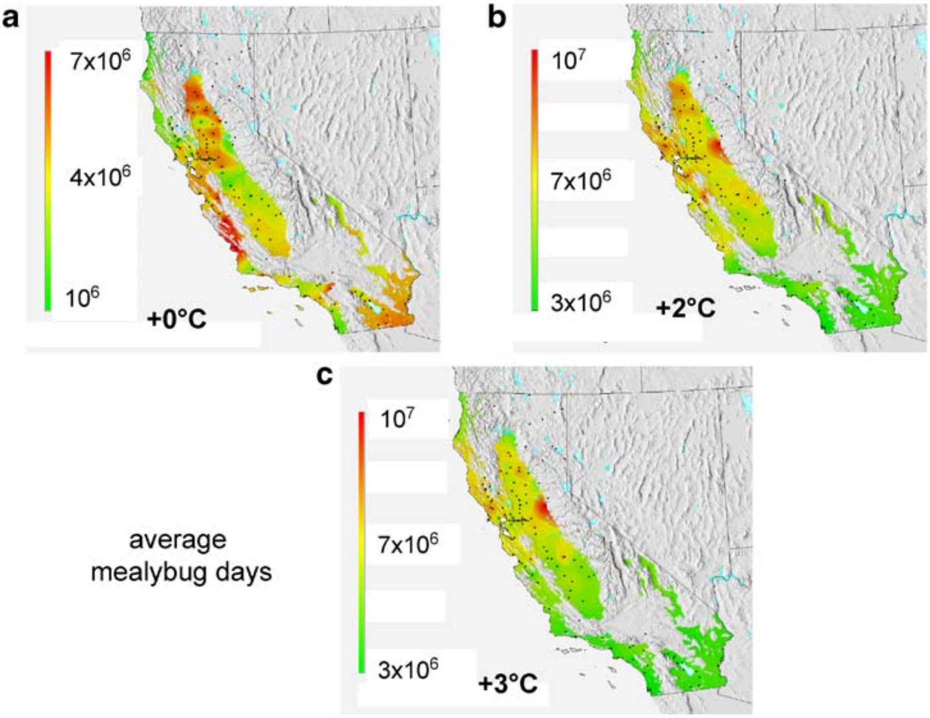

Fig. 7 Predicted areas of average favorableness for vine mealybug (VMB days) in the presence of natural enemies below 750 m elevation using: **a** observed weather, and with **b** +2°C and **c** +3°C increases in average daily temperature (cf. Gutierrez et al. 2007)

and high temperatures on olive (see also Dalla Marta et al. 2004), and their data were important components in the development of the PBD model for predicting the potential phenology and geographic distribution of olive (Gutierrez et al. submitted).

Like most temperate climate fruit trees (e.g. pome and stone fruits), olive requires some winter chilling (i.e. 450 h of chilling below 7.3°C for dormancy release (vernalization)) to stimulate fruit bud development. A further 500 degree-days (*dd*) above the threshold are required until the onset of flowering (see Hartmann and Opitz 1980). Among the approaches used to forecast chilling requirements for dormancy release and flowering in olive are neural networks (Mancuso et al. 2002) and thermal summing (De Melo-Abreu et al. 2004). In areas with insufficient chilling, olive may exhibit vegetative growth but produce only a sparse crop. Low or high temperatures during flowering may reduce fruit set. The pattern and timing of olive fruit development have important bottom up effects on the olive fly (*Bactrocera oleae*) that is a common pest in the Mediterranean region and was first recorded in California in 1998 (Fig. 3d).

Using observed weather for 1996–2006, average bloom dates ranged from Julian day 80 to 163 at elevations below 750 m across the ecological zones of California (Fig. 8a). Lack of vernalization may cause bloom failure, but this was not observed in our study. Heavy frost did limit olive in the far north of California. Yields ranged from 1.6 to 10.6 kg tree^{-1} with highest yields predicted in the desert regions (Fig. 8d). Areas with mid range bloom dates accord well with the predicted distribution of olive in California (Fig. 8a,d).

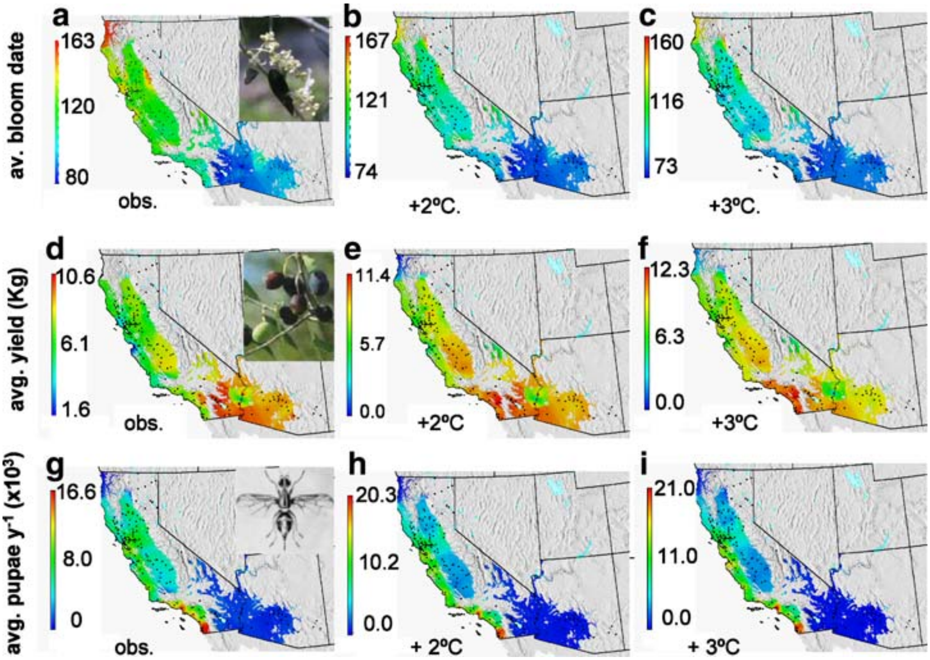

Fig. 8 Average simulated olive bloom dates and yield tree^{-1} without olive fly, and average total season long olive fly pupae using observed weather and with average 2.0 and 3°C increases in daily temperature: **a**–**c** average bloom date, **d**–**f** average yield tree^{-1} without olive fly and, **g**–**i** average cumulative season long olive fly pupae tree^{-1}. The period used in the analysis is 1996–2006 for areas below 750 m elevation. Average daily increases in temperature are indicated in each sub figure

The predicted range for olive fly, as measured by average total pupae tree^{-1}, is restricted to near coastal areas of southern California and regions of the Central Valley (Fig. 8g). The least favorable areas are the hot desert regions of southern California and Arizona where high summer temperatures reduce fly fecundity and survival (Gutierrez et al., submitted). The southern reaches of the great central valley are marginal for olive fly because of high temperature, while more northern areas are unfavorable because of low winter temperatures. In areas favorable for the fly, yields with unchecked infestations are expected to be reduced 85–90%.

Increasing daily temperature 2°C causes earlier more uniform bloom dates across much of California. The range of average bloom dates declines roughly 6–13 days (Fig. 8b). In the absence of olive fly, olive yields increase in many areas (range 1.6–11.4 kg tree^{-1}) but not in the desert regions of southern CA and Arizona where decreases occur (Fig. 8d vs e). Areas along the coast increase in favorability for both olive and olive fly, but the Central Valley of California decreased in favorability for the fly (Fig. 8g vs h).

Increasing daily temperatures 3°C cause average bloom dates to occur before day 100 in most areas (Fig. 8c; range 73–160). In the absence of olive fly, olive yields are again predicted to be highest near coastal areas of middle and southern California and Sierra Nevada foothills, while yield decreases are expected in the Central Valley and Southern California, and in the desert regions of Arizona (Fig. 8d vs. f) (range 0–12.3 kg tree^{-1}). The distribution and abundance of olive fly is expected to decrease further in the Central Valley

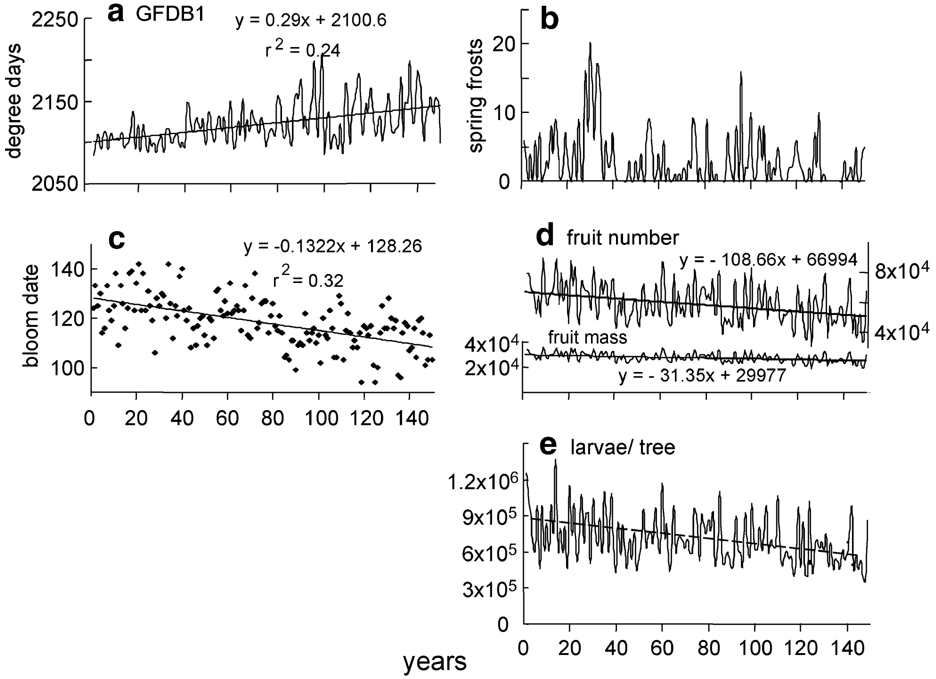

Fig. 9 Simulations for olive using 150 years of GFDL projected weather for Davis, CA: **a** season length in degree days, **b** number of spring frost days, **c** day of olive bloom, **d** olive fruit number and mass tree^{-1} in the absence of olive fly infestations, and **e** cumulative daily counts of olive fly larvae tree^{-1} year^{-1}

of California, but its importance is expected to increase in coastal areas (Fig. 8g, h vs i; range 0–21 × 10^{3}).

In summary, olive is not limited by increasing temperature but yield decreases can occur due to high temperatures. Warm winter temperatures may result in lack of chilling and bloom failure, but this was not found in any of our simulations. Low temperatures, however, will remain problematic in more northern locations. Time to flowering decreased with increasing temperature, and the geographic distribution of yield also changed. High temperatures are predicted to reduce olive fly infestations in hotter areas, but the pest will remain economic in coastal and middle California.

3.4.1 GFDL climate models scenario for Davis, California

Some of the predictions above on the effects of temperature on olive and olive fly are examined for Davis, CA using the 150 years of weather projected by the GFDL climate model (Fig. 9).

Degree-day accumulation (*dd*) increased 0.29 *dd* y^{-1} but with increasing variability from an initial average value of 2,100 *dd* (Fig. 9a). The frequency of spring frosts deceased (Fig. 9b), while average date of bloom declined at a rate of 0.13 days year^{-1} from an initial average value of 128.26 days (Fig. 9c). In the absence of olive fly, predicted yield decline 31.5 g plant^{-1} y–^{1} from an initial average of 29,977 g tree^{-1} (Fig. 9d). Yield decrease is due to increased plant respiration with climate warming. Fruit numbers decreased 108.7 year^{-1} (We note that the predicted values indicate only the direction of change.).

Olive fly infestations as measured by the season long sum of all daily counts of larvae decreased due to declining fruit numbers and increasingly unfavorable high temperatures near the fly's upper thermal threshold that decrease fecundity and increase mortality (Fig. 9e). Simulated yields with olive fly (not shown) were low during the first 120 years of simulation (i.e. <10–15% of potential), but increased, albeit slowing, due to adverse high temperature effects on olive fly.

> *Using climate model weather, olive bloom dates, yield and olive fly infestations at Davis, CA are predicted to decline annually with increasing temperatures due to global warming.*

3.5 Weather effects on the biological control of a noxious weed

Many exotic plants have become important weeds in aquatic and terrestrial systems worldwide. One of these is the noxious yellow starthistle (*Centaurea solstitialis*, YST) that invaded rangelands in the western United States reducing forage quantity and quality, causing injury to livestock, and becoming a severe nuisance in recreational areas. Several natural enemies that attack the seed head (capitula) of YST have been introduced for its control: two weevils (*Bangasternus orientalis* and *Eustenopus villosus*

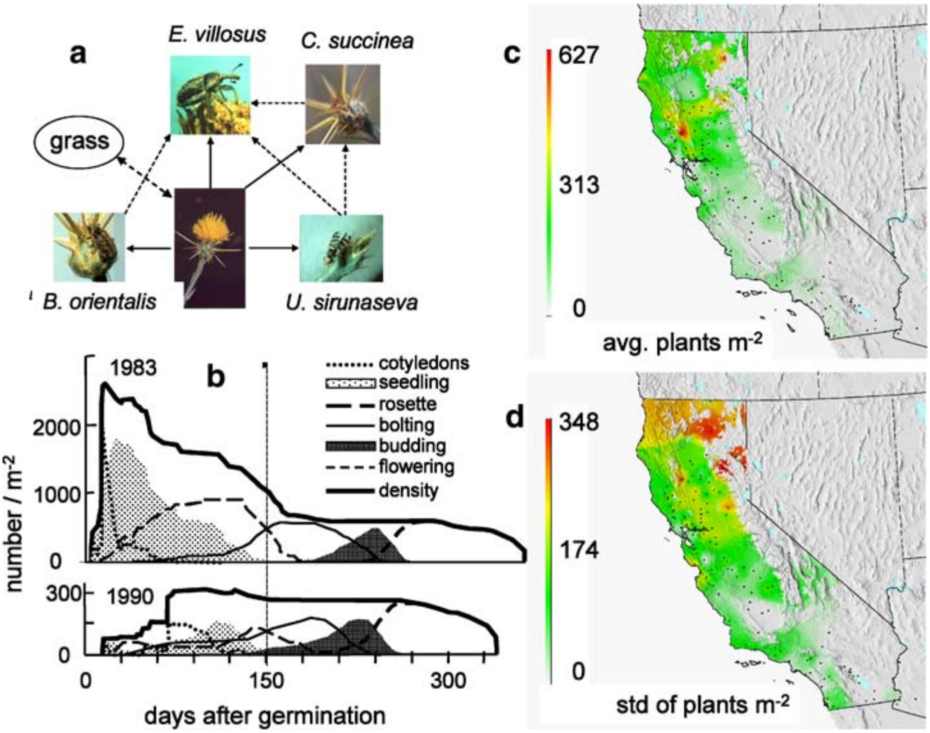

Fig. 10 Simulated average distribution and abundance of yellow starthistle seedlings below 1,500 m of elevation in California (see Gutierrez et al. 2005): **a** the interaction of four introduced natural enemies, **b** simulated plant phenology at Davis, CA during 1983 and 1990, **c** the predicted geographic distribution and abundance of YST seedling with natural enemies and **d** the SD

(Coleoptera: Curculionidae)) and two picture-winged flies (*Urophora sirunaseva* and *Chaetorellia succinea* (Diptera: Tephritidae)) (Fig. 10a). Solid arrows indicate the direction of energy flow, while dashed arrows indicate the victor in cases of multiple species attack in capitula. Competition for light and water from fast growing Mediterranean annual grasses is important during early spring and is included in the model (see Gutierrez et al. 2005).

Starthistle dynamics were simulated over the period 1995–2005 to see the evolution of the system under California conditions and with climate change. An initial soil seed bank density of 1,500 seed m^{-2} was assumed at all locations, but thereafter simulated local seed production and between season survival of seed provided the inoculums for the next season (see Gutierrez et al. 2005). Seed produced during the season may remain dormant for several years including years with abundant rainfall. The density and time of germination of starthistle seed is largely determined by the density of the seed in the soil, timing of rainfall and its intensity, and temperature above the plant's thermal threshold. These factors cause germination of YST to vary considerably across California and elsewhere. Predicted germination due to rainfall and the subsequent survival of plants due to competition during the different stages of growth are illustrated for the contrasting 1983 and 1990 seasons at Davis, CA (Fig. 10b). Note that seedling density may vary ten fold or more and that densities declines due to intra- and inter-specific competition for light and water, and disease. The effects of soil nutrients were not included in the model because geographic distribution of the initial conditions was not known.

Figure 10c shows the simulated average density of flowering plants at peak density and Fig. 10d shows the standard deviation (STD) of the ten years of simulation (1996–2006). The distribution of yellow starthistle accords well with the aggregate field survey data reported by the California Department of Food and Agriculture.

The model predicts the southern distribution of starthistle in California is limited by a lack of germinating rainfall and by low soil moisture during spring and early summer in some areas were seed germination occurred. In areas favorable for YST, herbivore feeding by all species and competition from grasses are insufficient to control the weed because of high seed production and survival, and plant compensation (Gutierrez et al. 2005). The geographic distribution of average seedling density with and without natural enemies is roughly the same suggesting low natural enemy efficacy.

3.5.1 Multivariate analysis

The regional impact of natural enemies on starthistle was assessed using multiple regression analysis of the simulation data for all combinations of natural enemies. Presence–absence dummy variables (0 or 1) for natural enemies were used as independent variables (Eq. 2, see Gutierrez et al. 2005).

$$\begin{gathered}\text{capitula}\,\text{m}^{-2} = 171.8 + 0.052\text{dd} + 0.16\text{mm} - 105.3E + 22.3C - 29.8E \times C \\ R^2 = 0.28,\ F = 248.6,\ df = 3,234\end{gathered} \tag{2}$$

Marginal analysis suggests that the number of flower heads (capitula) m^{-2} increases with season length (*dd* = degree days>8°C), cumulative rainfall during the season (*mm*), and with the presence of the fly C=*C. succinea*. In contrast, capitula density decreased due to the presence of the weevil *E*=*E. villosus* that attacks whole capitula and kills competing species in the same host. The interaction *ExC* plays a net minor role in suppressing YST because the positive effects of C alone. Substituting average values for *dd* (=2,656) and *mm*

(=466) in Eq. 2, the average capitula density across all regions was predicted to remain high (271 m^{-2}).The regression model for $\log_{10}$ seed bank density across all sites on season length (*dd*), total rainfall (*mm*), and the presence of *E. villosus* and *C. succinea* is given by Eq. 3. The weevil *B. orientalis* and the fly *U. sirunaseva* occurred in very low numbers region-wide and had no significant effect in reducing seed pool densities.

$$\begin{aligned}\log_{10}(\text{seed density}\,\text{m}^{-2}) &= 3.30 + 0.00007\text{dd} + 0.0002\text{mm} - 0.18E - 0.36C + 0.16E \times C \\ R^2 = 0.18,\ F &= 141.4,\ df = 3234\end{aligned} \tag{3}$$

Taking the antilog of Eq. 3 and substituting the mean value for *dd* and mm across sites shows that yellow starthistle seed densities increased with season length (dd) and total rainfall (mm), but decreased in order of importance with *C* and *E* presence.

$$\begin{aligned}\textit{seed density}\, m^{-2} &= 10^{3..3}10^{0.00007dd}10^{0.0002mm_{rain}}10^{-0.18E}10^{-0.36C}10^{0.16E\times C} \\ &= 1,581\, m^{-2}\end{aligned} \tag{4}$$

On average, the combined action of *E. villosus* and *C. succinea* reduced seed density 58% across the entire region with *C. succinea* having the greatest impact. The impact of *C. succinea* is reduced by its interaction with *E. villosus* that kills the fly's larvae when they co-occur in capitula. Note that the *ExC* interaction increases seed survival 12.8% offsetting much of *E. villosus's* contribution.

In summary, the predicted distribution and abundance of yellow starthistle accords well with field survey data. However, enough seed survives natural enemy attack to maintain high mature plant populations (i.e. 166 m^{-2}, computations not shown). The biology in the model was sufficiently complete to allow analysis of the role of the different enemies and their interactions on the checkered biological control of this highly invasive weed.

3.5.2 YST distribution and abundance using 150 year climate model projections

The predicted dynamics of YST was simulated at seven locations along a north–south axis in California (symbol o, Fig. 2) using the 150-year projections of the medium sensitivity scenarios of the GFDL and PCM climate models. The number of mature capitula m^{-2} was used as the dependent variable (i.e. a metric of density) while dd, mm and the total seasonal larvae m^{-2} of natural enemy larvae were used as independent variables (i.e. *E*=*E. villosus*, *B*=*B. orientalis*, *U*=*U. sirunaseva*, *C*=*C. succinea*) in the linear multiple regression analysis (Eqs. 5 and 6 respectively).

Using the PCM scenario, capitula (seed heads) densities (Eq. 5) increase an average 0.105 m^{-2} $year^{-1}$ but decrease 0.0083 dd^{-1}. Only the weevil *E. villosus* reduced seed head densities while the net effect of the two flies (*U. sirunaseva* and *C. succinea*) caused a net increase. The presence of *B. orientalis* was not significant. Total rainfall during the season was not significant because its effect was largely captured by season length (dd) that depends on soil moisture.

$$\begin{aligned}\text{capitula}_{\text{PCM}} &= -178.86 + 0.105\text{year} - 0.0083\text{dd} - 0.197E + 0.033U + 0.033C \\ &\quad -0.000025E \times U - 0.000019E \times C - 0.0000037U \times C \\ R^2 = 0.76,&\quad df = 1048,\quad F = 422.83\end{aligned} \tag{5}$$

Similarly, using the GFDL scenario, capitula densities (Eq. 6) increased an average of 0.124 m^{-2} $year^{-1}$, but decreased 0.0089 m^{-2} dd^{-1}. Of the natural enemies, only the snout beetle *E. villosus (E)* appreciably reduced capitula densities, while the net effect of the two flies (*U. sirunaseva* and *C. succinea*) increased capitula density. Neither total rainfall nor *B. orientalis* were significant.

$$\begin{aligned} \text{capitula}_{\text{GFDL}} = & -211.35 + 0.124\text{year} - 0.0089\text{dd} - 0.0924E \\ & + 0.027U + 0.041C + 0.000005E \times U - 0.000072E \times C + 0.000006U \times C \\ R^2 = 0.65, & \quad df = 1048, \quad F = 244.65 \end{aligned} \tag{6}$$

Projected temperatures were lower and rainfall higher in the PCM climate model scenario than in the GFDL scenario, and these effects are reflected in GFDL regression as a lower x-intercept, a reduction in the efficacy of *E. villosus* (E) and compared to the PCM scenario, changes in sign of some of the interaction terms that suggest they increase capitula density. In a separate regression, capitula density increased with increasing latitude (19 capitula m^{-2} degree^{-1}; results not shown) reflecting a weather gradient of increased rainfall and favorable temperatures.

> *In summary, capitula abundance increases northward but decreases in the hotter southern parts of YST's range where it was increasingly limited by low rainfall and high temperatures.*

4 Discussion

It is well known that weather in the short run is an important determinant of species abundance, and that climate in the long run determines the potential geographic distribution of species and their assemblages in food webs. Increases in global temperature due to elevated levels of green house gases and changes in rainfall are expected to have a profound effect on the distribution and abundance of species in all trophic levels. Temperatures in the range of +1.7–3°C and +2.2–4°C and decreased rainfall are predicted for California by two climate change models (see weather section above).

Pioneering studies on the effects of weather on the distribution and abundance of species are those of von Liebig (1840); Andrewartha and Birch (1954); Messenger (1964, 1968) and Fitzpatrick and Nix (1968). The importance of temperature on the regulation of pests in agriculture by natural enemies has been illustrated by examples from the field of biological control. For example, the cottony cushion scale in citrus was controlled by the vedalia beetle (*Rodolia cardinalis*) over a wide area including the hotter areas of citrus production, while the parasitic fly (*Cryptochaetum iceryae*) was restricted to cooler frost-free areas of coastal California (Quezada and DeBach 1973). In another case, DeBach and Sundby (1963) showed that successive introductions of parasitoids to control California red scale on citrus resulted in a sequence of climatically better-adapted parasitoids that displaced each other until each established itself in the subset of California's environments most favorable for its development. Huffaker and Kennett (1966) proposed that temperature affected differently the action of two parasitoids in the control of olive scale, and this was confirmed by Rochat and Gutierrez (2001) who provided further explanation based on PBDM analysis.

Classic studies of the effects of moisture on pest outbreaks are of locust species in North Africa and the Middle East where their numbers decline to extremely low levels during periods of drought, but may explode to biblical proportions during prolonged region-wide favorable periods (e.g. Roffey and Popov 1968). Control of Klamath weed (*Hypericum* *perforatum*) occurred using an introduced beetle (*Chrysolina quadrigemina*; see Huffaker 1971) that caused root damage and water stress during the dry summer period. This additional stress killed whole plants and/or reducing seed production in survivors resulting in exceedingly low plant densities.

Nutrients also play an important role in pest dynamics and outbreaks (see White 1984). Janssen (1993) demonstrated the important role of soil nutrient buildup during periods of drought and hence on plant nutrition and African armyworm outbreaks when the rains returned. Studies such as this demonstrate the need to incorporate the bottom up effects of the plant and of edaphic factors in analyses of weather effects on pests and their natural enemies. However, while soil nitrogen dynamics are included in our models structure, the data required to initialize the model regionally were not available, and hence were not part of our analyses.

4.1 Modeling plant/herbivore/natural enemy interactions

Quantitative evaluation of complex biological problems requires a modeling approach. The simplest approaches have been variants of the climate '*envelope approach*' used to determine the climatic conditions favorable for the distribution of species (Davis et al. 1998). A variant is the physiological index approach of Fitzpatrick and Nix (1968) that characterizes the growth response of a species to abiotic factors. This approach has been widely applied to field problems (e.g., Gutierrez et al. 1974; Gutierrez and Yaninek 1983; Hughes and Maywald 1990; Sutherst et al. 1991; Venette et al. 2000). Climate envelope approaches in general do not capture the dynamics of interacting species (Davis et al. 1998), and often, average weather is used in the analysis. Spatial variations in population responses to the environment and the rapid adaptations of phenotypes through developmental plasticity, acclimation, and hardening are typically ignored (Rogers and Randolph 2000). This kind of plasticity was demonstrated in tsetse species where reduction in the range of the flies occurs because of limited plasticity to upper critical temperatures (Rogers & Randolph 2000; Terblanche et al. 2006). Similar lack of upper (and lower) critical temperature plasticity likely occurs in many poikilotherm species.

In addition to temperature and rainfall, the composition of atmospheric gases (CO_2) may increase the severity of invasive weeds (Ziska 2003), their tolerance to herbicides (Ziska et al. 1999) and susceptibility of crops to pests (e.g. Hamilton et al. 2005). The effects of elevated levels of CO_2 were not included in our analyses.

Physiologically based demographic models (PBDM) capture the weather driven biology of species in tri-trophic systems (i.e. plant, pests and natural enemies) and circumvent many of the problems inherent in the climate envelope approach (Gutierrez and Baumgärtner 1984; Gutierrez 1996; Schreiber and Gutierrez 1998). These models make predictions that are independent of time and place, and as used here, can be used to assess what would happen to the distribution and abundance of species regionally under different climate change scenarios. This approach was used to examine selected aspects of climate change on some species associated with alfalfa, cotton, grape, olive and the invasive weed yellow starthistle (Fig. 2).

The model of the alfalfa system was used to examine how aphid species dominance would change if say, rainfall were to increase or decrease in California. The analysis illustrated how unexpected changes in aphid food webs could occur with changes in rainfall. Changes in food web composition could occur in many systems due to changes rainfall and temperature, and some of these could have potentially catastrophic results.

In irrigated cotton, the effect of climate warming on the geographic range and abundance of the frost intolerant pink bollworm in southern California and Arizona was examined. The model predicted that increases of 1.5 to 2.5°C in average temperatures would allow the pest to extend its range northward into the currently inhospitable cotton growing regions of the San Joaquin Valley of California. The pest is also predicted to become more severe in its extant range. The geographic range of other pests such as the Mediterranean fruit fly (*Ceratitis capitata*) and other pests could also change. Currently, its distribution is restricted to more southern frost-free areas of Southern California (Messenger and Flitters 1954) where incipient populations occur (Carey 1996). Occasional infestations and winter dieback occur in more northern areas. Climate warming, however, could allow medfly's range to expand putting at risk the fruit growing regions of Central California and other areas. Other pest species could be similarly affected as shown by Williams and Liebhold (2002) who predicted a northward shift of bark beetles in eastern forests of the United States. The geographic distribution of the cotton boll weevil is limited by desiccation of fruit buds in hot dry areas (De Michele et al. 1976), but an expansion of the range and abundance of boll weevil occurred during the early 1980s when a sequence of very wet years in Arizona and Southern California coupled with the cultivation of stub-cotton temporarily increased the favorableness of the region. Weevil infestations subsided when normal drier weather returned, but climate change could alter its distributions. How many other pest species will be similarly affected by climate change is unknowable, and some of the economically important ones require analysis.

A model of the grape/ vine mealybug was used to examine how weather and climate change affects biological control of this pest by two parasitoids and a ladybeetle predator across the ecological zones of California. First, the model predicted the areas favorable for each species and explained how spatial refuges under the bark and in the root zone reduced natural enemy efficacy. Then climate warming scenarios were examined and suggest that control of the vine mealybug would worsen throughout California with potential increase in its severity northward (Gutierrez et al. 2007). Similar analyses need to be made for other important newly arrived pest of grape (e.g., glassy-winged sharpshooter) and other crops.

A model of olive growth and development was used to evaluate the effects of historical weather and of projected climate change on chilling (vernalization), blooming and yield in olive. The results suggest that increasing temperatures could possibly inhibit flowering and reduce yield in olive in the southern reaches of California, while cold weather would limit its distribution in some northern areas. With global warming, olive production is predicted to consolidate in the central areas of California and along the coast. Yields would decline generally with increasing temperature in hotter areas. Climate change would affect not only olive culture, but also the distribution and abundance of pests such as the olive fly, and olive and oleander scales and the efficacy of their biological control (Rochat and Gutierrez 2001; Gutierrez and Pizzamiglio 2007 respectively).

Numerous terrestrial and aquatic weeds infest the United States, among which is the highly invasive yellow starthistle. This weed has degraded range lands throughout California and the western United States. Biological control of starthistle by seed heads attacking natural enemies has been checkered because the damage caused is insufficient to prevent compensation at lower plant densities where each plant grows larger and produces more seed. In addition, the herbivore species attacking starthistle have their own climatic requirements that limit their geographic range and effectiveness. Climate change would greatly alter their impact as ineffective as they might be. Climate warming is projected to increase the severity of starthistle in more northern regions of the California and elsewhere.

Currently, control of starthistle is reported in Oregon where the shorter growing season is thought to reduce the plant's capacity to compensate for herbivore damage (Gutierrez et al. 2005), but our analysis suggests that this could change with global warming and changes in rainfall patterns and intensity. Our analysis suggests that herbivores that attack whole starthistle plants and/or reduce the plant's capacity to compensate would be better candidates for introduction (Gutierrez et al. 2005). The control of Klamath weed by an introduced beetle that reduced root growth provides a good template for the control of starthistle and other terrestrial weeds in California and elsewhere.

4.2 Epilogue

Assessing the impact of climate change on natural systems is difficult, but we propose that the use of PBDMs simplifies the problem. These models build upon plant physiological models first developed in the Netherlands (see de Wit and Goudriaan 1978). The current limitations of this modeling approach include: a lack of funding and infrastructure for collecting the requisite biological data to develop, refine and test such models, and unexpectedly, the lack of appropriate weather data for implementing them on a large geographic scale. The cost to correct these deficiencies is relatively small, while the potential benefits are large. As an aside, the development of system models for the major crops in California was a major goal, now abandoned, of the UC/IPM Statewide Program when it was first started in 1978.

Last, successful biological control programs against insect pests and weeds have yielded billions of dollars in benefit to California, and globally since 1887 when modern biological control began, but tremendous losses continue to accrue as new exotic insect pests and weeds are introduced (Pimentel et al. 2000). Because of the cost effectiveness of biological control in general, additional support for it and for forecasting and analysis methods (Clark et al. 2001) is warranted.

Acknowledgments We acknowledge support from the California Energy Commission and Environmental Protection Agency and the California Agricultural Extension Service. We thank Mary Tyree and Dan Cayan for supplying the climate model scenarios and with Michael Hanemann and Guido Franco for their leadership in this project.

Appendix: Basic Mathematical Model

Resource acquisition and allocation

The mass (i.e. energy) flow consumer-resource population dynamics model (Eq. 7, Fig. 11) describes the dynamics at all trophic levels with the inflows and outflows having similar

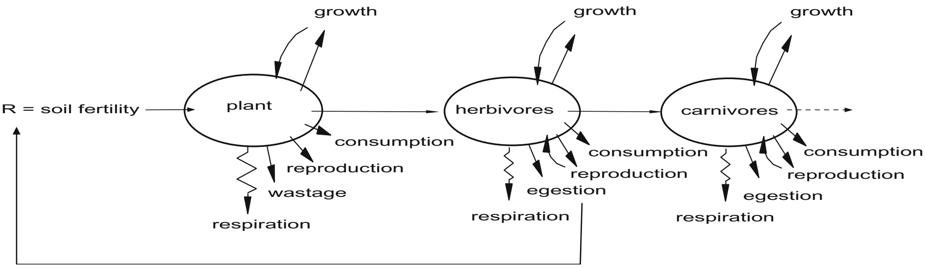

Fig. 11 Energy flow in a tritrophic system

shapes and characterized by the same functions. Note that multiplication by a constant converts the mass flow to numbers of individuals at any level or, say monetary units in human economies.

Physiologically based demographic models have been used to analyze biological systems in various regions of the world because the forcing variables are weather and the dynamics of soil nutrients and water (see Gutierrez and Baumgärtner 1984, 2007). These and other properties make their predictions independent of time and place. The basic model is reviewed below.

Let $M_i(i = 1,\ 2, \ldots,\ n)$ denote the mass of the ith trophic level in the food chain. The dynamics of any trophic level is governed by the following equation of motion:

$$\frac{d\,M_i(t)}{d\,t} \equiv \overset{\bullet}{M}_i = \theta_i M_i D_i h(u_i) - v_i\,(\dot{D}_i)\,M_i - M_{i+1}D_{i+1}h(u_{i+1}) \tag{7}$$

The components of the dynamics model are:

$h(u_i) = \left(1 - \exp\left(\frac{-\alpha_i M_{i-1}}{D_i M_i}\right)\right)$ is the resource acquisition model for resource trophic level i from level i-1 is the proportions of the demand D^i satisfied (i.e. the supply-demand ratio),

D^i is the maximum per unit demand of the ith trophic level for resources trophic level $i-1$ and may be viewed as the sum of maximum outflow for each species and includes consumption (C),

α_i is the proportion of level $i-1$ accessible to the ith level, and $1-\alpha$ is a refuge for the resource,

θ_i is the conversion rate of resource and includes the wastage rate,

$v_i(D_i)=vD$ is the cost rate per unit of consumer mass as a function of the demand rate (Q_{10} in physiologically based models).

The function $h(u)$ is a ratio-dependent concave predation functional response model that includes interspecific (and intraspecific) competition in the exponent and the possibility of several resource species with different α that may include consumer preference. The term $D_i\mathrm{M}_\mathrm{i}$ is the maximum per capita consumer population demand, and $D_i M_i h_i(u) \leq \alpha_i M_{i-1}$ is the actual rate of resource depletion by the ith level where $\alpha_\mathrm{i} \leq 1$ sets the limits on the extraction by consumers in level i from resource level $i-1$. If α_i is sufficiently small compared to the assimilation efficiency of the lower level $(\alpha_i \leq \theta_{i-1}D_{i-1} - v_{i-1}(D_{i-1}))$, then the lower tropic level will survive any population size and demand rate of its consumer, and can be viewed as a refuge of level $i-1$ from predation (see Gutierrez et al. 1994 for an analysis of model properties).

Distributed maturation time model

We use the distributed maturation time model of Vansickle (1977) to model the demography of all species, including the plant. Here only a brief introduction is given (see Gutierrez 1996; Gutierrez et al. 2005 for complete details). The use of a physiologically based model enables the incorporation of the rich biology that allows simulation of field data. The mathematical notation of Di Cola et al. (1999, p 523–524) is used here to develop a brief description of the systems. The demographic model is characterized by the following assumption.

$$v_i(t) = \frac{k}{\mathrm{del}(t)}\Delta a \qquad i = 0, 1, \ldots, k \tag{8}$$

The parameter k is the number of age intervals, del(t) is the expected mean emergence time from the delay model, and Δa is the change in age. From Eq. 8 we obtain

$$\frac{dN_i}{dt} = \frac{k}{\mathrm{del}(t)}\left[N_{i-1}(t) - N_i(t)\right] - \mu_i(t)N_i(t). \tag{9}$$

N_i is the density in the ith age cohort and $-\infty < \mu_i(t) < +\infty$ is the net age-specific proportional mortality (gains–losses). It is in $\mu_i(t)$ that the rich biology responsible for population fluctuations is incorporated. Aging occurs via flow rates $r_{i-1}(t)$ from N_{i-1} to N_i, births enter the first age class of the population, and deaths at maximum age exit the last or kth age class. From the mean developmental time del and its variance V, the number of age classes $k = \nu^2/V$ required to reproduce the observed distribution of developmental times of cohorts may be computed. If k is small, the variance of developmental times is large and *vice-versa*. The age width of an age class is del$(t)/k$, hence the number of individuals (or mass units) in age class i is $N_i(t) = r_i(t)\mathrm{del}(t)/k$, and that in the population is $N(t) = \sum_{i=1}^{k} N_i(t) = \frac{\nu(t)}{k}\sum_{i=1}^{k} r_i(t)$. Time and age in the model are in time-temperature units above specific thresholds (i.e. degree days or proportional development).

Seasonality is an important factor in the dynamics of plant and animal species. For example, the ability to enter and/or break dormancy during periods of extreme temperature and/or moisture stress and/or due to photoperiod stimuli may determine whether a species survives in an area (see Nechols et al. 1999). Plant diseases may require additional factors (e.g. periods of leaf wetness).

References

Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. The University of Chicago Press, Chicago

Bartlett BR (1974) Introduction into California USA of cold tolerant biotypes of the mealybug predator *Cryptolaemus montrouzieri* and laboratory procedures for testing natural enemies for cold hardiness. Environ Entomol 3:553–556

Carey JR (1996) The incipient Mediterranean fruit fly population in California: implications for invasion biology. Ecology 77:1690–1697

Clark JS, Carpenter SR, Barber M, Collins S, Dobson A, Foley JA, Lodge DM, Pascual M, Pielke R Jr, Pizer W, Pringle C, Reid WV, Rose KA, Sala O, Schlesinger WH, Wall DH, Wear D (2001) Ecological forecasts: an emerging imperative. Science 293:657–660

Coakley S, Scherm H, Chakraborty S (1999) Climate change and plant disease management. Annu Rev Phytopathol 37:399–426

Daane KM, Malakar-Kuenen R, Guillén M, Bentley WJ, Bianchi M, Gonzalez D (2003) Abiotic and biotic refuges hamper biological control of mealybug pests in California vineyards. In: van Driesch R (ed) Proceedings of the 1st International Symposium on Biological Control of Arthropods. USDA Forest Service, Morgantown, West Virginia, pp 389–398

Dalla Marta A, Orlandini S, Sacchetti P, Belcari A (2004) *Olea europaea*: integration of GIS and simulation modelling to define a map of “dacic attack risk” in Tuscany. Adv Hort Sci 18:168–172

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–786

DeBach P (1964) Biological control of insect pests and weeds. Chapman and Hall, London

DeBach P, Sundby RA (1963) Competitive displacement between ecological homologues. Hilgardia 34:105–166

De Melo-Abreu JP, Barranco D, Cordeiro AM, Tous J, Rogado BM, Villalobos FJ (2004) Modelling olive flowering date using chilling for dormancy release and thermal time. Agric For Meteorol 125:117–127

De Michele DW, Curry GL, Sharpe PJH, Barfield CS (1976) Cotton bud drying: a theoretical model. Environ Entomol 5:1011–1016

Denney JO, McEachern GR, Griffiths JF (1985) Modeling the thermal adaptability of the olive (*Olea europaea* L.) in Texas. Agric For Meteorol 35:309

de Wit CT, Goudriaan J (1978) Simulation of ecological processes. PUDOC, The Netherlands

Di Cola G, Gilioli G, Baumgärtner J (1999) Mathematical models for age-structured population dynamics. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology. Wiley, New York

Fitzpatrick EA, Nix HA (1968) The climatic factor in Australian grasslands ecology. In: Moore RM (ed) Australian Grasslands. Australian National University Press

Gilbert N, Gutierrez AP, Frazer BD, Jones RE (1976) Ecological relationships. Freeman, New York

Gutierrez AP (1992) The physiological basis of ratio dependent theory. Ecology 73:1552–1563

Gutierrez AP (1996) Applied population ecology: a supply-demand approach. Wiley, New York, USA

Gutierrez AP (2000) Climate change: effects on pest dynamics. In: Reddy KR, Hodges HF (eds) Climate change and global crop productivity. CABI, Wallingford, UK

Gutierrez AP, Baumgärtner JU (1984) Multitrophic level models of predator-prey energetics: I. Age-specific energetics models - pea aphid *Acyrthosiphon pisum* (Homoptera: Aphididae) as an example. Can Entomol 116:924–932

Gutierrez AP, Baumgärtner JU (2007) Modeling the dynamics of tritrophic population interactions. In: Kogan M, Jepson P (eds) Perspectives in ecological theory and integrated pest management. Cambridge University Press

Gutierrez AP, Pizzamiglio MA (2007) A regional analysis of weather mediated competition between a parasitoid and a coccinellid predator of oleander scale. Neotrop Entomol 36:70–83

Gutierrez AP, Regev U (2005) The bioeconomics of tritrophic systems: applications to invasive species. Ecol Econ 52:383

Gutierrez AP, Wang YH (1977) Applied population ecology: models for crop production and pest management. In: Norton GA, Holling CS (eds) Pest management. Proc. Ser.. Pergamon, Oxford

Gutierrez AP, Yaninek JS (1983) Responses to weather of eight aphid species commonly found in pastures in southeastern Australia. Can Entomol 115:1359–1364

Gutierrez AP, Nix HA, Havenstein DE, Moore PA (1974) The ecology of *Aphis craccivora* Koch and Subterranean Clover Stunt Virus in south-east Australia. III. A regional perspective of the phenology and migration of the cowpea aphid. J Appl Ecol 11:21–35

Gutierrez AP, Falcon LA, Loew W, Leipzig PA, van-den Bosch R (1975) An analysis of cotton production in California: a model for acala cotton and the effects of defoliators on its yields. Environ Entomol 4:125–136

Gutierrez AP, Butler GD Jr, Wang Y, Westphal D (1977) The interaction of pink bollworm (Lepidoptera: Gelichiidae), cotton, and weather: a detailed model. Can Entomol 109:1457–1468

Gutierrez AP, Baumgärtner JU, Summers CG (1984) Multitrophic level models of predator–prey energetics: III. A case study of an alfalfa ecosystem. Can Entomol 116:950–963

Gutierrez AP, Wermelinger B, Schulthess F, Baumgärtner JU, Herren HR, Ellis CK, Yaninek JS (1988) Analysis of biological control of cassava pests in Africa. I. Simulation of carbon, nitrogen and water dynamics in cassava. J Appl Ecol 25:901–920

Gutierrez AP, Mills NJ, Schreiber SJ, Ellis CK (1994) A physiologically based tritrophic perspective on bottom up-top down regulation of populations. Ecology 75:2227–2242

Gutierrez AP, Pitcairn MJ, Ellis CK, Carruthers N, Ghezelbash R (2005) Evaluating biological control of yellow starthistle (*Centaurea solstitialis*) in California: A GIS based supply-demand demographic model. Biol Control 34:115

Gutierrez AP, d'Oultremont T, Ellis CK, Ponti L (2006) Climatic limits of pink bollworm in Arizona and California: effects of climate warming. Acta Oecol 30:353–364

Gutierrez AP, Daane KM, Ponti L, Walton VM, Ellis CK (2007) Prospective evaluation of the biological control of vine mealybug: refuge effects and climate. J Appl Ecol (in press): DOI 10.1111/j.1365-2664.2007.01356.x

Gutierrez AP, Ponti L, Cossu QA (submitted) Effects of climate warming on the distribution of olive and olive fly (*Bactrocera oleae*) (Gmelin): Arizona, California and Italy. J Appl Ecol

Hamilton JG, Dermody O, Aldea M, Zangerl AR, Rogers A, Berenbaum MR, Delucia EH (2005) Anthropogenic changes in tropospheric composition increase susceptibility of soybean to insect herbivory. Environ Entomol 34:479–455

Hartmann HT, Opitz KW (1980) Olive production in California. Leaflet 2474 University of California Div. Agric. Sci.. Davis, USA

Hayhoe K, Cayan D, Field C, Frumhoff P, Maurer E, Miller N, Moser S, Schneider S, Cahill K, Cleland E, Dale L, Drapek R, Hanemann RM, Kalkstein L, Lenihan J, Lunch C, Neilson R, Sheridan S, Verville J (2004) Emissions pathways, climate change, and impacts on California. Proc Natl Acad Sci USA 101:12422–12427

Huffaker CB (1971) Biological control. Plenum, New York

Huffaker CB, Kennett CE (1966) Studies of the olive scale, *Parlatoria oleae* (Colvee) IV Biological control of *Parlatoria oleae* (Colvee) through the compensatory action of two introduced parasites. Hilgardia 37:283–334

Hughes RD, Maywald GW (1990) Forecasting the favorableness of the Australian environment for the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), and its potential impact on Australian wheat yields. Bull Entomol Res 80:165–175

Janssen JAM (1993) African armyworm outbreaks: why do they occur after drought. PhD Thesis, Wageningen Agricultural University, The Netherlands

Mancuso S, Pasquali G, Fiorino P (2002) Phenology modelling and forecasting in olive (*Olea europaea* L.) using artificial neural networks. Adv Hort Sci 16:155–164

Maurer EP (2007) Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. Clim Change 82:309–325

Maurer EP, Duffy PB (2005) Uncertainty in projections of stream flow changes due to climate change in California. Geophys Res Let 32:L03704 DOI 03710.01029/02004GL021462

Messenger PS (1964) Use of life-tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system. Ecology 45:119–131

Messenger PS (1968) Bioclimatic studies of the aphid parasite *Praon exsoletum*. 1. effects of temperature on the functional response of females to varying host densities. Can Entomol 100:728–741

Messenger PS, Flitters NE (1954) Bioclimatic studies of three species of fruit flies in Hawaii. J Econ Entomol 47:756–765

Nechols JR, Tauber MJ, Tauber CA, Masaki S (1999) Adaptations to hazardous seasonal conditions: dormancy, migration, and polyphenism. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology. Wiley, New York

Neuenschwander P, Hammond WNO, Gutierrez AP, Cudjoe AR, Adjakloe R, Baumgartner JU, Regev U (1989) Impact assessment of the biological control of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), by the introduced parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae). Bull Entomol Res 79:579–594

Noyes JS, Hayat M (1994) Oriental mealybug parasitoids of the Anagyrini (Hymenoptera: Encyrtidae). CAB International, Natural History Museum, London. University Press, Cambridge

Petrusewicz K, MacFayden A (1970) Productivity of terrestial animals: principles and methods. Blackwell, Oxford

Pickering J, Gutierrez AP (1991) Differential impact of the pathogen *Pandora neoaphidis* (R.&H.) Humber (Zygomycetes: Entomophthorales) on the species composition of *Acyrthosiphon* aphids in alfalfa. Can Entomol 123:315–320

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65

Quezada JR, DeBach P (1973) Bioecological and population studies of the cottony scale, *Icerya purchasi* Mask., and its natural enemies, *Rodolia cardinalis* Mul. and *Cryptochaetum iceryae* Wil., in southern California. Hilgardia 41:631–688

Reddy KR, Hodges HF (eds) (2000) Climate change and global crop productivity. CABI International, Wallingford, UK

Regev U, Gutierrez AP, Schreiber SJ, Zilberman D (1998) Biological and economic foundations of renewable resource exploitation. Ecol Econ 26:227–242

Ritchie JT (1972) Models for predicting evapotranspiration from a crop with incomplete cover. Water Resour Res 8:1204–1213

Rochat J, Gutierrez AP (2001) Weather-mediated regulation of olive scale by two parasitoids. J Anim Ecol 70:476–490

Roffey J, Popov G (1968) Environmental and behavioural processes in Desert locust outbreaks. Nature 219:446–450

Rogers DJ, Randolph SE (2000) The global spread of malaria in a future, warmer world. Science 289:1763–1766

Schreiber SJ, Gutierrez AP (1998) A supply/demand perspective of species invasions and coexistence: applications to biological control. Ecol Model 106:27–45

Shelford VE (1931) Some concepts of bioecology. Ecology 12:455–467

Sutherst RW (2004) Global change and human vulnerability to vector-borne diseases. Clin Microbiol Rev 17:136–173

Sutherst RW, Maywald GF, Bottomly W (1991) From CLIMEX to PESKY, a generic expert system for risk assessment. EPPO Bulletin 21:595–608

Terblanche JS, Klok CJ, Krafsur ES, Chown SL (2006) Phenotypic plasticity and geographic variation in thermal tolerance and water loss of the tsetse *Glossina pallidipes* (Diptera: Glossinidae): implications for distribution modelling. Am J Trop Med Hyg 74:786–794

Vansickle J (1977) Attrition in distributed delay models. IEEE T Syst Man Cyb 7:635–638

Venette RC, Naranjo SE, Hutchison WD (2000) Implications of larval mortality at low temperatures and high soil moistures for establishment of pink bollworm (Lepidoptera: Gelechiidae) in Southeastern United States cotton. Environ Entomol 29:1018–1026

von Liebig J (1840) Chemistry and its applications to agriculture and physiology. Taylor and Walton, London

Walther GR (2002) Ecological responses to recent climate change. Nature 416:389–395

Watson RT (2002) The future of the intergovernmental panel on climate change. Climate Policy 2(4):269–271

Wermelinger B, Baumgärtner J, Gutierrez AP (1991) A demographic model of assimilation and allocation of carbon and nitrogen in grapevines. Ecol Model 53:1–26

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105

Williams DW, Liebhold AM (2002) Climate change and the outbreak ranges of two North American bark beetles. Agric Forest Entomol 4:87–99

Ziska LH (2003) Evaluation of growth response of six invasive species to past, present, and future atmospheric CO2. J Exp Bot 54:395–406

Ziska LH, Teasdale JR, Bunce JA (1999) Future atmospheric CO2 may increase tolerance to glyphosate. Weed Sci 47:608–615