Climate Change Effects on Plant-Pest-Natural Enemy Interactions

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Abstract

Four approaches used to estimate the potential distribution of native and invasive species in agricultural, natural and medical/veterinary vector/disease systems in the face of climate change are reviewed: (1) time-series observations to document biological responses to changes in climatic variables; (2) remote sensing analysis of data; (3) climate envelope approaches (statistically-based ecological niche models and physiologically-based ecological niche models); (4) physiologically based demographic models. The bases and relative merits of the approaches are discussed. The chapter emphasizes physiologically based demographic models that may be used at the individual, population and regional scales. Such models easily include multiple trophic levels as demonstrated for the olive/olive scale system. The olive/olive-fly system embedded in a geographic information system (GIS) is used to illustrate the utility of the physiologically based demographic approach for climate change research. Applications to other crop/pest/natural enemy systems are also discussed. The use of marginal analysis to summarize regional simulation data is introduced.

Introduction

Climate change is expected to increase temperatures globally and alter patterns of rainfall (IPPC 2004) and other derivative factors that can alter species distribution, abundance and impact in natural, agricultural and medical/veterinary vector/disease systems in unknown ways. The term climate encompasses the long-run pattern of numerous meteorological factors (e.g., temperatures, humidity, relative humidity, atmospheric pressure, winds, rainfall, and others) in a given location or larger region, while the term weather refers to short-term current measures of these factors. Weather affects the physiology (e.g. development, growth and reproduction, survival, diurnal and seasonal phenology), interactions with other species, and other aspects of the biology of poikilotherm species (i.e., species unable to regulate body temperature) in time and space (see e.g., Andrewartha and Birch, 1954; Larcher, 1995; Wellington et al., 1999; Walther, 2002) (fig. 1). Projected climate changes could modify extant relationships and interactions in food chains and webs (i.e., plant-herbivore-natural enemy interactions) with unknown consequences in natural, and agricultural systems, and in medical and veterinary
diseases vectored by insects, ticks and other poikilotherm organisms (Gutierrez and Baumgärtner, 1984, 2007; Patz et al., 2003, Baylis and Githeco, 2006). The effects climate change on any trophic level may cascade to lower and high levels in food chains and webs affecting system regulation (sensu Hairston et al., 1960) and stability.

If the climate change is severe enough, the geographic range and the distribution and abundance of species will be altered in unknown ways leading to potentially disruptive effects on trophic and possibly ecosystem structure and function (see Schreiber and Gutierrez, 1998). Climate change may prove catastrophic for some species and human populations unable to adjust to habitat change and unable to migrate to favorable areas. The increasing introduction of invasive species with globalization is a further important complication. Current losses due to invasive species in agricultural and natural systems are in excess of a $130 billion per year in the United States alone (Pimentel et al., 2000), and hence they have become a major focus of much of the climate change research on biological systems (e.g., alien weeds, insect pests (aphids, mealybugs, fruit flies, bollworms, defoliators, forest bark beetles), and diseases).

Figure 1. A partial list of factors affecting species distribution and abundance.
The question of how best to study biological effects of climate change on complex biological systems across spatial and temporal scales remains unresolved (sensu Holling, 1992). Among the approaches are: (1) time-series observations to document biological responses to changes in climatic variables; (2) remote sensing analysis of data; (3) climate envelope approaches (statistically-based ecological niche models (Beaumont et al., 2009) and physiologically-based ecological niche models (Fitzpatrick and Nix, 1968; Gutierrez et al., 1974; Sutherst et al., 1991); (4) physiologically based demographic modeling (Gutierrez et al., 2006a).

Field Observations

Field studies conducted over several years have followed the effects of weather on the phenology of plant and animal species at both the local and regional levels. Some examples include bloom dates of apple, grape and lilac (Wolfe et al., 2005), olive (Galan et al., 2005) and other plants (Gordo and Sanz, 2009). In insects, expansions of geographic range have been predicted in pine processionary moth (Battisti et al., 2005), spruce budworm (Williams and Liebhold 1997); southern green stink bug (Tougou et al., 2009) and many others. In a six-decade long study, Gordo and Sanz (2005) found increasingly earlier time of first appearance for the honey bee; cabbage white butterfly, potato beetle and olive fly (fig. 2). Gordo and Sanz were concerned climate change could disrupt the synchrony between host plants and insect herbivores that in trophic chains and webs evolved to cope with expected range of fluctuations in their thermal and other requirements. A major drawback of the field survey approach is the length of time required to conduct the study, the lack of generality and explanatory power of the results, and the inability to project the results to other areas.
Remote Sensing

The coverage and resolution of biophysical data derived from remote sensing (RS) satellite data substantially increase our potential to assess the effects of climate change on ecosystems on a regional and global scale. Missing variables, low resolution, inadequate duration, temporal and spatial gaps, and declining coverage in remote sensing data are pervasive (Clark et al., 2001; Pettorelli et al., 2005), but many of the limitations of RS are being overcome (Turner et al., 2003; Mendelsohn et al., 2007; Camps-Valls et al., 2009). Although, satellite RS data are subject to errors that substantially reduce their ecological applications when not integrated with reliable field data (Kerr and Ostrovsky, 2003); an integration using new interdisciplinary approaches is emerging termed satellite ecology (Muraoka and Koizumi, 2009).

Spectral vegetation indices are widely used to assess ecological responses to environmental change (Tucker et al., 2005) including the very popular Normalised Difference Vegetation Index (NDVI) that measures canopy greenness (Shippert et al., 1995). Information derivable from NDVI (such as plant phenology, biomass, and distribution) is of prime importance for terrestrial
ecologists (Pettorelli et al., 2005), and novel methods are becoming available for measuring seasonal vegetation patterns and dynamics at the landscape level (i.e., landscape phenology) (see Liang and Schwartz, 2009). RS data are being used to map and monitor invasive plant species (see Pengra et al., 2007; DeFries, 2008). NDVI approaches have also been used for linking vegetation to animal distribution and dynamics (Jepsen et al., 2009).

NDVI and other satellite-derived vegetation indices have been used for monitoring and early warning of insect herbivore damage in a climate-change context for outbreaks of insect defoliators in forests (Eklundh et al., 2009), mortality of lodge pole pine induced by bark beetle (Coops et al., 2009), and especially locust outbreaks. Examples of the latter include FAO’s pioneering studies on desert locusts in Africa (Hielkema et al., 1986; Cherlet et al., 1991; Cressman, 1996; Voss and Dreiser 1997), Australian plague locust (McCulloch and Hunter, 1983), East Asian migratory locust in China (Ji et al., 2004; Ma et al., 2005; Liu et al., 2008), and locust infestations in Uzbekistan (Sivanpillai and Latchininsky, 2007).

Prediction of vector-borne diseases is difficult due to the complexity of human factors involved, but satellite imaging can play a critical role by monitoring major environmental drivers (Ford et al., 2009). Rift Valley fever (RVF) is a mosquito-borne viral disease in Africa that has been detected by RS (Linthicum et al., 1987). Using a combination of satellite measurements including NDVI, Anyamba et al., (2009) made the first prospective prediction of an RVF outbreak for the Horn of Africa. Satellite data are being harnessed to monitor and predict malaria, a mosquito-borne disease that kills more than a million people annually (Rogers et al., 2002). Remotely-sensed land surface temperature was used in Italy for early detection and risk assessment of tick-borne encephalitis (Rizzoli et al., 2007), a zoonotic vector-borne disease whose incidence has increased in Central Europe during the last few decades (Carpi et al., 2007). Remote sensing has also been successfully applied to the study of other arthropod vectors of disease such as blackflies (vectors of onchocerciasis), tsetse flies (sleeping sickness), and sandflies (leishmaniasis) (Kalluri et al., 2007).
Ecological Niche Approach

This approach attempts to characterize and climatically model the ecological niche \((ENM)\) of a species using observed weather and knowledge of its current distribution. These models may be either statistical or physiologically based, or be both. Another term used for this is the \textit{climate envelope} approach.

**Statistical Ecological Niche Models** – \textit{ENMs} developed using statistical methods correlate the current distributions of species based on surveys, museum collections and other records with climate variables. The \textit{ENM} for a species (i.e., a pest) may then be used to map its potential geographic distribution, its invasive potential in new regions, and using climate model scenarios to locate the future global areas of suitability (Estrada-Peña, 2008; Mitikka et al., 2008). Beaumont et al., (2009) summarized the assumptions underpinning statistical \textit{ENMs}: they are usually calibrated assuming the current distribution is the best indicator of its climatic requirements; that the distributions are in equilibrium with current climate; and that climate niche conservation is maintained in both space and time. Major applications of this approach have been to estimate the potential range of invasive species.

Araújo and Guisan (2006) discuss challenges to statistical \textit{ENMs} stating that …”\textit{In spite of the widespread use …} (e.g. Guisan and Thuiller, 2005), \textit{important conceptual, biotic and algorithmic uncertainties still need to be investigated if [these] models are to make important contributions for conservation and bio-geographical research [and agriculture].}” Araújo and Guisan reviewed Hutchinson’s (1957) \textit{fundamental} and \textit{realized niche concepts} that are core to ecological niche modeling (ENMs). They interpret the \textit{fundamental niche} as defined by the resources and limiting factors required for species persistence, while the \textit{realized niche} is defined by the constraints preventing the exploitation of resources. Inter-specific interactions are essential components of the realized niche as repeatedly demonstrated in the applied discipline of biological control (see Rosen and DeBach, 1979). Araújo and Guisan point to the general absence in \textit{ENMs} of facilitator species that influence resource utilization by other species, and further note that niche models explore only snapshot correlations that are difficult to use for assessing feedback mechanisms of species with their environment (see Davis et al., 1998).
Estrada-Peña, (2008) concludes ENMs are conceptually unable to distinguish between the transient and equilibrium response of a species to a stochastically and dynamically changing environment.

Roura-Pascual et al., (2009) compared five techniques for developing statistical ENMs to investigate the potential distribution of Argentine ants in the Iberian Peninsula: generalized linear models, generalized additive models, generalized boosted models, genetic algorithm for rule-set prediction, and maximum entropy models. They found geographic differences in the predictions of the different approaches and in their ability to identify areas of uncertainty regarding the species’ invasive potential. Latimer et al., (2006) showed that making distribution models spatially explicit improves the accuracy of characterizing the environmental response of species and drawing inference about species niche relations, distributions, and the effects of human disturbance. Thuiller et al., (2005) developed bioclimatic niche models for 96 plant species and subspecies endemic to South Africa that are invasive elsewhere. They posit that if species distribution patterns from the area of origin were available, ENM could be powerful tools for unbiased first-step screening of areas identified as potential invasive sites.

Hickler et al., (2009) studied the effects of changes in water availability on predictions by various ENM species distribution models. They concluded that future changes in species ranges and biodiversity should be interpreted with caution, and that more process-based representations of the water balance of terrestrial ecosystems should be considered in the models. In our context, accurate characterization of factors affecting the plant trophic level (e.g., water) is essential for accurate assessment of the geographic distribution and abundance of higher trophic levels.

**Ecological Niche Models based on Physiological Indices (ENPIM)** - This approach is based on the concept of plant growth indices proposed by Fitzpatrick and Nix (1968) for Australian pastures. The approach has quasi-mechanistic roots as it assumes that the normalized growth response of plants to various factors is hump-shaped with minimum and maximum values and an optimum. Hence at any time \( t \), the overall normalized growth response of a plant \( (0 \leq GI(t) < 1) \) is the product of indices for the effects of the different resources sought: e.g., light \( (LI(t)) \), temperature \( (TI(t)) \), moisture \( (MI(t)) \), nitrogen \( (NI(t)) \) and other factors. Low (shortfalls) or high
(toxic) concentrations away from the optimum are assumed to limit (sensu von Liebig, 1840) or slow the growth of the species. A hypothetical example of several growth indices is illustrated in Fig. 3 where the symbol (○) indicates the value at time \( t \). In our example, soil moisture is the major limiting factor, but shortfall or excesses predicted for other factors can also be compounding contributing factors (Eqn. 1).

\[
0 \leq GI(t) = LI(t) \times TI(t) \times MI(t) \times NI(t) \times \ldots < 1 \tag{1}
\]

A hypothetical trace of time-varying \( TI \) and \( MI \) values over a year at one location is plotted as a dashed line in fig. 4a. Superimposed on this trace are the overlapping tolerance limits (e.g., niches) for a plant, an herbivore and a natural enemy that interact in a food chain. In our first example (fig. 4a), the time trace of MI and TI is largely within the tolerance limits of favorability of all three species. While the tolerance of a species to a factor changes in evolutionary time, climate may change more rapidly and cause the trace of the indices to fall outside of the species’ tolerance. For example, if the climate in the area becomes hotter and drier, the degree of overlap
may become marginal for the herbivore and the predator while still being in the suitable range for the plant (fig. 4b). If climate becomes wetter and the range of temperature increases (fig. 4c), the trace of the indices could fall largely outside of the tolerance regions for all three species. Some species may be able to exploit brief periods of favorability by entering quiescence/dormancy during adverse periods (see below).

Figure 4. Climate matching of species tolerance limits to temperature (TI) and moisture (MI) at one location and the hypothetical one year trace of index values starting from Julian day 1 (- - - -): (a) good climatic match for all three trophic levels, (b) changes in climatic favorability within the range largely favorable for the plant but not for the herbivore or predator, and (c) climate change unfavorable for all three species.

The ENPIM approach was used to characterize the limits of favorability for several species of aphids in Australian pastures using soil moisture to characterize plant growth and temperature developmental effects on the aphids, and to map roughly the geographic limits of the cowpea aphid (*Aphis craccivora*) (Gutierrez et al., 1974; Gutierrez and Yaninek, 1983). Sutherst et al., (1991) embedded these notions as an algorithm (CLIMEX) in a geographic information system (GIS) that has been widely used to map the potential geographic distribution of invasive species (e.g., Venette et al., 2000; Coetzee et al., 2009; Rodda et al., 2009; Sutherst and Bourne, 2009).
Zalucki and van Klinken (2006) provided a recent summary of the biological and weather variables used in CLIMEX and some applications. Fig. 5 illustrates the ecological niche boundaries for three species of aphids using observed daily weather and a mechanistic water balance model (Gutierrez et al., 1974), the incorporation of the ENPIM in a GIS, and the prediction of the potential geographic range of the specie and its invasive potential into other geographic regions. There may be many other physiological dimensions than those of temperature and water illustrated in the figures 4 and 5.

Figure 5. Developing an ENM using the growth index approach: (a) ecological niches (ecological space defined using bi-variate normal regression) of three aphids (from Gutierrez et al., 1974); and (b) extrapolating the ecological space to geographic space beyond the original study area (adapted from Zalucki and van Klinken 2006).

In addition to climate, the distribution and abundance of a species is often limited by interacting species (Davis et al., 1998; Hodkinson, 1999), but this is difficult to implement in index models. In addition, weather patterns during short periods of the season may be critical and affect aspects of behavior, seasonality (e.g., dormancy or quiescence), survival and the dynamics of species in food webs. An example is the biological control of walnut aphid wherein
an introduced strain of parasitoid (*Trioxys pallidus*) from France failed to control walnut aphid during the hot dry summers in Central California, while a strain from Iran that was able to enter dormancy provided excellent control (van den Bosch et al., 1979). More complicated examples include the cosmopolitan cabbage root fly (Johnsen et al., 1997) and the pink bollworm in cotton (Gutierrez et al., 2006a) whose geographical distribution and abundance are severely limited by temperature and photoperiod that induce dormancy and alter their phenology and dynamics. Relevant interacting species such as host plants should be included in some analyses to obtain a more realistic estimate of distribution and abundance. However, these factors are difficult to incorporate in ENPIM that often use average weather as drivers.

**Medical and veterinary vector-borne diseases** - The potential impact of climate change on human diseases is of major concern. Vector borne diseases imposing large global burdens that are highly sensitive to climate and ecological change (Molyneux, 2003) include malaria, schistosomiasis, filariasis, dengue fever, leishmaniasis, Chagas disease, West Nile virus, Lyme disease, tick-borne encephalitis, African trypanosomiasis, onchocerciasis, and cholera (Patz et al., 2005). With some notable exceptions (e.g., tick borne diseases), the effect of climate change on animal diseases has received comparatively little attention (de la Rocque et al., 2008). Baylis and Githeco (2006) and Van den Bossche and Coetzer (2008) list the most important environmentally-driven epizootics that are expected to be influenced by climate change. Analyses of these systems have ranged from statistical ecological models, semi-quantitative methods or simplified dynamical models based on indexes (e.g., maximum daily reproductive rate of the disease also known as the vectorial capacity) to a few mechanistic models (Patz et al., 2003).

Among vector-borne human diseases, malaria has the greatest potential to increase its geographic distribution and epidemic patterns in response to climate change because of the effects on vector ecology and behavior (Martens et al., 1999). Attempts have been made to relate malaria resurgence in East African highlands to changes in temperature (Pascual et al., 2006) and climate variability caused by the El Niño-Southern Oscillation (ENSO) (Lindblade et al., 1999). However, temperature is but one part of the factors determining mosquito dynamics...
(Small et al., 2003), as spatial and temporal variations in rainfall also determine the nature and scale of malaria in highland and in low-lying semi-arid areas (Brown et al., 1998; Cox et al., 1999; Kilian et al., 1999; Poveda et al., 2001).

While many interpretations of the major role of climate change on vector-borne diseases are persuasive because they are intuitive, key factors in the transmission and epidemiology of the disease are often ignored (Reiter, 2008), and analyses based on simple models may not provide a holistic view of the complex ecology and disease-host interactions. In addition to physical variables, biological, ecological and evolutionary processes and dynamics in epidemiological systems need to be considered (Smith et al., 2005).

Process-based models offer more opportunities than statistical and semi-quantitative models for realistic representation of both physical and biological interacting component in eco-epidemiological systems (Patz et al., 2003). The biological and ecological realism of physiologically-based demographic models (Gutierrez et al., 2004) would seem to be a promising approach for vector-host-parasite interaction as the malaria systems (Gilioli et al., 2008; Mariani and Gilioli, 2009).

**Physiologically-based demographic ecological niche models (PBDM)**

This approach reverses the process used to develop statistical and physiological index environmental niche models. In these models, the physiological and demographic responses (processes) of the organism (species) to abiotic and biotic factors are modeled on a per capita basis (Gutierrez and Baumgärtner, 1984), and the model(s) at the population level is embedded in a GIS and used to explore the distribution and abundance of a species. The model driven by appropriate weather data and in a tritrophic context is expected to reproduce qualitatively the observed geographic distribution and abundance of the species.

This approach has its roots in the work of de Wit and Goudriaan (1978) on physiologically-based plant canopy models. van Ittersum et al., (2003) summarized de Wit’s concept as follows: **defining factors** (e.g., CO₂, temperature, radiation, and crop characteristics and genetics) determine the potential growth rate, **limiting factors** (water and nutrients, etc.) that constrain this potential, and **reducing (or biotic) factors** (herbivores, weeds and diseases,
pollution) that may further reduce growth. These factors have parallels in Hutchinson’s concept of the fundamental and realized niche, but as we shall see PBDM can also include food web interactions. The physiologically-based approach assumes that the per capita maximum rate of growth is reduced by conditions the organism experiences and by its interactions with other species. This concept of factors reducing the maximum growth rate to the observed was proposed independently in entomology by Hughes (1968). Combining the de Wit - Hughes notions enables PBDM development at all trophic levels - at the individual (Gutierrez et al., 1981, 1987), population, food webs and meta-population (Gutierrez and Baumgärtner 1984, Gutierrez et al., 1988), and the regional levels (e.g. Gutierrez et al., 2007, 2008, 2009, Ponti et al., 2009, 2010) (figure 6a).

Figure 6. Levels of physiologically based models: (a) individual, population, across ecological zones and across large geographic regions, and (b) ecosystem analysis using site-specific weather, GIS maps and marginal analysis.

Tritrophic systems are composed of interacting populations with: (i) the resource and consumer populations characterized by resource-limited growth; (ii) the plant population
integrating the bottom-up effects of weather and edaphic factors (moisture, nutrients and others) (Eqn. 1) and is in turn regulated by the top-down effect of consumers that may also be influenced from lower and higher trophic levels (Hairston et al., 1960; Rosenzweig, 1973); (iii) the attack and consumption rate of all populations are regulated by the same functional response model; and (iv) the life-history strategies of both populations are forced by environmental-driving variables. Nutritional quality and phenology of the resource population also affect the demography and phenology of consumer trophic levels.

The same numerical and functional response models are used for all trophic levels and the linkages between them (Gutierrez and Baumgärtner, 1984; Gutierrez, 1992). The underlying mathematics for the population dynamics is found in Gutierrez (1996) and DiCola et al., (1999). The models are driven by observed weather to predict site-specific dynamics or the dynamics across a landscape. When imbedded in a GIS (e.g., GRASS\(^1\)), the model can be used to estimate the range and relative abundance of the species (fig. 6b). Marginal analyses of multi-variate models of the simulation data can be used to quantify the trends in the data and may prove more useful than the insights gained from the maps of range shifts alone (Gutierrez et al., 2007).

Food webs in systems as diverse as alfalfa, cassava, cotton, coffee, bean, olive, rice, wheat, yellow starthistle, and aquatic systems have been modeled using this approach, and many of the models have been tested with field data and used to develop IPM strategies and to explore theory (see Gutierrez et al., 2005; Gutierrez and Baumgärtner, 2007). Other physiologically-based models include those for forest defoliators (Williams and Liebhold, 1997; Logan et al., 2007; Abbott and Dwyer, 2008), mosquitoes (Focks et al., 1993; Kearney et al., 2009), and bark beetles (Ungerer et al., 1999) and others, but none of these have included the plant level.

Considerable realism can be added in PBDM as illustrated by the examples below and in especially in Gutierrez et al. (2008). PBDMs may be used to explore how weather and climate change may affect trophic interactions that may determine the geographic range of species. We first examine the effects of temperature on the control of olive scale (Parlatoria oleae) by two parasitoids. In our second example, we review the effects of weather and climate change

\(^{1}\) GRASS was originally developed by the US Army Corp of Engineers, but the version we used is maintained and further developed by the Geographic Resources Analysis Support System (GRASS GIS) Software, ITC-irst, Trento, Italy (http://grass.itc.it).
scenarios on the olive/olive-fly system and the influence their geographic range, phenology and abundance. These examples illustrate some of the applications and processes illustrated in fig. 6b. These unified models are part of a suite called CASAS models (see http://cnr.berkeley.edu/casas).

The Olive System

Olive scale/parasitoid system – Weather has considerable influence on the complex developmental biology and dynamics of the sexual olive scale and the two parasitoids that attack it in California olive (Rochat and Gutierrez, 2001; fig.7a). The asexual parasitoid *Aphytis maculicornis* produces only females and only on olive scale. In contrast, the sexual parasitoid *Coccophagoides utilis* produces females on olive scale hosts and males by parasitizing pupae of female siblings. *A. maculicornis* operates at lower temperatures than *C. utilis* and is the victor in cases of larval competition within a single host. The model incorporates the effect of temperature on development, reproduction and survival of the scale and the parasitoids as well as their preference for olive scale life stages. The biology and the mathematics of these processes are too extensive to review here, and hence interested readers are referred to the original article.

Huffaker and Kennett (1966) and Kennett et al., (1966), based on field studies and intuition, concluded that only the combined action of the two parasitoids could provide the high level of control of olive scale observed in Californian olive. To explore this, different combinations of maximum and minimum daily temperatures were used to drive the model to examine the effects on parasitoid regulation and control of olive scale populations – i.e., a demographic ecological niche model was developed. In the absence of natural enemies, olive scale densities are uniformly high across all temperature regimes (fig. 7b). However, including the parasitoids one at a time in the model shows that *C. utilis* was able to suppress olive scale densities only in higher max-min temperature regimes (i.e. the hotter parts of the season in the field, fig. 7c), while *A. maculicornis* alone could suppressed olive scale only in the cooler max-min regimes (i.e., the cooler periods in the field, fig. 7d). The model suggests that only the combined action of the two parasitoids acting largely in different but partially overlapping regions of the max-min temperature state space can control olive scale (fig. 7e), mimicking the effects of seasonal shifts.
in temperature that occur during the year. The question of whether good biological control of olive scale will continue in the face of climate change across the large geographic range of this pest requires embedding the model into a geographic information system (GIS). This is demonstrated using the olive-olive fly system.

Rochat and Gutierrez 2001
Figure 7. The biology (a) of the sexual olive scale (OS) and two parasitoids: the sexual autonomous hyperparasitoid (C, *Coccophagoides utilis*) and asexual thelytokous parasitoid (A, *Aphytis maculicornis*), and (b) the effects of the different combinations of the two parasitoids on olive scale population densities plotted on combinations of max-min temperatures (cf. Rochat and Gutierrez, 2001).

**Olive/Olive Fly System** - Olive and olive fly are of African origin. A review of the biology of both species is found in Gutierrez et al. (2009), and only a brief overview is presented here.

Olive is a drought-tolerant, long-lived species that exhibits little response to photoperiod; its distribution is limited largely by low and high temperatures, and less so by soil water and other factors. Temperature affects the rates of development, photosynthesis, respiration, and subunit initiation rates (i.e., of leaves, stem, root), and mortality. The response of olive to average temperature is non-linear, but all plant subunits are assumed to have the same lower (9.1°C) and upper (38°C) thresholds. Note that these thresholds may be exceeded for short periods during the day with marginal effects. The normalized net of the photosynthetic rate minus the respiration rate over temperature defines the upper and lower thermal thresholds for development and the optimum. Freezing temperature causes mortality to plant subunits and in the extreme may kill the whole plant.

The maximum number of flower buds in the current season is a function of the amount of fruit wood produced in the previous season, but some of buds may be killed by freezing temperatures. Approximately 450 h < 7.3°C are required to stimulate spring fruit bud initiation leading to flowering and 400 degree-days (*dd*) are required from bud swelling to flowering with the period of flowering being approximately 7–10 days. Massive shedding of young post flower fruit occurs due to lack of pollination, cold weather, and shortfalls of photosynthate. A mean of 1495 degree-days are required from flowering to fruit maturation with the fruit becoming susceptible to olive fly when the seed begins to harden. These parameters vary with variety.

Olive fly is endemic in much of the Mediterranean Basin and Middle East, and was discovered in 1998 in California, where it is now widely distributed. The biology of the fly is closely linked to olive fruit age and availability. Adult flies over-winter in facultative reproductive-dormancy that begins to break when fruit of increasingly preferred ages become available, reaching its maximum when the seed begins to harden. Dormancy is also induced
during summer when fruits are in short supply, when mean temperatures fall below 15ºC, and during periods of high summer temperatures. Olive fly females prefer to lay single eggs in unattacked fruit, but multiple attacks may occur when fruit numbers are limiting. When very ripe, fruit fall to the ground and may play an important role in the fly’s dynamics as immature stages in them continue development during the winter.

The lower temperature thresholds for olive fly were computed from the literature: 6.3ºC for egg–larval stages and 8ºC for pupae and adults with the upper threshold for all stages being approximately 33ºC. Low and high temperatures increase fly mortality in all stages. Four to five generations may develop in highly favorable areas.

The model predicts many aspects of olive and olive-fly dynamics and biology, but only flowering phenology, average total fly pupae per tree, and final infestation rates in the absence of control are reviewed and used to assess the possible effects of observed weather and three climate change scenarios: Ten years of observed weather in Arizona-California and Italy and three climate change scenarios where daily weather was increased an average of 1, 2 and 3ºC (see Gutierrez et al., 2009 for full details). The analysis can be done at the field, local area, national or regional scale.

**Olive flowering** - Sufficient chilling for flower bud initiation accrued at all locations and years in Arizona-California and Italy. The range of mean bloom dates using historical weather ranged from Julian day 80 to 163, with the earliest bloom date occurring in the hotter areas of southern California and Arizona (fig. 8a, see histograms). In AZ-CA, a dramatic shift toward earlier blooming occurs throughout much of north and central California with increasing temperatures. Specifically, a three-day decrease in bloom dates occurs per 1°C rise in mean temperature at the lower end of the range, while the effect on the upper end is less clear. Blooming occurs later in Italy where the range of bloom dates is 114 – 178 (fig. 8b). In Italy, the lower and upper end of the range of blooming dates decreases 6-8 days per 1°C increase in mean temperature. These changes are seen as shifts in the histograms for each increment of temperature.
Figure 8. Simulated average Julian bloom dates for olive in Arizona/California and Italy using observed weather (a, b), and the distribution of bloom dates across both regions using observed weather and three climate warming scenarios (adapted from Gutierrez et al., 2009).

**Olive fly abundance** - Olive fly’s dynamics are closely linked to olive fruiting, but as described above there are independent effects of temperature on development, reproduction, survival and dormancy. Total season-long number of pupae produced is used as a metric of the fly’s invasive potential given the bottom-up effects of olive fruit abundance, phenology, and temperature. The infestation levels in California (fig. 9a) coincide quite well with its reported distribution in California (Hannah Nadel and colleagues, [http://arcims.uckac.edu/CIMIS/](http://arcims.uckac.edu/CIMIS/)). The areas predicted to be most favorable for olive fly are along the southern coast of California, where temperatures remain mild throughout the year, while the desert regions of AZ-CA are generally unfavorable because of high summer temperatures that increase fly mortality and decrease reproduction directly and cause reproductive dormancy. The effects of high temperature on olive fly are most obvious in the lower part of the Central Valley of California and the deserts of Southern California and Arizona where high summer temperatures allow only low to intermediate
densities of the fly to develop. Climate warming is expected to cause the favorable range for olive fly to contract further in the Central Valley and desert regions of AZ-CA, but to increase in coastal areas (fig. 9b-d)).

Figure 9. Predicted average number of pupae/tree in Arizona-California (a-d) and Italy (e-h)) under observed and three climate-warming scenarios (+1, +2 and +3°C) (adapted from Gutierrez et al., 2009). The right inset is an enlargement for the Guarda Lake region in northern Italy.

Linear multiple linear regression may be used to summarize the GIS data (see Gutierrez et al., 2005, 2008) on olive fly pupae abundance for Arizona-California (eqn. 2). The coefficients of the regression model for log₁₀ pupae on total $dda<0°C$, date of bloom ($Blm$) and cumulative year long rainfall ($mm$) were highly significant ($p<0.01$), while the significance level for $dda$ was $p<0.05$. Only the coefficient for $dda$ and $ddb$ were negative.

$$Log_{10}pupae = 5.151 - 0.000646dda - 0.00187ddb + 0.0018Blm + 0.00039mm$$

\( df = 6,567 \), \( R^2 = 0.44 \), \( F = 1288.4 \)

(means: $dda=2612$; $ddb=231.40$; $Blm=104.8$, $mm=418.9$)
Substituting mean values for the independent variables shows that $dda$ (i.e., $0.000646 \times 2612 = -1.688$) followed by $ddb$ (-0.433) have the greatest mean negative impact on log pupal density, while $Blm$ (0.189) and $mm$ (0.163) have positive effects resulting in a mean of 2,421.0 pupae per tree across AZ-CA. [As an important aside, this marginal approach bridges biology and economics as it can be used to estimate the effects on yield (or other factors) of weather, pests and say natural enemies in complicated biological systems (see Gutierrez et al., 2005, 2006b).]

while the restricting effects of cold weather are seen in Northern Italy (fig. 9e). In Italy, only the northern regions and the mountains of central Italy are unfavorable due to winter temperatures (fig. 9e), but with climate warming, olive fly distribution moves increasingly northward into previously inhospitable cold areas, and deceases in the more southern areas due to increased summer temperature (fig. 9f-h). The inset in fig. 9e shows the favorable area around Guarda Lake in Northern Italy where olive and olive fly are protected to flourish in what would otherwise be an inhospitable region.

Preliminary results for average olive fly densities and levels of infestations are shown for two decades (e.g. 1956-67 and 1988-97) across the Mediterranean Basin (fig. 10) (Ponti et al., 2010). The results over this much larger area are more difficult to summarize and interpret because of the numerous ecological zones that comprise the region, the grid size of the analysis, and the need to include better water balance models for very arid regions. Despite these caveats, the model gives a very reasonable picture of the distribution of olive fly (fig. 10a, b). Note that the geographic range of high infestation levels during the period 1988-97 is greater than for 1956-67 (10c vs. 10d).
Lest this section be interpreted as being the final word on appropriate methodology, we point out some important shortcomings of PBDM model: the biology of the relevant interacting species must be described in a quantitative manner, but often the biological data to do this are sparse, daily weather data (e.g., max-min temperature, solar radiation, rainfall, RH, wind) are used to drive the model and ideally, calibrated water and nutrient balance models should be available to capture the bottom-up effects of the plant on higher trophic levels. Large scale data to test the model are rarely available. From a mathematical perspective, only numerical solutions of the models are possible, greatly limiting its use in analysis. However, although development of these models is often deemed difficult and extensive computing capacity to implement the model is assumed, this is not the case. A comparison with the CLIMEX approach (see Zalucki and van Klinken, 2006) suggests that the number of parameters is less and that they can all be measured directly with the added benefit that several trophic levels can be included (see examples in Gutierrez et al., 2008, 2009).
Discussion

Species in all trophic levels will be affected by climate change either directly or indirectly, but the greatest impact is expected to occur when the lower trophic levels in a food web or chain are affected (i.e., the pyramid of energy). Important changes may also occur when intermediate levels are adversely affected. The literature is replete with studies that posit weather effects on species and species interactions, but few of them have been studied in sufficient detail to be useful in analyses of the impacts of climate change. Because of their economic importance (Pimentel et al., 2000), data on invasive species tend to be more available. For example, weather was inferred to influence the dynamics and abundance of the founding case of modern biological control in California: the control of cottony cushion scale (Icerya purchasi, a pest of citrus) by the exotic parasitic fly (Cryptocheatum iceryae) and the predacious vedalia beetle (Rodalia cardinalis) (Quesada and DeBach, 1973). The distribution of the fly C. iceryae is restricted to the cooler near-coastal areas, while the vedalia beetle is active across a wide range of ecosystems, including the hotter inland areas of California. However, to determine the geographic ranges of these species and estimate how climate change might affect them requires more biological information than is currently in the literature. The displacement of successive species of red scale parasitoids by later introductions that were better adapted to conditions of Southern California (Rosen and DeBach, 1979) was analyzed by Murdoch et al., (1996), but the analysis was not extended to the regional level.

Surprisingly, the effects of weather on host plants and the cascading-up effects on higher trophic interactions are usually not included in ENM studies. The classic example is the outbreak of locust when the confluence of rains increases host plant abundance in space and time, and favorable winds occur that carry building locust populations from one favorable place to another until massive swarms occur (Roffey and Popov, 1968). Rapid buildups in response to host plant availability may occur in some species (e.g., cowpea aphid; Gutierrez et al., 1974; and African armyworms, see Janssen, 1993), while in other cases outbreaks develop more slowly due to cyclic changes in host plants over time [e.g., spruce budworm (Thompson et al., 1979); bark beetles (Rebetez and Dobbertin, 2004); some vertebrate species (e.g., snowshoe hare/lynx, Krebs et al., 2002) and others]. The capacity to model such systems realistically is critical if we are to
assess the impact of climate change on native and invasive species, but these require sound models of the plant dynamics.

RS satellite data hold unprecedented potential for assessing the effects of climate change on ecosystems on regional and global scales, but they need integration with reliable field data (Kerr and Ostrovsky 2003) in an interdisciplinary framework (Muraoka and Koizumi, 2009). Among the most widely used RS data are measures of canopy greenness called NDVI (Normalized Difference Vegetation Index). Successful applications of NDVI were reviewed showing the potential of this approach to the study of climate change effects on species in managed and natural systems.

Ecological niche/climate envelope modeling approaches are used to examine the effects of weather variables on the geographic distribution and abundance of species in a food web context. These approaches may be statistical or physiological index based, but in both cases the area of current distribution of a species is characterized climatically and using observed weather or climate model projections. The models may be used to project the potential range of the species and its invasive potential into other areas (sensu Estrada-Peña, 2008, Mitikka et al., 2008). Some underpinning assumptions of statistical ENMs include: the current distribution of a species is the best indicator of climatic requirements; the distributions are in equilibrium with current climate (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005); and climate niche conservatism is maintained in both space and time (Peterson et al., 1999). These may hold true for some species, but not for other. Feedbacks of other interacting species may help determine the geographic range of a species, but this is difficult to include in ENMs. Araújo and Luoto (2007) provide support that biotic interactions significantly affect both the explanatory and predictive powers of ENM models at macro scales.

A variety of physiologically-based ENM models have been used to predict the potential distribution of invasive species (Coetzee et al., 2009; Rodda et al., 2009; Sutherst and Bourne, 2009). These physiological based models seek to describe the physiological response of plant and animal species to weather and abiotic variables as growth indices. These indices may be developed by fitting hump shaped response curves for species based on their known distribution or they could be determined using laboratory or field studies (Gutierrez et al., 1974). The best
known of these systems is the widely used CLIMEX system (Sutherst et al., 1991). Including feedback of interacting species that are determinants of the geographic range of a species is difficult (Davis et al., 1998).

There have been many physiologically-based demographic models of local dynamics that include biotic interactions (e.g., Gutierrez and Baumgärtner, 1984; Wu and Wilson, 1997; Holst and Ruggle, 1997) and that can be extended to regional analyses (e.g. Gutierrez et al., 2005, 2006a,b, 2007, 2009; Ponti et al., 2009). The ability to include biotic interactions and feedback potentially makes them more accurate for assessing the geographic distribution and abundance of species, and for examining the potential effects of climate change on them. Drawbacks to this approach include the need for more extensive biological data to formulate the model and more weather data at closer intervals to run the model.

When available, these physiologically-based demographic models often give very different predictions than the physiological index approach. For example, Venette et al., (2000) using CLIMEX concluded that abiotic factors did not preclude the establishment of the pink bollworm in cotton over much of the cotton growing regions of the SE United States, and that its absence in “favorable regions” may be the result of federal monitoring, quarantine, and eradication programs but did not rule out climate and other ecological factors. In contrast, using PBDM that included the dynamics of cotton and the factors affecting PBW reproduction, development, survival, and induction and termination of diapause gave a more restricted distribution for this pest in Arizona and California. This analysis also predicted that a 2.5°C increase in temperatures would increase considerably the range of this pest in California.

The newly-discovered polyphagous light brown apple moth (LBAM) (Epiphyas postvittana) in the area around the San Francisco Bay area prompted a quarantine of the infested area and the initiation of an eradication program. Using two simple criteria - degree days sufficient for the development of three or more LBAM generations and winter temperatures that do not drop below -16°C for one full day to ensure winter survival - Fowler et al., (2009) predicted that most of California and the southern half of the United States could be invaded by this pest. In contrast, Gutierrez, Mills and Ponti (submitted), using biological data from Danthanarayana (1975) in a PBDM, showed that the distribution of LBAM in California was restricted largely to near-coastal
areas with some extension eastward into the northern part of the Central Valley. Most of the Central Valley and southern Arizona are of less than intermediate favourability, particularly when high summer temperatures exceed the tolerance of LBAM. Including the limiting effect of rainfall on annual host plants (e.g. Gutierrez et al., 2005) further restricts the distribution of the pest to the coastal regions. Climate warming would further restrict LBAM’s distribution in central California, but could extend it northward along the coast.

Conclusion
While the goal of all of the pest simulation approaches used is to analyze climate change effects on the distribution and possibly abundance of species (invasive and otherwise), the methods cannot be applied with equal success. Each of the methods has different data requirements and will provide different insights into how climate change may affect host-pest interactions. Hence the method of analysis selected will depend on data availability and on the technical expertise and bias of the researcher(s). On the positive side, many problems may be solved using more direct or simpler approaches such as remote sensing or ecological niche models obviating the need to include more biological detail. However, for analyses of tri-trophic systems, the details may matter. Considerable care must be exercised in modeling approach selection, construction and evaluation because the model will always give an answer but it may simply be wrong (sensu Wang and Gutierrez, 1980).

Literature cited


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**Figure legends**

Figure 1. A partial list of factors affecting species distribution and abundance.

Figure 2. The time of first appearance of four insect species at Tortosa, Spain, beginning 1943 (modified from Gordo and Sanz, 2005).

Figure 3. Growth index models (cf. Fitzpatrick and Nix 1968).

Figure 4. Climate matching of species tolerance limits to temperature (TI) and moisture (MI) at one location and the hypothetical trace (- - - -) of index values starting from Julian day 1 (dashed line): (a) good climatic match for all three trophic levels, (b) changes in climatic favorability within the range largely favorable for the plant but not for the herbivore or predator, and (c) climate change unfavorable for all three species.

Figure 5. Developing an ENM using the growth index approach: (a) ecological niches (ecological space defined using bi-variate normal regression) of three aphids (from Gutierrez et al., 1974); and (b) extrapolating the ecological space to geographic space beyond the original study area (adapted from Zalucki and van Klinken 2006).

Figure 6. Levels of physiologically based models: (a) individual, population, across ecological zones and across large geographic regions, and (b) ecosystem analysis using site-specific weather, GIS maps and marginal analysis.

Figure 7. The biology (a) of the sexual olive scale (OS) and two parasitoids: the sexual autonomous hyperparasitoid (C, Coccophagoides utilis) and asexual thelytokous parasitoid (A, Aphytis maculicornis), and (b) the effects of the different combinations of the two parasitoids on olive scale population densities plotted on combinations of max-min temperatures (cf. Rochat and Gutierrez, 2001).

Figure 8. Simulated average Julian bloom dates for olive in Arizona/California and Italy using observed weather (a, b), and the distribution of bloom dates across both regions using observed weather and three climate warming scenarios (from Gutierrez et al., 2009).

Figure 9. Predicted average number of pupae/tree in Arizona-California (a-d) and Italy (e-h) under observed and three climate-warming scenarios (+1, +2 and +3°C) (from Gutierrez et al., 2009). The right inset is an enlargement for the Guarda Lake region in northern Italy.

Figure 10. Predicted olive fly levels across the Mediterranean Basin (a, b) and the predicted percentage infested fruit (c, d) during two decades (158-1967 and 1988-1997) (Ponti et al., 2010).
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