

Chapter 17

Assessing and managing the ecological and economic impact of climate change on invasive species

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Abstract

Assessing the geographic distribution and abundance of invasive species is critical for developing sound management and/or eradication policies. Ecological niche modeling approaches that make implicit assumptions about the biology and mathematics are commonly used to predict the potential distribution of invasive species based on their recorded distribution. An alternative approach is physiologically- based demographic modeling (PBDMs) that make explicit assumptions about the biology and mathematics based on data and the observed field biology, include trophic interactions, and predict the temporal phenology and dynamics of the species across wide geographic areas independent of pest distribution records. Contrary to common perceptions, the data requirements for developing PBDMs are not onerous.

A weather driven PBDM system model for the noxious yellow starthistle (YST) and its interactions with annual grasses and four seed head feeding herbivorous biological control agents is used to demonstrate the utility of the PBDM approach for analyzing complex invasive species problems (see Gutierrez et al., 2005). The model predicts the geographic distribution and relative abundance of YST across the western USA, and the results are used to assess the effects of temperature, rainfall, competition from grasses, and the four herbivorous insects introduced for its control. The inter-specific competition among the biological control agents is also reviewed. Observed increases in YST growth rates with increasing CO₂ could exacerbate the management problem and complicate the biological control and management of this noxious weed (Dukes et al., 2011). A heuristic bioeconomic model is developed to show how the YST PBDM can be used to assess the biological and economic effects of climate change on YST infestation levels regionally.

Last, a call is made to develop a unified system for assessing invasive species problems at the field, regional and global levels with the goal of enhancing the development of policy and management decisions.

1. Introduction

A critical step to assessing biological invasions is to predict their potential geographic distribution and dynamics in time and space. This capacity is a critical component in developing strategies for their management, including eradication. To do this we must recognize that species are affected not only by climatic change, but also by trophic relationships (Davis et al., 1998). However, assessing the impact of these factors on invasive species biology has proven difficult (Gallien, 2010).

The most commonly used methods to characterize the ecological niche space of species fall under the ambit of *ecological niche modeling* (ENMs) approaches that attempt to characterize the distribution of species using aggregate weather and other factors in areas where the species has been recorded. ENMs are often used to predict the potential range of invasive species following introduction. ENMs may be statistical models (e.g., generalized linear models, generalized additive models, generalized boosted models, genetic algorithm for rule-set prediction, principal components analysis; see Estrada-Peña, 2008), physiological index models (e.g., *CLIMEX*; Sutherst and Maywald 1985; Sutherst et al. 2007), models based on information theory (*MaxEnt*; Phillips et al., 2006; Phillips and Dudík, 2008) and other methods (see Elith and Leathwick, 2009). Elith et al. (2011) provides a useful exposé of the *MaxEnt* approach.

ENMs assume the current geographic distribution of a species is the best indicator of its climatic requirements, that the distribution is in equilibrium with current climate, and climate niche conservatism will be maintained in both space and time (Beaumont et al., 2009). But there are several deficiencies: incorporating trophic interactions in ENMs is difficult (Davis et al., 1998); the assumed native range may be in error (e.g., the species may have been misidentified); a single species may be composed of different ecotypes; aggregate weather data used to delineate distribution may miss important short-term weather effects. Different ENM approaches may also give different results as the region considered and sample size affect the demographic projection (Wisz et al. 2008), and other factors (see Lozier et al., 2009 for additional important cautions). An additional deficiency is that ENMs make **implicit** ecological and mathematical assumptions having no mechanistic basis (Soberón and Nakamura, 2009). For these reasons, the results and transferability (validation) of ENMs are often conjectural with the predictive power being potentially lower than spatial interpolation (Bahn and McGill, 2007). As a result, ENM predictions of invasive species ranges in response to climate change may also be unsound, as climate change effects not captured by the ENM may influence species abundance and subsequent trophic interactions (van der Putten et al., 2010; Wardle et al. 2011). Despite these acknowledged shortcomings, ENMs have been used to assess the potential distribution of invasive species under climate change (Jeschke and Strayer, 2008). Because ENMs are unable to predict the dynamics of invasive species, we suggest they are marginally useful for developing management strategies.

The main advantage of ENM approaches is their relative simplicity to implement and low biological data requirements. Thuiller et al. (2005) has suggested ENMs may provide an unbiased first-step for screening the potential range of invasive plants in new areas; but as Hickler et al. (2009) caution, process-based representations of water balance in terrestrial ecosystems need to be included. The use of ENMs for heterothermic animal species such as insects have also provided useful insights when based on species biology (see Lozier and Mills 2011).

A more direct approach, however, is to model **explicitly** the mechanistic weather driven age structured biology and dynamics of a species and of important species in its food chain or web (i.e. the system) using weather driven physiologically based demographic models (PBDMs). This approach is independent of data concerning the assumed native range of the species. PBDMs estimate prospectively the phenology, dynamics and distribution of species in time and space as driven by observed or climate model scenarios. The PBDM approach has early roots in the work

of Fitzpatrick and Nix (1968), Gutierrez et al. (1974) and de Wit and Goudriaan (1978). The underpinning concepts were summarized in Gutierrez and Baumgärtner (1984) and Gutierrez (1992, 1996). PBDMs may be developed for an individual, a single species population or a tri-trophic food web system that includes bottom-up effects of plant growth and development on herbivores and the top-down action of natural enemies (Gutierrez et al., 2010b). In their most complete form, PBDMs capture the daily age structured dynamics of dry matter acquisition and allocation (**See Chapter 3**). The same model may be used to model the growth dynamics of plants or animals having very different resource acquisition and allocation biology (Gutierrez et al., 1987). As such, we believe that PBDMs may be a more effective method to capture biogeographical and physiologically relevant parameters likely to be influenced with climate change.

2. Estimating the physiological effects of weather

Biological functioning of a species is highly dependent on local weather, and if climate changes, the species dynamics will respond to the new weather regime. For example, if temperature increases, the ontogenetic development and growth rates of plants and other heterothermic species may change in positive or negative ways. Additional factors associated with climatic change such as moisture and CO₂ concentration [CO₂] are likely to change globally as well. For example, the highly invasive weed, yellow starthistle (*Centaurea solstitialis* L.) grew more than six times faster in response to elevated CO₂ in community settings (Dukes et al., 2011). In some plants, increases in the potential growth rates may be slowed by extant physical, morphological and physiological constraints, and in some cases photoperiod and other factors may act as developmental switches (e.g., Morison and Lawlor, 1999). These are important considerations that call for physiological based modeling approaches to capture the expression of the biology as it varies with changes in weather, including climate change.

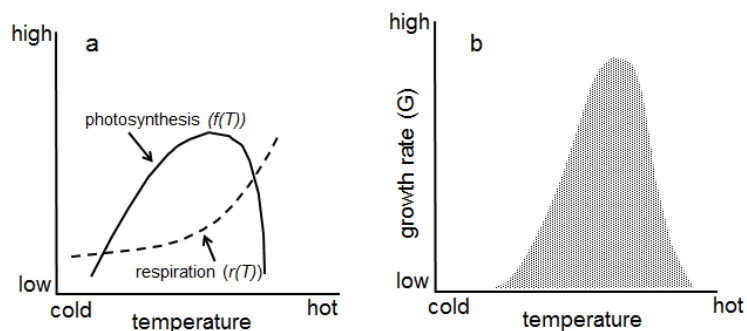


Figure 1. The effects of temperature on growth rates: (a) photosynthesis and respiration and (b) plant growth rate (i.e., $f(T)-r(T)$) at given light and [CO₂].

2.1 Physiological index model

The origins of the PBDM approach is the concept of plant growth indices proposed by Fitzpatrick and Nix (1968) for Australian pastures which Gutierrez et al. (1974) extended to the study of the effects of weather on the distribution of insect populations. The Fitzpatrick-Nix physiological indices were also the basis for the development of the widely used CLIMEX ENM algorithm (Sutherst and Maywald 1985). The growth index approach was an important bridge to the development of PBDMs and hence is reviewed in greater detail here.

Fitzpatrick and Nix (1968) proposed that plants have a concave growth response to various factors, that when normalized yields growth indices having minimum and maximum limits and

optimal values (Fig. 1b). Assuming current [CO₂], the effects of temperature T on the photosynthetic ($f(T)$) and respiration ($r(T)$) rates (i.e., the Q_{10} rule) in a hypothetical plant given constant light is illustrated in Fig 1a. The difference $f(T) - r(T)$ is the potential assimilation rate ($G(T)$) (Fig. 1b). The normalized growth response (an index) is computed by dividing $G(T) = f(T) - r(T)$ by the maximum potential growth rate $G_{max}(T)$ (eqn. 1).

$$0 \leq GI(t) = (f(T) - r(T))/G_{max} < 1 \quad (1)$$

Normalized growth responses to other factors may also be computed in a similar fashion, with the limiting effects of all factors estimated as the product of the various indices (e.g., light ($LI(t)$), temperature ($TI(t)$), moisture ($MI(t)$), nitrogen ($NI(t)$), etc.) (eqn. 2, see Fitzpatrick and Nix 1968).

$$0 \leq \phi = GI(t) = LI(t) \times TI(t) \times MI(t) \times NI(t) \times \dots < 1 \quad (2)$$

This model assumes that concentrations of any factor or combination of factors away from the optimum slows plant growth rates, and in the extreme may be limiting. This is not a new idea (see von Liebig, 1840, Shelford 1931, Andrewartha and Birch 1954). The same approach can be applied to other organisms (say arthropods) with limiting factors being weather variables, resource levels, availability of mates, oviposition sites, density, etc. (see below). One enduring example of this approach is Haefner (1970) who mapped the effects of temperature, salinity and dissolved oxygen on the survival of sand shrimp. A major difficulty, however, is a priori determining the limits and optimum for each index.

The physiological index niches of three hypothetical species in three weather dimensions are depicted in a stylized manner in Fig. 2a. In practice, the physiological indices can be computed using weather data during periods when the species are active in the field, and used to define their ecological niches. For example, the average MI index for the plant and TI indices for three aphids (*Rhopalosiphum padi* Koch, *R. maidis* Fitch, and *Aphis craccivora* Koch) were estimated during periods when winged aphids (alate) were trapped in some of 40 pasture sites across SE Australia during 1968-70 (Fig. 2b; Gutierrez et al. 1974; see also Gutierrez and Yaninek 1983 for other species). During periods when the aphids were active, MI was computed using a soil water balance model based on pan evaporation data, and TI was computed using average daily temperatures. Weather varied greatly across SE Australia during this period and only a few locations were favorable. A bivariate normal model was fit to average MI and TI values for the periods of activity (i.e. the $MI \times TI$ space is the 95% tolerance region), with highest favorability occurring in the middle of the bivariate distribution space.

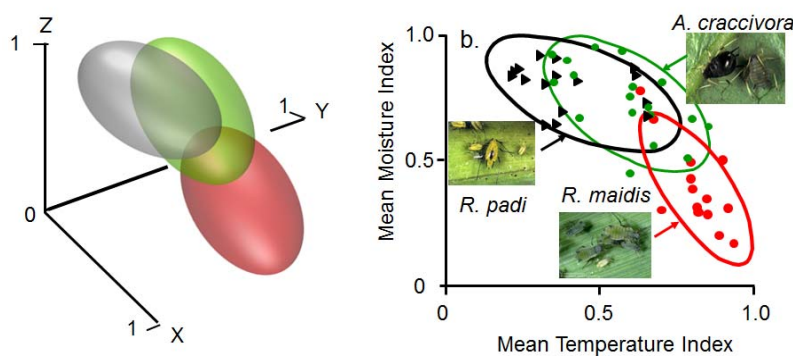


Figure 2. The ecological niche space: (a) three hypothetical species, and (b) three aphids in Australian pastures with the data being the average MI and TI values during the period when aphids were present (Gutierrez et al. 1974). The ellipses are bi-variate normal fits to the data.

As observed in the field, the model suggests that *R. padi* was active during the cooler wetter periods (fall-mild winters), *A. craccivora* was active during periods with mild temperatures and adequate soil moisture for pasture growth (fall or spring), and *R. maidis* winged forms were active during warmer and drier periods (late spring-early summer). Interpreting the model for future time and other locations suggests that populations of each species could develop only when the computed indices fall within the species' ecological niche tolerance region. Further, we note that the geographic distribution of these species is not static, and migration of alate forms plays a key role in the life cycle of these aphids. Hence, whether populations of these species develop in an area also depend on the arrival of migrants during the favorable period.

Different species may have different responses to weather, and this problem is illustrated in a tri-trophic setting where the trace of weekly *MI* and *TI* values at one location during a year is the line circumscribing the grey area in Fig. 3a. Other years and other locations would have different *MI* and *TI* traces indicating different weather patterns and hence levels of favorability. The ecological niche tolerance regions for the plant, an herbivorous species, and its natural enemy are superimposed in the same *MI* x *TI* space in Fig. 3a. The relationships suggest that the different populations may grow during periods when the *MI* x *TI* trace falls within their ecological niche boundary provided its resource (species) is also present. Some species may enter dormancy or survive in microclimates during unfavorable periods, or as in our cowpea aphid examples may survive in the larger region via migration from areas of permanence.

Fig. 3a shows a good climatic match for the three species to current climate for relatively long periods. In contrast, the weather scenario in Fig. 3b shows suggests marginal favorability.

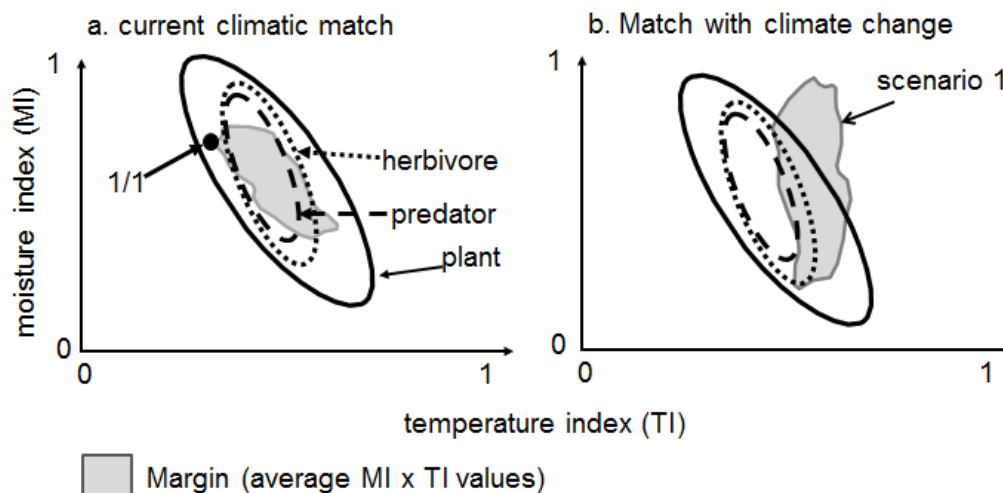


Figure 3. Hypothetical ecological space on temperature (TI) and moisture (MI): (a) a well-adapted tritrophic system, and (b) an alternate scenario of decreasing favorability. The margins of the grey areas are the average weekly TI x MI values starting 1 January.

The weather scenarios, say from Fig. 3a to 3b could be viewed as climate change. We note that in the short run the physiological niches of the species does not change, though in some species selection may occur on a shorter time scale (see Meineke et al., 2013), but predicting the rate of that change remains vexing. Climate change could lead to trophic and spatial mismatches (Schweiger et al., 2008), disruption of pollination (Schweiger et al., 2010), and, potentially, new communities composed of more adapted species (i.e. succession) (George et al. 2009).

Although figure 3 relates weather to trophic interactions, how to extrapolate this link to project demographic change, particularly in a rapidly shifting climate, is the crux of this chapter. Sakai et al. (2001) proposed that population biology holds promise for understanding and

managing invasive species demography, but we argue that, in a climate change context, the models must be weather driven (e.g., Aurambout et al., 2009). In doing so, greater realism can be added to the PBDM approach with subsequent improvements in our understanding of climate driven invasive species dynamics.

2.2 Age structured physiologically based demographic model (PBDM)

We first make the links to the physiological index concepts using a single species model lacking age structure where N is species density and R is its resource density. In dynamics model eqn. 3, $f(R, N, T)$ is the functional response of N to R , T is temperature, θ is the efficiency of converting resource R to N (number or mass), $r(T)$ is the respiration rate (i.e. the Q_{10} rule in a time varying environment) (Fig. 1), $\mu(T)$ is the temperature dependent net death rates, and ϕ is the product of all limiting factors affecting the growth rate of N (eqn. 2) (see Gutierrez and Baumgartner 1984; Gutierrez, 1992; Gutierrez et al., 1994).

$$\frac{dN}{dt} = \phi\theta[f(R, N, T) - r(T)]N - \mu(T)N \quad (3)$$

The single species model may be recast with parallel structure to include mass structure (not shown) and one or more higher-trophic level consumers (C) may be added where $f_c(N, C, T)$, θ_c , r_c , μ_c and ϕ_c have analogous definitions as given above (see Gutierrez et al. 1994; eqn. 4).

$$\frac{dN}{dt} = \phi\theta\{f(R, N, T) - r(T)\}N - \mu(T)N - g(N, C, T)C \quad (4)$$

$$\frac{dC}{dt} = \phi_c\theta_c\{g(N, C, T) - r_c(T)\}C - \mu_c(T)C$$

Adding age structure to eqn. 4 (Gutierrez, 1996) enables more nuanced modeling of the interactions of R , N and C . A variety of age/mass structured models may be used to imbed the time varying dynamics in an age specific manner (see Di Cola et al., 1999). Such models may be used at the individual or population level, and apply equally well to plant and animal species (see Chapter 3). For example, plants pass through various life stages, and each plant has subunit populations (e.g. leaves, stem root, fruit), with fruit having distinct developmental stages and potential growth rates (i.e. bud stage, growing buds, flowers, maturing growing fruit and ripe fruit). Similarly, a holometabolous insect species has distinct stages: egg (i.e., e = eggs) larval (l), pupal (p) and adults (a), but the model can be structured for hemimetabolous life cycles as well. Individuals enter the first age class, say as an egg, and age through the life stages at temperature dependent rates exiting from the final age class, or via mortality (the double arrows) from any age or stage (Figure 4). One may also add developmental variability using models such as those developed by Manetsch (1976) and Vansickle (1977) (see Di Cola et al. 1999 for a review) wherein the distribution of maturation times depends on the number of age classes in each stage. The numerical solution for the time varying form of this model is given in the appendix (see Severini et al., 2005).

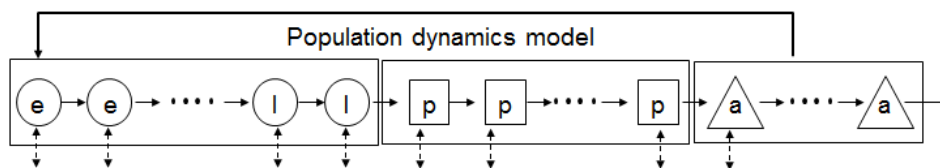


Figure 4. Population dynamics: (a) an age structure models for the dynamics for the egg (symbol e), larval (l), pupal (p) and adult (a) stages with flows (aging) between age classes and stages, with the double arrows indicating net age specific mortality.

2.3 Parameterizing PBDMs

PBDMs are time varying life tables (*sensu* Gilbert et al., 1976), and the parameters may be estimated from laboratory and field age-specific life table studies conducted across gradients of ecological factors (e.g., temperature). Optimally, studies on dry matter allocation and growth would also be performed at the same time. The parameterization process is simplified by the fact that models for all species have similar sub components models that may vary with temperature and other factors (e.g., density, nutrition) and can be captured using simple functions. PBDMs may include aspects of behavior such as host preferences, physiology, dormancy, and other factors. At a minimum, developmental times of life stages, and age specific resource acquisition, reproduction and mortality rates, and dormancy as applicable must be estimated (see review in Gutierrez and Ponti, in press a; see appendix). While this may appear to be a difficult task, in reality it is quite simple and straight forward.

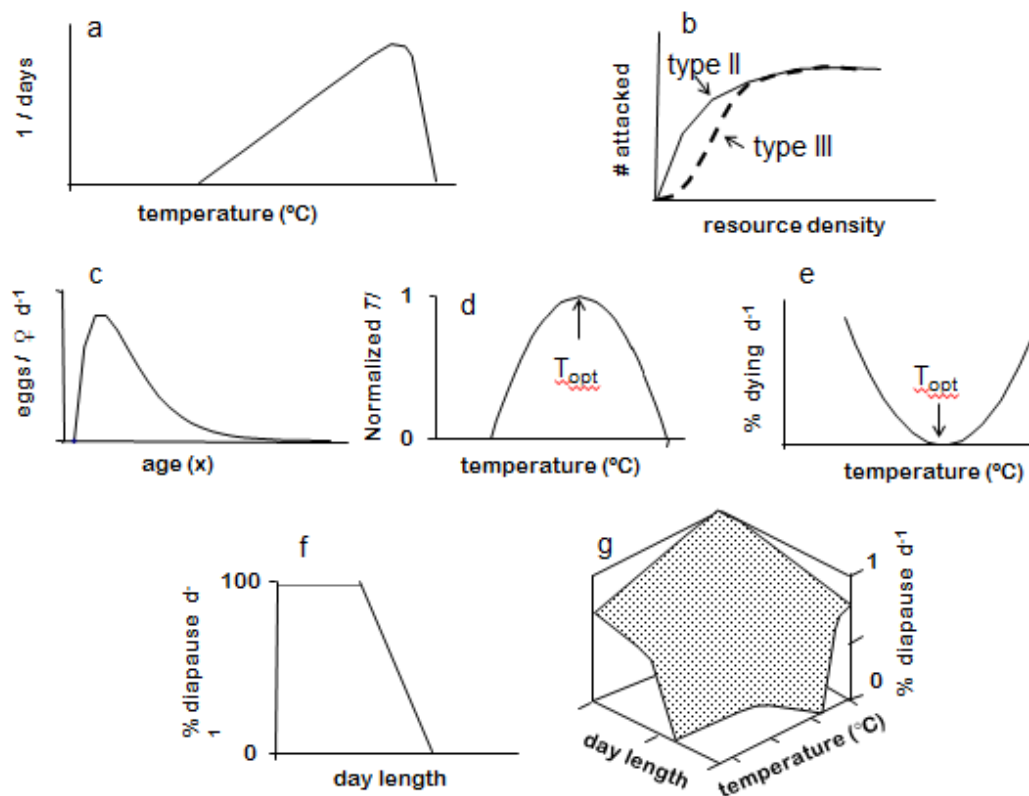


Figure 5. Biological sub models: (a) the rate of development on temperature (Brière, et al. 1999), (b) type II and type III functional responses, (c) the per capita fecundity profile on female age in days at the optimum temperature (T_{opt} in Fig. 5d, e) (Bieri et al., 1983), (d) the normalized effects of temperature on longevity (and gross fecundity) (Gutierrez, 1996), (e) effects of temperature on mortality, and two examples of diapause induction; (f) the proportion diapause induction as a function of day length (e.g., grape vine moth, Gutierrez et al., 2012), and (g) as a function of day length and temperature (e.g., pink bollworm, Gutierrez et al., 1981). Figure modified from Gutierrez et al. in press a).

The effect of temperature on the developmental rate is illustrated in fig. 5a (Brière et al. 1999). Similar demand and search driven resource acquisition processes (functional response) occur in all trophic levels (e.g., photosynthesis, water and nitrogen acquisition by plants, and resource acquisition by higher trophic levels; Gutierrez, 1992, 1996; Gutierrez and Baumgärtner,

1984, 2007) and at the economic level (Regev et al., 1998), and all can be modeled using the same functional form (Fig. 5b). Depending on the biology of search, the functional response model (e.g., $f(R, N, T)$) may be type II if the search rate is a constant, or type III if it is an increasing function of consumer density C . The choice of predator (single attacks) or parasitoid (multiple attacks per host) form of the model depends on the acquisition biology being modeled. For example, a predator model is used for photosynthesis because a quantum of light can be captured only once, while a parasitoid form might be used for herbivores (or parasitoid) when multiple attacks are possible (e.g., on fruit).

Per capita age-specific fecundity at the optimum temperature (i.e., T_{opt} in Fig. 5d, e) may be captured by a simple function (Fig. 5c; Bieri et al., 1983) and scaled for the effects of temperature by the function $\varphi(T)$ (Fig. 5d) and other factors (eqn. 2). Mortality varies with temperature and may be captured by a convex function (e.g., Fig. 5e). Of course, in trophic interactions, we must include predation by higher trophic levels (e.g., $g(N, C, T)$, see eqn. 4). Dormancy in some species may allow them to survive unfavorable periods (see Hahn and Denlinger, 2011). We note however that dormancy may be absent in some species, may be transient in others, may be induced by low host density and/or high temperatures, or day length (Fig. 5f), or it may depend on multiple factors (e.g., temperature, day length (Fig. 5g) and nutrition). As appropriate, the time of dormancy initiation and termination, and the daily rates of dormancy induction must be computed in the model.

Energy (dry matter) flow in an age structured tri-trophic system model consisting of a plant/herbivore/pathogen/parasitoid/predator system) is illustrated in Fig. 6a-c (e.g., Gutierrez et al., 2008a, 2011). The plant provides bottom up effects via resource availability to herbivores, while higher trophic levels provide top down regulation.

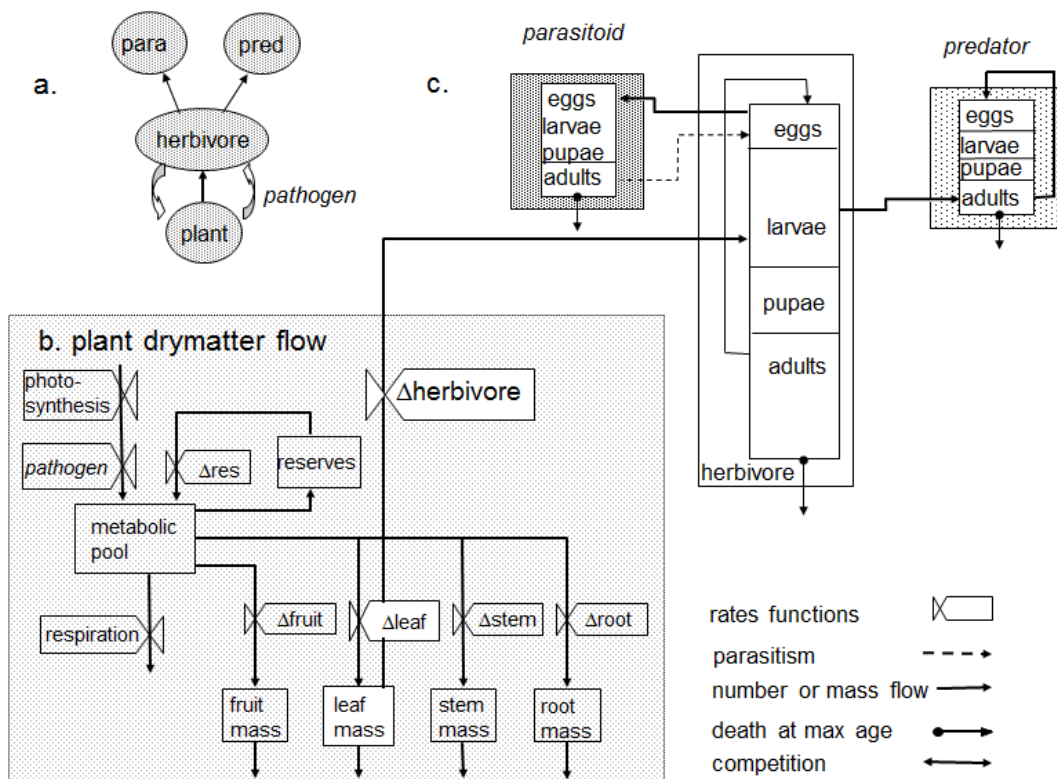


Figure 6. A plant/herbivore/pathogen/parasitoid/predator system: (a) the basic tri-trophic relationships, (b) dry matter flow in the plant as modified by the pathogen, and (c) to the herbivore and a parasitoid and predator showing stage-specific attack preferences (modified from Gutierrez et al., 2008a, 2011).

Table 1. Summary of PBDM systems evaluated in a GIS context.

host plant	herbivores	parasitoids	predators	pathogens	regions	reference	Origins
alfalfa	spotted alfalfa aphid	<i>Aphelinus semiflavus</i> , <i>Praon palitans</i> , <i>Trioxys</i> <i>complanatus</i>	<i>Hippodamia</i> <i>convergens</i>	<i>Erynia neoaphidis</i> (insect)	California	Gutierrez and Ponti (in press b)	temperate
cotton	pink bollworm				USA/Mexico	Gutierrez et al. (2006a, in press)	tropical
citrus	Asian citrus psyllid	<i>Tamarixia</i> <i>radiata</i>	coccinellid beetles		USA/Mexico	Gutierrez and Ponti submitted c	tropical
grapevine	European grapevine moth,				USA/Mexico	Gutierrez et al. 2012, in press)	temperate
	glassy-winged sharpshooter,	<i>Gonatocerus ashmeadi</i> , <i>G. triguttatus</i>		<i>Xylella fastidiosa</i> ^a (plant)	USA/Mexico	Gutierrez et al. 2011, in press	sub tropical
	grapevine mealybug	<i>Anagyrus pseudococci</i> , <i>Leptomastidea abnormis</i>)	<i>Cryptolaemus</i> <i>montrouzieri</i>		California	Gutierrez et al. 2008	temperate
olive	olive fly				USA/Mexico Mediterranean Basin	Gutierrez et al. 2009, in press; Ponti et al. 2009a,b; in press	sub tropical
perennial plant^b	light brown apple moth				USA/Mexico	Gutierrez et al. 2010a	temperate
fruit tree hosts^b	medfly				USA/Mexico/ Italy	Gutierrez and Ponti 2011	tropical
California laurel^b	oleander scale	<i>Aphytis chilensis</i>	<i>Rhysoobius</i> <i>lophanthae</i>		California	Gutierrez and Pizzamiglio 2007	temperate
vertebrate host^a	screwworm				USA/Mexico	Gutierrez and Ponti in press	tropical
yellowstar thistle	<i>Bangasternus orientalis</i> , <i>Eustenopus</i> <i>villosus</i> , <i>Urophora sirunaseva</i> , <i>Chaetorellia succinea</i>				California	Gutierrez et al. 2005	temperate

^a not modeled, ^b generalized host.

3. Regional analysis

Several systems have been modeled using this basic structure in a GIS context (Table 1). The analysis path is as follows: (1) run the model using daily weather data (observed or climate model data) across all grid points in the landscape, (2) map the geo-referenced data using GIS, (3) perform marginal analysis of the output data (i.e., $\partial y / \partial x_i$) to assess the relative contribution of various factors in the regulation of the pest, and (4) use the model as the objective function in a bio-economic analysis of the invasive species problem. To illustrate these phases, we review the biological control of the invasive Mediterranean annual yellow starthistle (YST) in California (Gutierrez et al., 2005).

3.1 The yellow starthistle system

YST is an important noxious weed that heavily infests pastures in the Western USA, and has been the focus of an ongoing biological control effort for more than 25 years. Growth of the thistle is affected by competition for light and water from exotic Mediterranean annual grasses (*G*), and attack from introduced exotic seed head (= capitula) feeding insect herbivores introduced for its biological control (Fig. 7a).

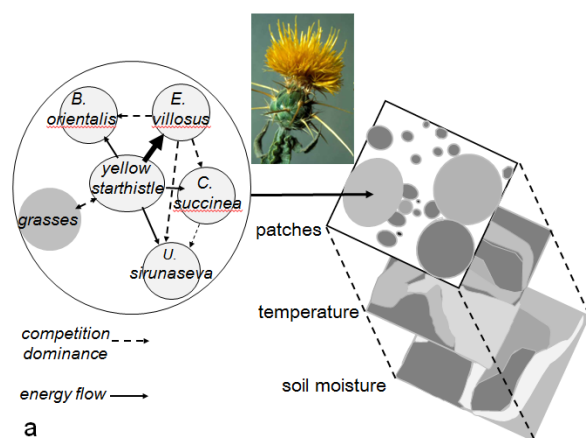
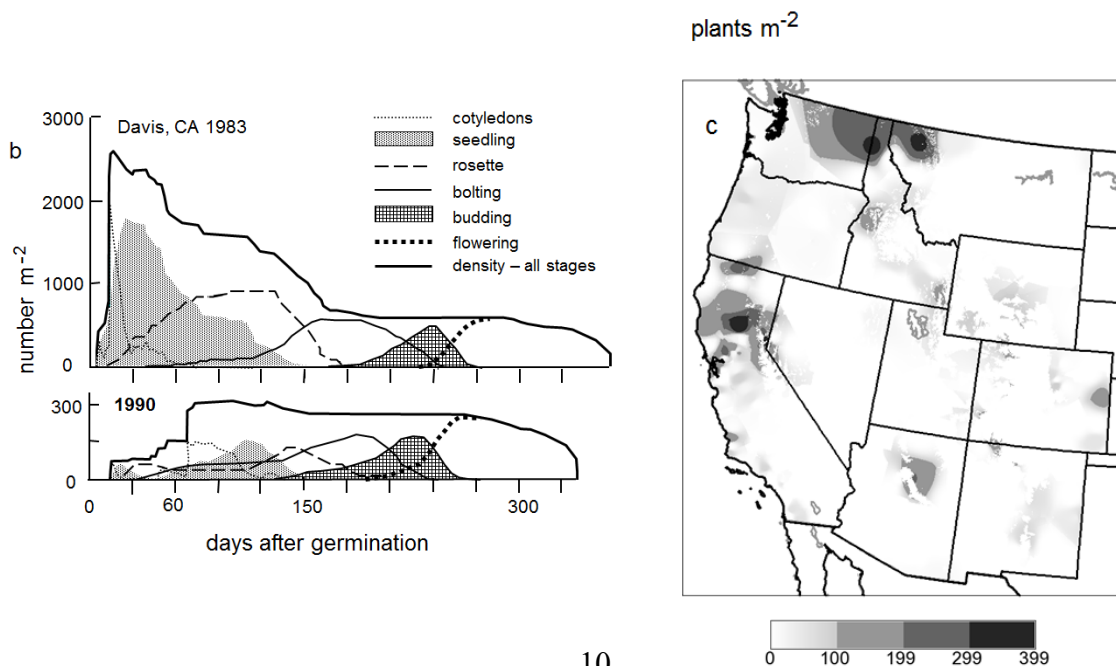


Figure 7. The yellow starthistle PBDM system: (a) trophic interactions (competition between yellow starthistle and exotic annual grasses and herbivory by seed feeding insects as affected by temperature and soil moisture (see text), (b) the simulated phenology of YST from germination through senescence during a wet (1983) and a dry year (1990) (see Gutierrez et al., 2005), and (c) the prospective average distribution of flowering plants m^{-2} during the period September 1982 to September 2003 in the western USA.



Among the species introduced are two weevils (*Bangasternus orientalis* (abbreviation *BO*) and *Eustenopus villosus* (*EV*)), and two picture winged flies (*Chaetorellia succinea* (*CS*) and *Urophora sirunaseva* (*US*)). Gutierrez et al. (2005) analyzed the system using the PBDM approach to estimate the distribution and abundance of YST, and to estimate the impact of the interacting herbivores on YST and each other across the varied ecological zones of California. Here, the analysis is extended to the western USA.

Germination of YST (and Mediterranean grasses) in California normally begins during fall with the intensity and patterns determined by seed bank density and the timing and quantity of autumn-fall-spring rains and favorable temperatures. The germination patterns vary greatly across years, location and regionally. Germination of an annual cohort of seed occurs over several years providing an important stabilizing mechanism for coping with variable rainfall. Winter dormancy in the insect herbivores provides a bridging mechanism between seasons. Season-length for YST is determined mostly by temperature and the availability of soil-moisture estimated using a mechanistic soil water balance model that predicts the evapo-transpiration rate in response to weather and developing leaf area index (Ritchie, 1972).

The phenology and population dynamics of plant stages at Davis, California from germination in fall to senescence and death during a wet (1983) and a dry (1990) year are illustrated in Fig 7b (see Gutierrez et al., 2005). The number of germinating seed (cotyledon stage) during the wet 1983 period was ten-fold that in 1990, with the steep pattern of germination in 1983 starting after the first heavy rains. In contrast, germination during dry 1990 occurred over a protracted 110 day period due to low infrequent rainfall. Fig. 7c shows the predicted average distribution of flowering YST plants across the varied ecological zones of the western USA. In California, the average distribution of YST is restricted to areas with more than 350mm of annual rainfall. Similar maps can be drawn for each plant stage, and for the herbivorous insect species, but aside from illustrating the predicted distribution, the maps are not highly informative.

3.2 Marginal analysis of simulated yellow starthistle data

Using marginal analysis we review the average impact of each herbivore species and grass in suppressing YST, their competitive interactions, and the effect of competition from grasses on YST populations. The simulated action of the different combinations of herbivores and grass (abbreviations *Bo*, *Ev*, *Us*, *Cs* and *G*) at the 72 sites across the varied ecological zones of California were summarized using linear multiple regression wherein species absence or presence (i.e., 0 or 1) and the interactions were used as the independent variables. Only independent variable having slopes significantly different from zero were retained in the multiple regression models (see Gutierrez et al., 2005 for full details). The goal of the regression analysis was not prediction (explained variance), but rather to estimate the direction and average impact of the various factors. (We note, however, that prediction increases with decreasing geographic scale.)

Regressing mature flowering plant density on season length (*dd*), total rainfall (*mm*), and presence-absence of the four herbivores, grass and their interactions yielded multiple regression eqn. 5. The weevil *B. orientalis* and the fly *U. sirunaseva* had no significant effect in reducing plant densities, and are not included in the final model.

$$\text{plants } m^{-2} = 219.4 - 0.012dd - 0.01mm - 12.0Ev - 30.0Cs + 8.6EvCs - 7.9G \quad (5)$$

$$R = 0.22, F = 27.6, df = 3, 233$$

Plants density declines with factors that increase season length (*dd*, *mm*) and with *E. villosus*, *C. succinea* and competition from annual grasses. A longer season enables more generations of *Ev*

and *Cs*. The interaction *EvCs* decreases control and is a measure of interspecific competition. Using marginal analysis, average *dd* (2,656) and *mm* (466) and herbivore presence, the predicted high average plant density is 142m⁻² indicating, as observed, poor control.

A regression of log₁₀ seed density on the same independent variables yielded eqn. 6.

$$\log_{10} \text{ seed density} = 3.30 + 0.00007dd + 0.0002mm - 0.18Ev - 0.36Cs + 0.16Ev \times Cs \quad (6)$$

$$R = 0.42, F = 141.4, df = 3,234$$

Again, *B. orientalis* and *U. sirunaseva* on average had no significant effect in reducing seed densities. Taking the antilog of eqn. 6 and substituting mean values for *dd* and *mm* across sites shows that yellow starthistle seed densities increase with season length and total rainfall, but decrease with *Ev* and *Cs* presence. The action of *E. villosus* and *C. succinea* on average reduce seed production 58% across California with *C. succinea* having the greatest impact. The impact of *C. succinea* was reduced by its interaction with *E. villosus* because it kills fly larvae when they co-occur in capitula. The interaction *EvCs* increases seed survival 12.8% offsetting much of *Ev*'s contribution to seed reduction. Most important, the proportion of seeds that survive in attacked capitula is far higher than required for plant replacement.

3.3 Inter-specific competition among YST herbivores

The interactions of the four herbivore species (and grass) were also examined using log₁₀ cumulative larval days during the season (i.e. abundance) as the dependent variable and the presence-absence and interactions terms of the other species and grass as the independent variables. The results of the marginal analyses suggest (see Gutierrez et al., 2005):

B. orientalis - Only the presence of the weevil *E. villosus* has a significant large negative effect on the abundance of the weevil *B. orientalis*. Without *E. villosus*, average cumulative *B. orientalis* abundance would be 1,096m⁻² larval days but with *E. villosus* the average of *B. orientalis* drops to 3.5m⁻² because *E. villosus* is a superior competitor.

E. villosus - Competition from *B. orientalis*, *C. succinea* and *U. sirunaseva* on log *E. villosus* are not significant, but the indirect effects of grass competition on YST growth and hence capitula production reduced average *E. villosus* larval days by 23%.

C. succinea - *E. villosus* reduces average abundance of the fly *C. succinea* an average of 62%.

U. sirunaseva - The combined action of *E. villosus* (weevil) and *C. succinea* (fly) decreased average larval days of the fly *U. sirunaseva* with *C. succinea* having the larger effect. In the absence of competitors, *U. sirunaseva* average larval days would be 10,715m⁻², but with competition it is reduced to 19.5 m⁻² because both *E. villosus* and *C. succinea* are superior competitors in cases of multiple occurrences in capitula.

In summary, lack of control of yellow starthistle is due to the high survivorship of seed and to plant compensation that increase per plant seed production at lower plant densities. The analysis suggests that herbivory that reduces the plant's ability to compensate and/or kills whole plants before seed maturity would be most likely to lead to the control of yellow starthistle. This is what occurred in the control of the noxious Klamath weed in California by the root feeding Klamath weed beetle (Huffaker and Kennett, 1959). The results of our YST model are consistent with field observations and illustrate the utility of a well parameterized PBDM. However, increases in CO₂ levels have been shown to increase greatly YST growth rates, and this will likely complicate the biological control and management of this weed (Dukes et al., 2011). The effects of increasing [CO₂] can be incorporated in the current PBDM via the demand parameter (see appendix eqn. A3), though a more physiologically nuanced sub models could also

be incorporated. In addition, the modular structure of the PBDM allows integration of the effects of additional biological control species, and used to assess the evolving temporal and spatial changes in YST density with climate change, and used as an aid in guiding ongoing management policy. It could also be used as a template to assess other weed species. Below, we examine the YST problem heuristically from a bio-economic perspective.

3.4 Analyzing the bio-economics of climate change in yellow starthistle

The static production and damage control function approach is commonly used in agricultural economic analyses (e.g., Lichtenberg and Zilberman, 1986), but a PBDM model could be substituted for the production function (Pemsl et al., 2007). For example, the YST model (i.e. $Y(\cdot)$) could be used as the production function to estimate the effects of YST infestation levels (I) on changes in land value under current (\bar{w}_o) and future climate change (\bar{w}_F , e.g., Dell'Aquila *et al.* 2012)) weather including $[CO_2]$ (eqn. 7). The revenues per unit of uninfested grazing land (ρ) are assumed to decrease with infestation level (i.e., $\rho e^{-\alpha I}$) where α is the parameter for change. Control costs enter as the product of the number of control interventions (n) and unit price p_x , while \bar{X}_o and \bar{X}_F are the dynamics of current and potential future sets of biological control agents. Ignoring location coordinates subscripts for convenience in eqn. 7, and assuming p and p_x are constants, profits (Π_o and Π_F) under \bar{w}_o and \bar{w}_F could be estimated as follows.

$$\Pi(\bar{w}_o) = Y(\bar{w}_o, [CO_2]_o, \bar{X}_o) \rho e^{-\alpha I(\bar{w}_o)} - n_o p_x \quad (7)$$

$$\Pi(\bar{w}_F) = Y(\bar{w}_F, [CO_2]_F, \bar{X}_F) \rho e^{-\alpha I(\bar{w}_F)} - n_F p_x$$

The effects of climate change on profits at any location under \bar{w}_o and \bar{w}_F is $\Delta\Pi = \Pi(\bar{w}_F) - \Pi(\bar{w}_o)$, and could be mapped but also used in marginal analyses.

4. Management of invasive insects: a policy perspective

Effective management of invasive species requires approaches that go beyond the existing environmental policy (Pyšek and Richardson, 2010). Some invasive species may disrupt extant food webs, while others may be of minor consequence (see Tylianakis *et al.*, 2008). It is to our advantage to differentiate the threat posed once an invasive pest is introduced. Currently, the presence of invasive species does not include differentiation of actual risk, and as a result, invasives are often handled in a crisis mode by government agencies (Larson 2005). Yet, such agencies often lack the capacity to predict the potential geographic range and relative abundance of the exotic species (i.e., invasiveness) under current weather, much less under future climate change (Gutierrez and Ponti *in press a*). McNeely *et al.* (2001) have suggested that eradication of an invasive species is but one component of invasion policy, which must include a combination of prevention measures and early detection, with effective management (including eradication) being the last resort (see Simberloff *et al.*, 2011). The capacity to predict the occurrence and resulting impact of an invasive species is pivotal to developing science based policy, including environmental, social and economic decisions (Larson *et al.*, 2010). Policy decisions should also extend to invasive species management, including eradication, control, and

in some cases acceptance (Myers et al., 2000). Decisions made for the management of invasive species based on a ENM approach are likely suboptimal, as discussed herein, and hence there is a greater need to be able to assess the effects of species interactions and other factors including the effects of climate change. To that end, we propose that knowledge gaps can be effectively bridged by developing biologically comprehensive, weather driven models such as PBDMs that can utilize sound data in a GIS setting with fine space/time resolution, including data from satellite remote sensing (e.g., Roiz et al., 2011, Table 1) and climate models (e.g., Ponti et al., 2009b).

Venette et al. (2010) have argued that pest risk models that incorporate a high degree of biological complexity (e.g., PBDMs) are less utilized because substantially more biological data at temporal and spatial scales are required, and that decision makers with political and legislative constraints cannot wait for research to fill the data gaps. Policy decisions based on simple assessments may, over time, prove to result in greater environmental and economic damage as illustrated by some of the cases reviewed in chapter 3 and in Table 1 of this chapter.

It is widely acknowledged that mmanagement/eradication efforts against some invasive pests have been ongoing for decades. In the absence of basic biological information, large sums of public monies are often spent in control efforts, efforts that could be strengthened if a fraction of the funds could be applied to the research needed to develop the requisite biological data and models that could improve policy and management decisions (Gutierrez and Ponti, in press a). The recent termination of eradication efforts against the light brown apple moth (*Epiphyas postvittana*) in California is a poignant case in point (see Gutierrez et al., 2010a; Lozier and Mills, 2011).

Overall, propensity to dismiss biologically intense approaches in favor of short-term “solutions” can be counterproductive and often leads to inadequate and/or misdirected research funding and continuing gaps in scientific knowledge regarding the long-term failures or success of invasive species management programs (e.g., the YST example above, see Simberloff et al., 2005). The field of invasion biology has matured sufficiently so that a synthesis and global policy framework for research and implementation for dealing with diverse invasive species can be developed. This synthesis would harness extant and develop new tools such as PBDMs to enhance scientifically-based decision making at the policy level (e.g., Yemshanov et al. 2009).

References

- Andrewartha, H.G., and Birch, L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Aurambout, J.P., Finlay, K.J., Luck, J. and Beattie, G.A.C. (2009). A concept model to estimate the potential distribution of the Asiatic citrus psyllid (*Diaphorina citri* Kuwayama) in Australia under climate change—A means for assessing biosecurity risk. *Ecological Modelling* 220, 2512–2524.
- Bahn, V. and McGill, B.J. (2007). Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography* 16, 733-742.
- Beaumont, L.J., Gallagher, R.V., Thuiller, W., Downey, P.O., Leishman, M.R. and Hughes, L. (2009) Different climatic envelopes among invasive populations may lead to under estimations of current and future biological invasions. *Diversity Distribution* 15, 409–420.
- Bieri, M., Baumgärtner, J., Bianchi, G., Delucchi, V. and von Arx, R. (1983) Development and fecundity of pea aphid (*Acyrtosiphon pisum* Harris) as affected by constant temperatures and by pea varieties. *Mitteilungen der Schweizerischen entomologischen Gesellschaft* 56, 163-171.
- Brière, J.F., Pracros, P., Le Roux, A.Y. and Pierre, J.S. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology* 28, 22–29.

- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. and Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391, 783-786.
- De Wit, C.T. and Goudriaan, J. (1978). *Simulation of Ecological Processes*, 2nd Edn. Pudoc Publishers, Wageningen, Netherlands.
- Dell'Aquila, A., Calmanti, S., Ruti, P., Struglia, M.V., Pisacane, G., Carillo, A. and Sannino, G. (2012) Effects of seasonal cycle fluctuations in an A1B scenario over the Euro-Mediterranean region. *Climate Research*, **52**, 135-157.
- Di Cola, G., Gilioli, G. and Baumgärtner, J. (1999) Mathematical models for age-structured population dynamics. In C. B. Huffaker and A. P. Gutierrez [eds.], *Ecological Entomology*, Second ed. John Wiley and Sons, New York, , pp. 503-534.
- Dukes, J., Chiariello, N.R., Loarie, S.R. and Field, C.B. (2011) Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. *Ecological Applications*, 21(6), 1887-1894
- Elith, J., and Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*. 40, 677-697.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. and Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distribution*, 17, 43-57.
- Estrada-Peña, A. (2008) Climate, niche, ticks, and models: what they are and how we should interpret them. *Parasitology Research* 103, 87-95.
- Fitzpatrick, E.A. and Nix, H.A. (1968) The climatic factor in Australian grasslands ecology, In R.M. Moore (ed.). *Australian grasslands*. Australian National University Press, Canberra, pp. 3-26.
- Frazer, B.D., and Gilbert, N.E. (1976) Coccinellids and aphids: A qualitative study of the impact of adult lady birds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *Journal of the Entomological Society of British Columbia* 73, 33-56.
- Gallien, L., Münkemüller, T., Albert, C.H., Boulangéat, I. and Thuiller, W. (2010) Predicting potential distributions of invasive species: where to go from here? *Diversity and Distribution* 16, 331-342.
- George, K., Ziska, L.H., Bunce, J.A., Quebedeaux, B., Hom, J.L., Wolf, J. and J.R. Teasdale. 2009. Macroclimate associated with urbanization increases the rate of secondary succession from fallow soil. *Oecologia* 159:637-647.
- Gilbert, N., Gutierrez, A.P., Frazer, B.D. and Jones, R.E. 1976. *Ecological Relationships*. Freeman and Co., New York.
- GRASS Development Team (2010) Geographic Resources Analysis Support System (GRASS) Software, Version 6.4.0. Open Source Geospatial Foundation. URL <http://grass.osgeo.org>.
- Gutierrez, A.P. (1992) The physiological basis of ratio-dependent predator-prey theory: the metabolic pool model as a paradigm. *Ecology* 73, 1552-63.
- Gutierrez, A.P. (1996) *Applied population ecology: a supply-demand approach*. John Wiley and Sons, New York, USA.
- Gutierrez, A.P., and Baumgärtner, J.U. (1984) Multitrophic level models of predator-prey energetics: II. A realistic model of plant-herbivore-parasitoid-predator interactions. *Canadian Entomologist* 116, 933-949.
- Gutierrez, A.P. and Baumgärtner, J.U. (2007) Modeling the dynamics of tritrophic population interactions. In M. Kogan and P. Jepson [eds.], *Perspectives in ecological theory and integrated pest management*. Cambridge University Press, Cambridge, UK, , pp. 301-360.
- Gutierrez, A.P., Butler, Jr., G.D. and Ellis, C.K. (1981) Pink bollworm: diapause induction and termination in relation to fluctuating temperatures and decreasing photophases. *Environmental Entomology* 10, 936-942.

- Gutierrez, A.P., Daane, K.M., Ponti, L., Walton, V.M. and Ellis, C.K. (2008a) Prospective evaluation of the biological control of vine mealybug: refuge effects and climate. *Journal of Applied Ecology* 45, 524–536.
- Gutierrez, A.P., d'Oultremont, T., Ellis, C.K. and Ponti L. (2006a). Climatic limits of pink bollworm in Arizona and California: effects of climate warming. *Acta Oecologica* 30, 353-364.
- Gutierrez, A.P., Havenstein, D.E. Nix H.A. and Moore, P.A. (1974) The ecology of *Aphis craccivora* Koch and subterranean clover stunt virus. III. A regional perspective of the phenology and migration of the cowpea aphid. *Journal of Applied Ecology* 11, 21-35.
- Gutierrez, A.P., Mills, N.J. and Ponti, L. (2010a) Limits to the potential distribution of light brown apple moth in Arizona-California based on climate suitability and host plant availability. *Biological Invasions* 12, 3319-3331.
- Gutierrez, A.P., Mills, N.J. Schreiber, S.J. and Ellis, C.K. (1994) A physiologically based tritrophic perspective on bottom-up-top-down regulation of populations. *Ecology* 75, 2227-2242.
- Gutierrez, A.P., Pitcairn, M.J., Ellis, C.K., Carruthers, N. and Ghezelbash, R. (2005) Evaluating biological control of yellow starthistle (*Centaurea solstitialis*) in California: A GIS based supply-demand demographic model. *Biological Control* 34, 115-131.
- Gutierrez, A.P., and Pizzamiglio, M.A. (2007) A regional analysis of weather mediated competition between a parasitoid and a coccinellid predator of oleander scale. *Neotropical Entomology* 36(1),70-83.
- Gutierrez, A.P., and Ponti, L. (in press a) Eradication of Invasive Species: why the biology matters. *Environmental Entomology*
- Gutierrez, A.P., and Ponti, L. (in press b) Deconstructing the control of the spotted alfalfa aphid (*Therioaphis maculata*). *Agricultural and Forest Entomology*.
- Gutierrez, A.P., and Ponti, L. (in review c) Prospective analysis of the geographic distribution and relative abundance of Asian citrus psyllid (Hemiptera: Psyllidae) and citrus greening disease in North America and the Mediterranean Basin. *Florida Entomologist*
- Gutierrez, A.P., and Ponti, L. (in review d) The new world screwworm: exploring effects of temperature and rainfall on the prospective distribution in North America and the Mediterranean Basin. *Agricultural and Forest Entomology*
- Gutierrez, A.P., and Ponti, L. (2011) Assessing the invasive potential of the Mediterranean fruit fly in California and Italy. *Biological Invasion* 13, 2661-2676.
- Gutierrez, A.P., Ponti, L., Cooper, M.L., Gilioli, G., Baumgärtner, J. and Duso, C. (2012) Prospective analysis of the invasive potential of the European grapevine moth (*Lobesia botrana* (Den. & Schiff.)) in California. *Agricultural and Forest Entomology* 14(3), 225-238 DOI: 10.1111/j.1461-9563.2011.00566.x
- Gutierrez, A.P., Ponti, L. and Cossu, Q.A. (2009) Effects of climate warming on olive and olive fly (*Bactrocera oleae* (Gmelin)) in California and Italy. *Climatic Change* 95, 195-217.
- Gutierrez, A.P., Ponti, L. and Gilioli, G. (2010b) Climate Change Effects on Plant-Pest-Natural Enemy Interactions. In *Handbook of Climate Change and Agroecosystems: Impact, adaptation and mitigation*, (Ed.) D. Hillel and C. Rosenzweig. Imperial College Press, UK. 452Pp.
- Gutierrez, A.P., Ponti, L., Hoddle, M., Almeida, R.P.P. and Irvin, N.A. (2011) Geographic distribution and relative abundance of the invasive glassy-winged sharpshooter: effects of temperature and egg parasitoids. *Environmental Entomology* 40, 755-769.
- Gutierrez, A.P., Schulthess, F., Wilson, L.T., Villacorta, A.M., Ellis, C.K. and Baumgärtner, J.U. (1987) Energy acquisition and allocation in plants and insects: A hypothesis for the possible role of hormones in insect feeding patterns. *Canadian Entomologist* 119, 109-129.
- Gutierrez, A.P., and Yaninek, J.S. (1983) Responses to weather of eight aphid species commonly found in pastures in southeastern Australia. *Canadian Entomologist* 115, 1359-1364.

- Haefner, P.A. (1970) The effects of low dissolved oxygen concentrations on temperature-salinity tolerance of the sand shrimp, *Crangon septemspinosa* Say. *Physiological Zoology* 43, 30-37.
- Hahn, D.A. and Denlinger, D.L. (2011) Energetics of insect diapause. *Annual Review of Entomology* 56, 103-121.
- Hickler, T., Fronzek, S., Araújo, M.B., Schweiger, O., Thuiller, W. and Sykes, M.T. (2009) An ecosystem model-based estimate of changes in water availability differs from water proxies that are commonly used in species distribution models. *Global Ecology and Biogeography* 18, 304–313.
- Huffaker, C.B. and Kennett, C.E. (1959) A ten year study of the vegetational changes associated with biological control of Klamath weed. *Journal of Range Management* 12, 69-82.
- Jeschke, J. M., and Strayer, D. L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals New York Academy of Science* 1134, 1-24.
- Larson, B.M.H. (2005) The war of the roses: demilitarizing invasion biology. *Frontiers in Ecology and the Environment* 3, 495-500.
- Larson D.L., Phillips-Mao, L., Quiram, G., Sharpe, L., Stark, R., Sugita, S. and Weiler, A. (2010) A framework for sustainable invasive species management: Environmental, social, and economic objectives. *Journal of Environmental Management* 92, 14-22.
- Lichtenberg, E. and Zilberman, D. (1986) The econometrics of damage control: why specification matters. *American Journal of Agricultural Economics* 68, 261–273.
- Lorraine, H. (1991) The California 1980 Medfly eradication program - An analysis of decision making under nonroutine conditions. *Technological Forecasting and Social Change* 40, 1-32.
- Lozier, J.D., Aniello, P. and Hickerson, M.J. (2009) Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modeling. *Journal of Biogeography* 36, 1623–1627
- Lozier, J.D. and Mills, N.J. (2011) Predicting the potential invasive range of the light brown apple moth (*Epiphyas postvittana*) using biologically informed and correlative species models. *Biological Invasions* 13, 2409-2421.
- Manetsch, T.J. (1976) Time-varying distributed delays and their use in aggregate models of large systems. *IEEE Transactions on Systems, Man, and Cybernetics* 6, 547-553.
- McNeely, J.A., Mooney, H.A., Neville, L.E., Schei, P.J. and Waage, J.K. (Eds.) (2001) *A Global Strategy on Invasive Alien Species*. IUCN, Gland, Switzerland, 50 pp.
- Meineke, E.K., Dunn, R.R., Sexton, J.O. and Frank, S.D. (2013) Urban warming drives insect pest abundance on street trees. *PLoS ONE* 8(3), e59687. doi:10.1371/journal.pone.0059687
- Monteith, J.L. (1965) Light distribution and photosynthesis in field crops. *Annals of Botany* (London) [N.S.] 29, 17-38.
- Morison, J. I. L. and Lawlor, D.W. (1999) Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant, Cell and Environment* 22, 659–682
- Myers, J.H., Simberloff, D., Kuris, A.M. and Carey, J.R. (2000) Eradication revisited: dealing with exotic species. *Trends Ecology and Evolution* 15, 316-320.
- Nicholson, A.J. and Bailey, V.A. (1935) The balance of animal populations. Part 1, *Proceedings of the Zoological Society of London* 3, 551-598.
- Pemsl, D., Gutierrez, A.P., Waibel, H. (2007) The Economics of Biotechnology under Ecosystems Disruption. *Ecological Economics* 66, 177-183.
- Phillips, S.J., and Dudík, M. (2008) Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31,161–175.
- Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling* 190, 231–259.

- Ponti, L., Cossu, Q.A. and Gutierrez, A.P. (2009a) Climate warming effects on the *Olea europaea*–*Bactrocera oleae* system in Mediterranean islands: Sardinia as an example. *Global Change Biology* 15, 2874-2884.
- Ponti, L., Gutierrez, A.P. and Ruti, P.M. (2009b) The olive-*Bactrocera oleae* (Diptera Tephritidae) system in the Mediterranean Basin: a physiologically based analysis driven by the ERA-40 climate data. *Notiziario sulla Protezione delle Piante – III Serie* 1, 113-128.
- Pyšek, P., and Richardson, D.M. (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35, 25-55.
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Regev, U., Gutierrez, A.P., Schreiber, S.J. and Zilberman, D. (1998) Biological and economic foundations of renewable resource exploitation. *Ecological Economics* 26, 227-242.
- Ritchie, J.T. (1972) Model for predicting evaporation from a row crop with incomplete cover. *Water Resources Research*. 8, 1204-1213.
- Roiz, D., Neteler, M., Castellani, C., Arnoldi, D. and Rizzoli, A. (2011) Climatic factors driving invasion of the tiger mosquito (*Aedes albopictus*) into new areas of Trentino, northern Italy. *PLoS ONE* 6, e14800.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E. O'Neil, P. Parker, I.M., Thompson, J.N. and Weller, S.G. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32,305–32.
- Schweiger, O., Settele, J., Kudrna, O., Klotz, S. and Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89, 3472-3479.
- Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., Kühn, I., Moora, M., Nielsen, A. and Ohlemüller, R. (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews* 85, 777-795.
- Severini, M., Alilla, R., Pesolillo, S. and Baumgärtner, J. (2005) Grapevine and *Lobesia botrana* (lep. Tortricidae) phenology in the Castelli Romani area. *Rivista Italiana di Agrometeorologia* 3, 34-39.
- Shelford, V. E. (1931) Some concepts of bioecology. *Ecology* 12, 455-467.
- Simberloff, D., Parker, I.M. and Windle, P.N. (2005) Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* 3, 12-20.
- Simberloff, D., Genovesi, P., Pyšek, P. and Campbell, K. (2011) Recognizing conservation success. *Science* 332, 419
- Soberón, J., and Nakamura, M. (2009) Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Science USA* 106, 19644-19650.
- Sutherst R.W. and Maywald G.F. (1985) A computerized system for matching climates in ecology. *Agriculture, Ecosystems & Environment* 13, 281-299.
- Sutherst, R.W., Maywald, G.F. and Bourne, A.S. (2007) Including species interactions in risk assessments for global change. *Global Change Biology* 13, 1843-1859.
- Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes G.O. and Rouget, M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11,2234-2250.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. and Wardle, D.A. (2008) Global change and species interactions in terrestrial. Ecosystems. *Ecology Letters* 11, 1351–1363
- van der Putten, W.H., Macel, M. and Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B* 365, 2025-2034.

- Vansickle, J., (1977) Attrition in distributed delay models. *IEEE Transactions on Systems, Man, and Cybernetics* 7, 635-638.
- Venette, R.C., Kriticos, D.J., Magarey, R.D., Koch, F.H., Baker, R.H.A., Worner, S.P., Gómez Raboteaux, N.N., Dobesberger, E.J., Yemshanov, D. and De Barro, P.J. (2010) Pest risk maps for invasive alien species: a roadmap for improvement. *Bioscience* 60, 349-362.
- von Liebig, J. (1840) *Chemistry and its Applications to Agriculture and Physiology*. London, Taylor and Walton. (4th edition 1847).
- Wardle, D. A., Bardgett, R.D., Callaway, R.M. and Van der Putten, W.H. (2011) Terrestrial ecosystem responses to species gains and losses. *Science* 332, 1273-1277.
- Watt, K.E.F. (1959) A mathematical model for the effects of densities of attacked and attacking species on the number attacked. *Canadian Entomologist* 91, 129-144.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. and Guisan, A. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14, 763-773.
- Yemshanov, D., McKenney, D.W., Pedlar, J.H., Koch F.H. and Cook, D. (2009) Towards an integrated approach to modeling the risks and impact of invasive forest species. *Environmental Reviews* 17,163-178.
- Ziska, L.H., Blumenthal, D. M., Runion, G. B., Hunt Jr., E. R. and Diaz-Soltero, H. (2011) Invasive species and climate change: an agronomic perspective. *Climatic Change* 105,13-42.

Appendix 1. Distributed maturation time model.

The numerical solution of this model for a life stage i with $i = 1, \dots, K$ age classes is eqn. A1 (text Fig. 4; see Manetsch, 1976; Vansickle, 1977; Di Cola et al. 1999; Severini et al., 2005). The state variable is density (as a rate, $n_i(t)$) in units of number (or mass). Births flow into the first age class ($i=1$), survivors exit at the maximum age ($i = k$). Note that this is the time-varying form (Vansickle, 1977; Severini et al., 2005). The model can be adapted for flows in other dimensions as well (mass, etc).

$$n_i(t+1) = n_i(t) + \frac{V}{\Delta(t)} \left\{ n_{i-1}(t) - \left(1 + \frac{\Delta(t) + [\mu_i - 1] \cdot \Delta(t-1)}{V} \right) \cdot n_i(t) \right\} \quad (A1)$$

The forcing variable is temperature (T), and time (t) is a day that from the perspective of the heterotherm organisms is of variable length in physiological time units above its lower thermal threshold (see below). The variable V is the proportional change in development (aging), $\Delta(T_{opt})$ is the mean developmental time under optimal T_{opt} , and $\Delta x(T(t))$ is an increment of age (x), and $R(T(t))$ is the rate of development at temperature $T(t)$. The function variable $\mu_i(t)$ is the proportional net loss rate that includes the rich biology affecting the age specific births, deaths, growth, predation, net immigration, and other factors including text eqn.1.

The density of cohort i is $N_i(t) = n_i(t) \cdot \Delta(T(t)) / k$, the total density in the life stage is $N(t) = \sum_1^k N_i(t)$ and $k = \Delta(T_{opt})^2 / \text{var}$. The model allows multiple thermal thresholds and multiple age and time scales for the different species and their sub-stages. The definitions of variables in eqn. A1 are expanded below.

Parameterizing the dynamics model

All of the sub models below are parameterized by fits to data.

The developmental rates and times – In PBDMs, the time step is a day while the change in age is in physiological time units (e.g., degree days) above the lower thermal threshold for development. The effect of temperature and other factors on the developmental rate (fig. 5a) is captured by eqn. A2 (Brière et al., 1999, see).

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

The constants a and b , and the lower and upper thresholds T_L and T_U are estimated from data. The average developmental of a cohort initiated at some time t_0 is completed when the daily rates sum to 1 (i.e., $\int_{t_0}^t R(T(t)) dt = 1$). Development can also be affected by nutrition and other factors.

Resource acquisition ($f(R,N)$) - Similar demand and search driven resource acquisition processes occur in all trophic levels (e.g., photosynthesis, water and nitrogen acquisition by plants, and resource acquisition by higher trophic levels; Gutierrez, 1992, 1996; Gutierrez and Baumgärtner, 1984, 2007) including the economic one (Regev et al., 1998). The per capita resource acquisition rate S (=supply) is computed using the ratio-dependent functional response model (eqn. A3; Fig. 5b, solid line) where D is the per capita consumer demand that varies with temperature and other factors (e.g., $[\text{CO}_2]$, see also Gutierrez, 1992).

$$S = f(N, C) = D(1 - e^{-\frac{\alpha N}{DC}}) \quad (A3)$$

Depending on the biology of search, eqn. A3 is type II if α is constant, but is type III if α is an increasing function of C (i.e. $\alpha(C)$). In plant physiology, the function $\alpha C = LAI/\alpha$ would be the well-known Monteith (1965) light extinction model and in animal ecology the equally well-known Nicholson and Bailey model (1935) (see Gutierrez, 1996). The type II model is related to the model proposed by Watt (1959) and is the predator form of the Frazer and Gilbert (1976) parasitoid model. The choice of predator (single attacks) or parasitoid (multiple attacks) form of the model depends on the attack biology being modeled. Dividing both side of eqn. A3 by D yields the supply-demand ratio ($0 \leq S/D < 1$) (i.e., search is always imperfect).

Per capita age-specific fecundity ($F(T, x)$, Fig. 5c) may be captured by a simple per capita reproduction function $f(x)$ (Biere et al., 1983) scaled by the effects of temperature ($\phi(T)$, Fig. 5d).

$$F(T, x) = \phi(T)h(x), \quad (A4)$$

$$\text{where } h(x) = \frac{cx}{d^x}$$

Temperature dependent mortality - Similarly, mortality varies with temperature and the rate per unit time may be capture by upward convex functions such as Fig. 5e with constants d and e .

$$0 \leq \mu(T) = d \times (T - T_{opt})^2 + e \leq 1 \quad (A5)$$

Of course, in trophic interactions, we must include predation effects of higher trophic levels ($g(N, C, T)$, see text eqns. 3, 4).

Dormancy - Various forms of dormancy allow different species to survive unfavorable periods. Dormancy is absent in many species, it may be transient in some, may be induced by low host density and/or high temperatures, it may be induced by day length (Fig. 5f), or it may depend on temperature and day length (Fig. 5g), but may also be influenced by nutrition and other factors (see (e.g., pink bollworm, Gutierrez et al., 1981). As appropriate, the time of dormancy initiation, the daily rates of dormancy induction, and dormancy termination must be computed in the model (see Gutierrez et al., 2006, 2011).