

## Physiologically based demographic models streamline identification and collection of data in evidence-based pest risk assessment

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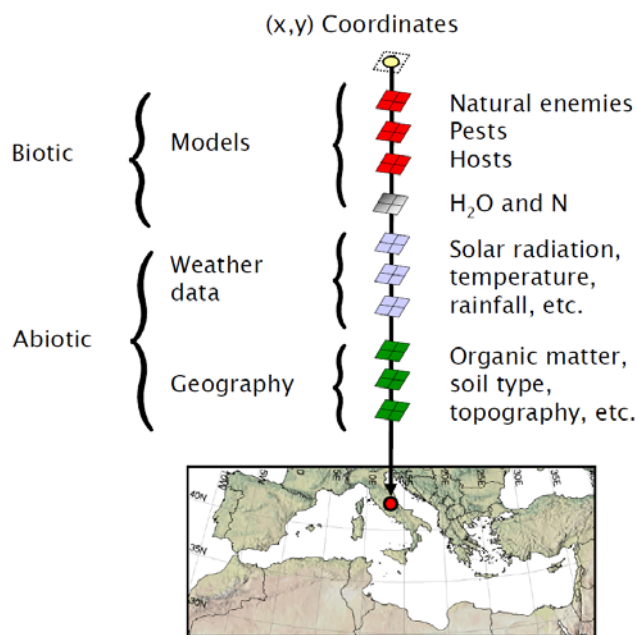
**Running head:** A process-based guide to data collection

**Abstract.** The distribution and abundance of species that cause economic loss (i.e., pests) in crops, forests or livestock depends on many biotic and abiotic factors that are thought difficult to separate and quantify on geographical and temporal scales. However, the weather-driven biology and dynamics of such species and of relevant interacting species in their food chain or web can be captured via mechanistic physiologically based demographic models (PBDMs) that can be implemented in the context of a geographic information system (GIS) to project their potential geographic distribution and relative abundance given observed or climate change scenarios of weather. PBDMs may include bottom-up effects of the host on pest dynamics and, if appropriate, the top-down action of natural enemies. When driven by weather, PBDMs predict the phenology, age structure and abundance dynamics at one or many locations enabling projecting the distribution of the interacting species across wide geographic areas. PBDMs are able to capture relevant ecosystem complexity within a modest number of measurable parameters because they use the same ecological models of analogous resource acquisition and allocation processes across all trophic levels. The use of these analogies makes parameter estimation easier as the underlying functions are known. This is a significant advantage in cases where the available biological data is sparse.

### Introduction

A pest species in any taxon, be it native or exotic, is defined as causing economic loss to resource species harvested by humans or is of medical or veterinary concern. The distribution, phenology and abundance of a pest species (say an herbivore) depends on biotic (e.g., plant host, natural enemies) and abiotic (e.g., weather) factors (Andrewartha & Birch, 1954; Larcher, 1995; Wellington *et al.*, 1999; Walther *et al.*, 2002). These effects are often difficult

to separate and quantify on a geographic scale (Fig 1; see e.g. Gutierrez *et al.*, 1974), and yet determining whether a species is a pest or not is cornerstone for developing the economic justification for local and regional management (Kogan, 1998; Ponti *et al.*, 2015). To put regional pest management programs on solid scientific grounds, such studies of pest impact are best implemented as tritrophic systems and best performed in a geographical context.



**Figure 1.** A partial list of factors affecting the distribution and abundance of pest species (modified from Gutierrez *et al.*, 2010b). Note such models are best implemented as tritrophic systems so that any component of the system can be assessed.

Assessment of whether a species in any trophic level is a pest and whether it must be controlled, must include realistic estimates of its potential geographic distribution, phenology and relative abundance in time and space with assessments of the damage it causes (e.g., Gutierrez *et al.*, 2010a). This may sound straightforward in principle, but it has been a difficult recurring problem (see Gutierrez *et al.*, 2010b), the need for which will only worsen with global climate and environmental changes (e.g., Estay *et al.*, 2009). The difficulty of such analyses is due to the multi-factor time-varying complexity of pest systems and their underlying ecology that remain a fundamental challenge to assess reliably under current climate and with climate change (Tylianakis *et al.*, 2008). All species have different requirements for growth, survival and reproduction that determine their geographic distribution, abundance, and interactions with other species, and hence to analyze this complexity requires the development of models that include the relevant effects of biotic and abiotic factors on species dynamics (Gutierrez *et al.*, 2008).

One approach to model this complexity is to develop mechanistic descriptions – i.e., process-based models – that capture the weather-driven biology of the species and of relevant interacting species in its food chain or web. Physiologically based demographic models (PBDMs) of species have been used to capture these processes (Gutierrez, 1996) using observed daily weather or climate scenarios to drive model dynamics across time and

geographic space, and to map the results via a geographic information system (GIS; e.g. GRASS GIS, see Neteler *et al.*, 2012). Some recent examples are Gutierrez *et al.* (2005) and Gutierrez & Ponti (2011, 2013, 2014a). Here we illustrate how PBDMs can streamline pest risk assessment by providing a process-based guide to identify knowledge gaps, and guide the collection of the data required to develop the PBDM to determine whether a species should or should not be considered a current or potential pest in a region.

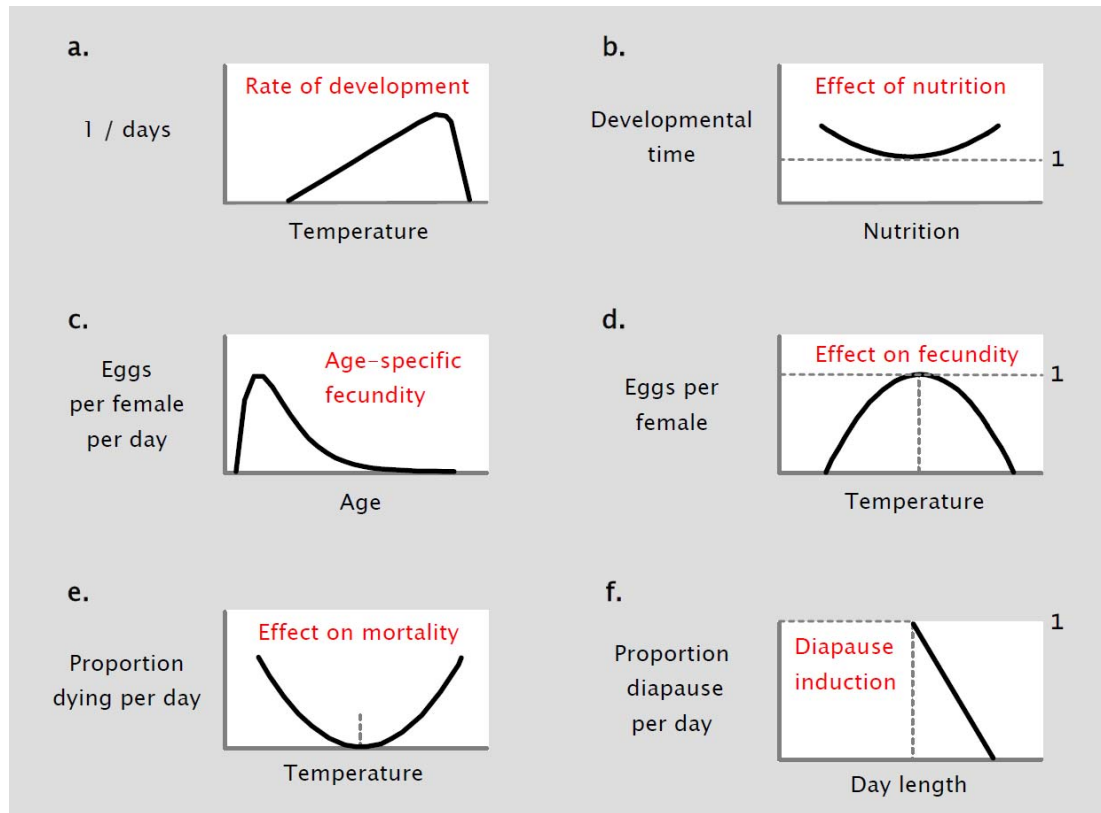
### **A physiologically based approach to pest risk assessment**

PBDMs in the context of a GIS can help provide an appropriate level of mechanistic synthesis for capturing the complex interactions that underpin evidence-based pest risk assessment and decision making in plant health. PBDMs often include bottom-up effects of host plant growth and development on pest dynamics and, in some cases, the top-down action of natural enemies (see Gutierrez *et al.*, 2010b; Gutierrez & Ponti, 2014b). The models may also be used for studies of medical and veterinary pests (e.g., Gutierrez & Ponti, 2014a). When driven by weather including climate change scenarios, PBDMs predict the phenology, age structure and abundance dynamics, and distribution of the interacting species across wide geographic areas (e.g., Gutierrez *et al.*, 2008; Gutierrez & Ponti, 2013). Several weather data sources can be used to drive weather-driven PBDMs (see Ponti *et al.*, 2013; Rocchini *et al.*, 2015), including satellite remote sensing (e.g., Neteler, 2010) and regional climate change projections (e.g., Artale *et al.*, 2010; Dell'Aquila *et al.*, 2012).

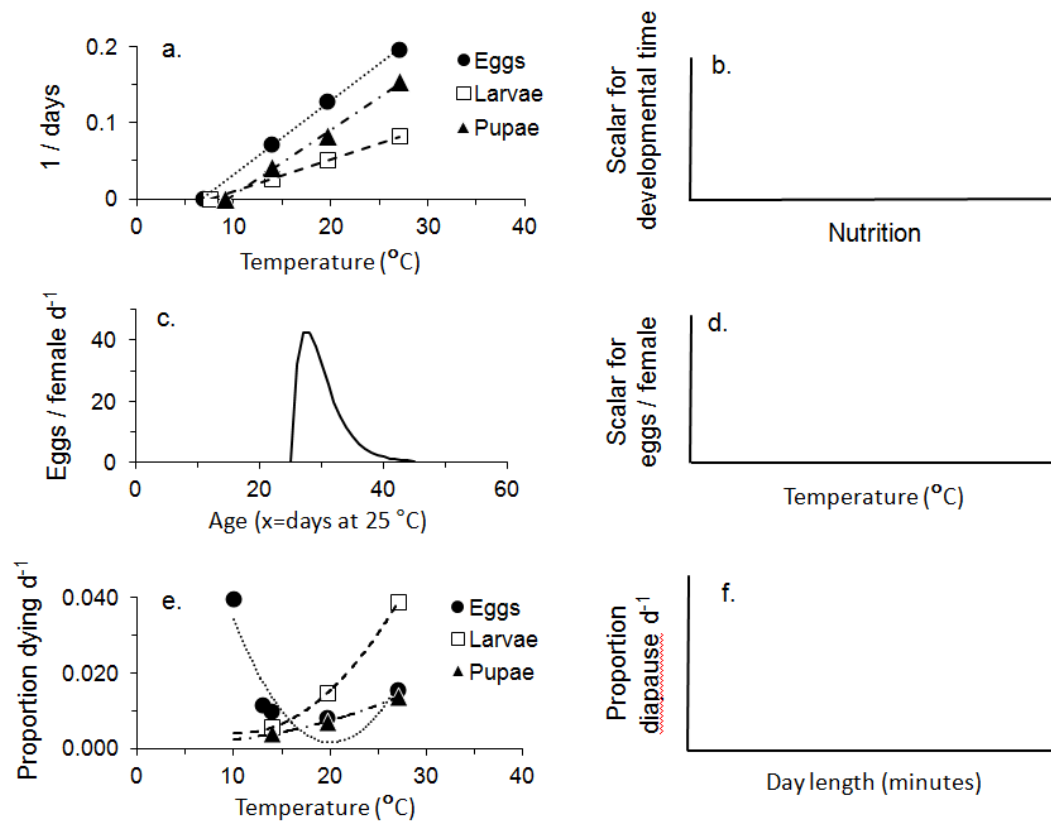
PBDMs build on the idea that all organisms in all trophic levels are consumers with resource acquisition processes having similar shapes described by the same mathematical functions, and with analogous allocation priorities (Gutierrez & Baumgärtner, 1984; Gutierrez *et al.*, 1994; Gutierrez, 1996; Regev *et al.*, 1998). These analogies enable PBDMs to capture relevant ecosystem complexity at all trophic levels using a modest number of measurable parameters. By analogy, the dynamics of all species can be captured using the same resource acquisition and same shape birth-death rates sub-models embedded in age-mass structured population models that describe sub processes such as temperature-dependent developmental rates, age-specific fecundity and mortality as modified by temperature and other factors, diapause and the interaction with resource species and with natural enemies (see sub model shapes in Fig. 2; modified from Gutierrez & Ponti, 2013). As the underlying functions are known (Fig. 2), parameter estimation is easier, and is a significant advantage in case the required set of sound biological data is not fully available.

PBDMs are especially useful in assessing whether a species should or should not be considered a current or potential pest in a specific geographic area. PBDMs streamline the identification and collection of missing data that may have prevented evidence-based pest risk assessment. The highly destructive South American tomato leafminer (*Tuta absoluta*) that recently invaded the Mediterranean Basin (Desneux *et al.*, 2011) is an example of how the PBDM modeling framework is providing clear guidance for a collaborative effort by identifying data gaps in the biology of this species, and for guiding data collection (Ponti *et al.*, 2015). Comparison of Fig. 3 vs. Fig. 2 shows available information on the biology of *T. absoluta* that is insufficient to estimate the limiting effects of temperature on its dynamics in cold and hot regions, and hence to predict correctly the potential geographic distribution and relative abundance over the vast invasive range of the species. This does not mean that all the experience gained in recent years about *T. absoluta* is not useful, but rather that PBDM

analysis helps summarize the data and focus new research efforts to collect vital missing biological data. PBDMs simply describe species biology in a concise mechanistic way making few assumptions to enable realistic projections of species biology on a geographic scale based on physiology as driven by daily weather. The models can explain the current range and project where the species might spread, estimate infestation patterns, and become the basis for evaluating and evolving control strategies.



**Figure 2.** PBDM sub-models used for all species (modified from Gutierrez & Ponti, 2013): (a) the rate of development on temperature (modified from Brière *et al.*, 1999); (b) the effects of for example nutrition on developmental time (for example, nutrients in plants may negatively affect developmental time both when in shortfall by acting as a limiting factor, and also when in excess due to a toxic effect); (c) the per capita fecundity profile on female age in days (Bieri *et al.*, 1983) at the optimum temperature (i.e., the vertical dashed line in (d)); (d) the effects of temperature on normalized fecundity; (e) the effects of temperature on normalized mortality (Gutierrez, 1996); and (f) the proportion diapause induction as a function of day length (e.g., grapevine moth, Gutierrez *et al.*, 2012). The biology of plants, herbivores, and natural enemies are modeled in a similar way in PBDMs. The same dynamics model and submodels for analogous processes in the life histories across trophic levels (e.g., for plants and for insects that feed on them) have similar shapes described by the same functions. Plants may not lay eggs, but the population dynamics of plant subunits (e.g., leaves) are modeled in a way similar to that used to model insect populations. The figure provides examples that are illustrative of the plant health domain, but the results are more general. Full details are given in the literature cited.

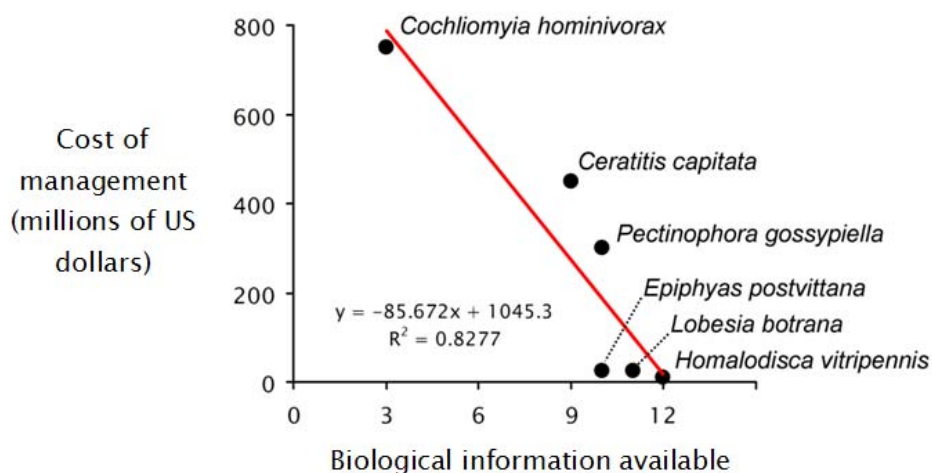


**Figure 3.** Gaps in knowledge about the biology of *T. absoluta* as identified using the PBDM approach: only sub-models for developmental times (a), age-specific fecundity (c) and mortality (e) can be partially parameterized. See Fig. 2 for comparison (from Ponti *et al.*, 2015). Age-specific fecundity profile shown in subfigure (c) was modeled after Bieri *et al.* (1983) using data digitized from Fig. 1 in Pereyra and Sanchez (2006) using WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>).

### Why the biology matters to pest risk assessment

The importance of taking a process-based PBDM approach to pest risk analysis is exemplified by assessments of several invasive species (Gutierrez & Ponti, 2013). A PBDM analysis of pink bollworm (*Pectinophora gossypiella*), a major pest of cotton worldwide that invaded southern Arizona and southern California about 50 years ago, explained that the Central Valley of California was outside of its permanent geographic range of year-round persistence, and that the ongoing eradication program to prevent establishment there was not needed (Gutierrez *et al.*, 2006). Mediterranean fruit fly (*Ceratitis capitata*) was first detected in California in 1975, and since then a large-scale detection/eradication campaign has been in place in the absence of sound knowledge of the fly's potential invasiveness and geographic distribution, and in the absence of measurable populations of the pest. A PBDM analysis suggests that temperatures are unfavorable for medfly in much of California and hence questions the scientific basis for the ongoing eradication program (Gutierrez & Ponti, 2011). Another example is light brown apple moth (*Epiphyas postvittana*), a polyphagous species native to Australia known to feed on 545 plant species including pome fruits and grape (Brockerhoff *et al.*, 2011). However, despite its broad host range, *E. postvittana* has not caused the projected economic damage after it was first found in the state in 2006 (Hogg *et*

*al.*, 2014). In 2007, a controversial eradication program including aerial sprays was initiated over urban and suburban areas to eradicate *E. postvittana* based on predicted wide geographic range and prospective economic losses estimated by the United States Department of Agriculture (USDA; see Fowler *et al.*, 2009). Predictions using a PBDM for *E. postvittana* differed markedly from those made by the USDA, and show as observed that the potential distribution of *E. postvittana* in California is largely restricted to near coastal areas (Gutierrez *et al.*, 2010a). The *E. postvittana* eradication program has since been switched to regional containment and quarantine programs (see Gutierrez & Ponti, 2013). A larger set of examples with full description found in Gutierrez & Ponti (2013) suggests that expenditures made to manage invasive pest species are inversely related to the amount of biological information available (Fig. 4). The lack of basic biological information for the screwworm *Cochliomyia hominivorax*, a parasitic fly the larvae of which feed on the flesh of living warm blooded animals (e.g., Gutierrez & Ponti, 2014a) illustrates the importance of gathering appropriate biological data and using sound methods for evaluating the potential distribution and relative abundance of pest species before costly eradication programs are begun. It doesn't matter whether a pest attacks plants or animals, PBDMs may help allocate scarce resources more efficiently in assessment and management actions.



**Figure 4.** The biology matters: a process-based approach is key to managing pests effectively. The plot shows expenditures made to manage six invasive species versus the amount of information available on each species. Information available was scored using a scale from 0 to 12 indicating how many of the following items were known for each species: name, origin, host specificity, host model, functional response, developmental rate, fecundity, temperature-dependent mortality, biotic mortality, dormancy, costs, and eradications success (see Table 1 in Gutierrez & Ponti, 2013). The eradication of the native *C. hominivorax* in North America during the 1960s and 1970s was the hallmark of the eradication paradigm (USDA 2012), and yet the biological data to support it was sparse. The fact that screwworm is a parasite of warm blooded animals whereas the rest of the species shown in the figure are plant pests is irrelevant as the figure is meant to illustrate a trend. More important is that the same PBDM paradigm was used to analyze the seven pest species in the study (Gutierrez & Ponti, 2013).

## Conclusions

Evidence-based pest risk assessment can be made more efficient if mechanistic models (e.g., PBDMs) are used to identify data needs and for streamlining data collection. Once the modest number of measurable parameters required to capture relevant ecosystem complexity are present, PBDMs can be used in a GIS context as driven by weather and other information layers representative of the abiotic factors affecting the distribution and relative abundance of a species, and used to assess the regional pest status. The PBDM modeling framework provides clear guidance for interdisciplinary collaborative efforts in evidence-based pest risk assessment.

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