

Holistic approach in invasive species research: the case of the tomato leaf miner in the Mediterranean Basin

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Abstract The Mediterranean Basin is a climate change and biological invasion hotspot where recent warming is facilitating the establishment and spread of invasive species, one of which is the highly destructive South American tomato leaf-miner (*Tuta absoluta*). This pest recently invaded the Mediterranean Basin where it threatens solanaceous crops. Holistic approaches are required to project the potential geographic distribution and relative abundance of invasive species and hence are pivotal to developing sound policy for their management. This need is increasing dramatically in the face of a surge in biological invasions and climate change. However, while holistic analyses of invasive species are often advocated, they are rarely implemented.

We propose that physiologically-based demographic models (PBDMs) in the context of a geographic information system (GIS) can provide the appropriate level of synthesis required to capture the complex interactions basic to manage invasive species such as *T. absoluta*. We review the PBDMs for two invasive flies, and use them as a basis for assessing the biological data available for the development of a PBDM for *T. absoluta*, and in the process identify large data gaps that using the PBDM as a guide can be easily filled. Other components for an ecologically-based management program for this pest (habitat modification, natural and classical biocontrol, pheromones, and others) are also reviewed. The development of a PBDM for *T. absoluta* would provide the basis for an interdisciplinary agroecological synthesis of the problem and the role different control tactics would play in region-specific control of the pest.

Key words: *Tuta absoluta*, invasive species, agroecology, physiologically-based weather-driven demographic models, geographic information systems (GIS), climate change effects, ecologically-based pest management, holistic analysis.

1. The Mediterranean Basin as a hotspot for biological invasion

The Mediterranean Basin is a biodiversity (Myers et al., 2000) and climate change hotspot (Giorgi, 2006) challenged by biological invasions of exotic species (Sala et al., 2000; Drake & Lodge, 2004; Gritti et al., 2006; Hulme et al., 2008; Tatem, 2009; Robinet & Roques, 2010; Pyšek & Hulme, 2011). Because of this, methods must be developed for assessing these invasive species and for assessing management strategies and tactics (Pyšek & Richardson, 2010; Simberloff et al., 2013). This paper reviews the progress in assessing such problems using the tomato leaf miner *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) as the foil for discussion.

The status of the Mediterranean Basins as a climate change hotspot is based on a consensus of climate projections (Giorgi, 2006; Diffenbaugh & Giorgi, 2012) across forcing scenarios, future time periods, and a range of global and regional climate models (Giorgi & Lionello, 2008; Lionello et al., 2012). This consensus suggests that the Basin and other areas of Europe are at increased risk of exotic species invasions (e.g., pests). This problem is compounded by the numerous airports in the area with voluminous incoming traffic from regions with similar climates, and by gaps in phyto-sanitary controls (Bacon et al., 2012). This combination of factors is projected to increase invasive species establishment (Tatem, 2009) as illustrated by the establishment of several tropical insect species in the Basin (Robinet & Roques, 2010). Geographical barriers previously limited entry of exotic species, but these have been made ineffective by rapid global commercial traffic, making climate mismatches the major natural barrier against the global spread of invasive species, (Tatem & Hay, 2007; Tatem, 2009).

Invasive species may be of any taxa and yearly cause an estimated trillion US dollars in losses worldwide (Oerke & Dehne, 2004). This figure is nearly an order of magnitude higher than losses due to natural disasters (see Ricciardi et al., 2011). Plants are a major group of invasive organisms, but their introduction has mostly been intentional or as contaminants in seed (Pimentel et al., 2005). Insects are common invasive species and constitute one-third of insect pests (Ward & Masters, 2007), and their economic impact has been considerable (Pyšek et al., 2008). The potential geographic distribution and relative abundance (i.e., measures of invasiveness) of invasive species are poorly understood, even after costly and long-standing management/eradication programs (Gutierrez & Ponti, 2013b).

The fields of integrated pest management (IPM)/agroecology (see Apple & Smith, 1976; Altieri, 1995; Altieri & Nicholls, 2004) are a holistic vision of the agricultural sustainability problem (Tomich et al., 2011). Based on analysis of definitions spanning 35 years, Kogan (1998) proposed a definition of IPM as “a decision support system for the selection and use of pest control tactics, singly or harmoniously coordinated into a management strategy, based on cost/benefit analyses that take into account the interests of and impacts on producers, society, and the environment”. Because it involves the use of science to solve problems, IPM can be seen as a technology (see definition on www.merriam-webster.com)

stemming from the recognition that the control of pest populations is a complex ecological problem where the food system must be considered in its entirety, including simultaneous consideration of insects, diseases, plant nutrition, plant physiology, and plant resistance, as well as the economics of the crops (see Stern et al., 1959). On the other hand, agroecology has been defined as “the science of applying ecological concepts and principles to the design and management of sustainable food systems” (Gliessman, 2007). In theory, as evident from e.g. Figure 1 in Kogan (1998), the degree of distinction between IPM and agroecology depends on the level of IPM integration achieved within the context of the ecological, socioeconomic, and agricultural scales. In practice, however, the gap between the concept of agroecology and the capacity to analyze agroecosystems is wide. Holistic analyses are often advocated (Zavaleta et al., 2001; Hulme, 2006; Sutherst & Bourne, 2009; Gilman et al., 2010), but are rarely achieved – there are simply too many factors, and the best we can do is to examine sub sets of the agroecosystem (e.g., Gutierrez & Ponti, 2013a). What is possible are analyses and regional projections of the dynamics of sub systems as driven by weather and as constrained by interactions with other species and elements of the abiotic environment (see Gutierrez, 1996). Focusing on invasive species, key issues include predicting their potential distribution and relative abundance, the effects of natural enemies, and assessing the efficacy of available control methods with the effects of future climate change being an additional layer of evolving complexity (Gutierrez et al., 2010; Gutierrez & Ponti, 2013b; Gutierrez & Ponti, 2013a, in press-a, in press-b).

In this paper, we first review the shortcomings of mainstream approaches commonly used to assess exotic species invasiveness, and as an alternative propose that the physiologically-based demographic modeling (PBDM) approach provides a quantitative framework for the holistic management of pests. As examples, we review recent PBDM analyses of Mediterranean fruit fly (*Ceratitis capitata*) (Gutierrez & Ponti, 2011, 2013b) and olive fly (*Bactrocera oleae*) (Gutierrez et al., 2009; Ponti et al., 2009a; Ponti et al., 2009b; Gutierrez & Ponti, 2013b) to illustrate the utility of PBDM methods to the analysis of *T. absoluta*, a serious highly invasive pest that threatens tomato and other solanaceous crops in the Mediterranean Basin and globally (Desneux et al., 2010; Desneux et al., 2011). We review the available biological data on *T. absoluta*, with an eye cast to its adequacy for developing a PBDM for this pest. In addition, we review progress in the development of options for the management of *T. absoluta* given that resistance in *T. absoluta* to a wide range of insecticides makes the need for ecologically-based management even more stringent.

2. Predicting geographic distribution and relative abundance

Pivotal to developing sound policy for control and management of invasive species, or their eradication, is the capacity to predict their potential geographic distribution and relative abundance (i.e., invasiveness) under current and climate change scenarios (Gutierrez et al., 2011). Climate is an important determinant of species distribution and abundance (Andrewartha & Birch, 1954), and is a major barrier against the global spread of invasive species (Tatem & Hay, 2007; Tatem, 2009). However, predicting the geographic distribution and dynamics of invasive species in time and space has been a difficult recurring problem (see review by Gilioli & Baumgärtner, 2009) that may only increase with global climate and environmental change (see e.g., Hulme, 2012; Sorte et al., 2013). Climate is the long-run pattern of meteorological factors that organisms experience as short-term (e.g., daily) weather dynamics affecting their physiology (e.g., development, growth and reproduction, survival, diurnal and seasonal phenology), interactions with other species, and other aspects of their biology in time and space (see e.g., Andrewartha & Birch, 1954; Larcher, 1995; Wellington et al., 1999). Analyzing this complexity remains the greatest single challenge to assess reliably ecosystems (including invasive species) under climate change (Tylianakis et al., 2008).

In the Mediterranean Basin, recent climate warming has been concentrated in the summer period (Mariotti & Dell'Aquila, 2011), especially during the last decade of the twentieth century (Bartolini et al., 2012). This level of warming is consistent with climate change projections for the region (Barkhordarian et al., 2011) and readily demonstrable when compared to historical temperature variability spanning the last millennium (Guiot, 2012; Joël, 2012).

3. A review of methods used to predict the geographic distribution of invasive species

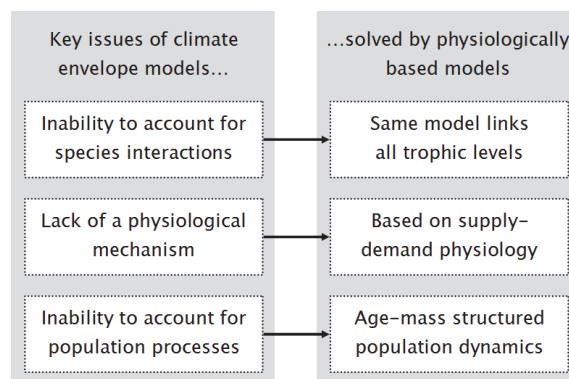
In this section we review the use of ecological niche models and physiologically-based demographic models used to predict the distribution and abundance of species.

3.1. Ecological niche models (ENMs)

Common methods fall under the ambit of *climate envelope* approaches (i.e., ENMs) wherein distribution records of the species are used as a basis to characterize climatically the ecological niche of the species using statistical techniques (see Estrada-Peña, 2008), physiological indices (e.g., CLIMEX; Sutherst et al., 2007), methods based on information theory (Maxent; Phillips et al., 2006;

Phillips & Dudik, 2008) and other methods reviewed by Elith and Leathwick (2009). ENMs assume the current geographic distribution of a species is the best indicator of its climatic requirements, the distribution is in equilibrium with current climate, and climate niche conservatism is maintained in both space and time (Beaumont et al., 2009). However, because of the correlative nature of ENMs, a number of problems arise (see also Tab. 1): difficulty incorporating trophic interactions (Davis et al., 1998a; Davis et al., 1998b; van der Putten et al., 2010), the assumed native range may be in error as the records may be of presence in ephemeral habitats or the species may have been misidentified (Soberón & Peterson, 2011; Warren, 2012), aggregate weather data are often used that miss important short-term weather effects (see Tab. 2), different ENM approaches give different results (Lawler et al., 2006), and other factors (see Lozier et al., 2009). These models make implicit ecological and mathematical assumptions that lack mechanistic underpinnings (Soberón & Nakamura, 2009) (Tab. 1).

Table 1. Limitations of *climate envelope* models acknowledged in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Fischlin et al., 2007) and how these limitations are addressed by physiologically-based demographic models.

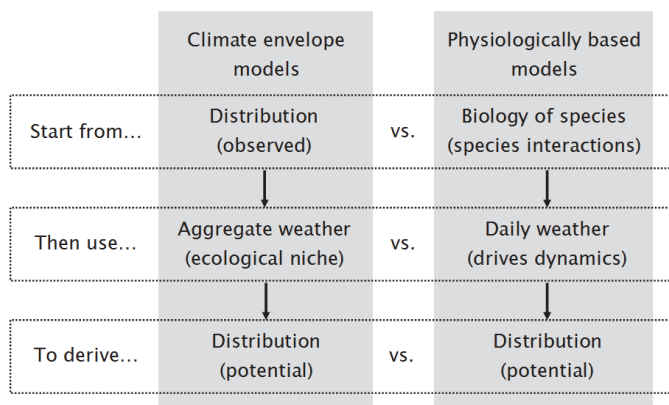


ENMs are often good at characterizing the current ranges of species, but they are not as good at projecting range shifts due to the spread of the invaders or due to climate change (Jeschke & Strayer, 2008; Wiens et al., 2009; Sinclair et al., 2010; Barve et al., 2011; Veloz et al., 2012). Despite shortcomings, ENMs are in many cases the only readily available methods for estimating the ecological niche of an invasive species (Warren, 2012), and may provide a useful first approximation if the results are interpreted with due consideration of the limitations of the models (Pearson & Dawson, 2003). However, correlative analyses leave significant gaps in our understanding of biological invasions, and more mechanistic approaches have been increasingly advocated recently (see e.g., Dawson et al., 2011; Hulme, 2011; Hulme & Barrett, 2013).

3.2. Physiologically-based demographic models (PBDMs)

PBDMs address some of the shortcomings of ENMs by explicitly capturing the mechanistic weather-driven biology of the species and of relevant interacting species in its food chain or web. Instead of beginning with the assumed native range of a species, PBDMs model the biology of the target species and other species in the same food chain or web (i.e., the system) (Tab. 2), and when driven by weather the PBDM predicts the phenology, age structured dynamics and distribution of the interacting species across wide geographic areas independent of distribution records (Gutierrez et al., 2005, 2008; Gutierrez & Ponti, in press-a) (see Tab. 1). PBDMs may include bottom-up effects of plant growth and development on herbivore dynamics and in some cases the top-down action of natural enemies (see Gutierrez & Baumgärtner, 1984; Gutierrez et al., 1994). Because the weather-driven biology is modeled explicitly, the PBDM system easily deals with the effects of climate change. Apart from background immigration rates, movement is not included explicitly in PBDMs limiting their use in predicting the regional spread and dynamics of the species with great accuracy (see e.g., Battisti et al., 2006). Recently, Gilioli et al. (2013) have developed a model for local and long-distance dispersal of the exotic chestnut gall wasp (*Dryocosmus kuriphilus*) that accurately reproduces the observed spatio-temporal invasion dynamics of the species in Europe for the period 2002-2009, and could provide a necessary link for the PBDM approach.

Table 2. Comparison of the *climate envelope* approaches and the physiologically-based demographic modeling approach.



The underlying idea of PBDMs is that all organisms (in all trophic levels including the economic one; see Gutierrez, 1996; Regev et al., 1998) are consumers and have analogous resource acquisition (inputs) and allocation (outputs) priorities (Gutierrez et al., 1994). Based on these analogies, the dynamics of all spe-

cies can be captured using the same resource acquisition and same shape birth-death rates sub-models embedded in an age-mass structured population models that capture 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. 1; modified from Gutierrez & Ponti, 2013b).

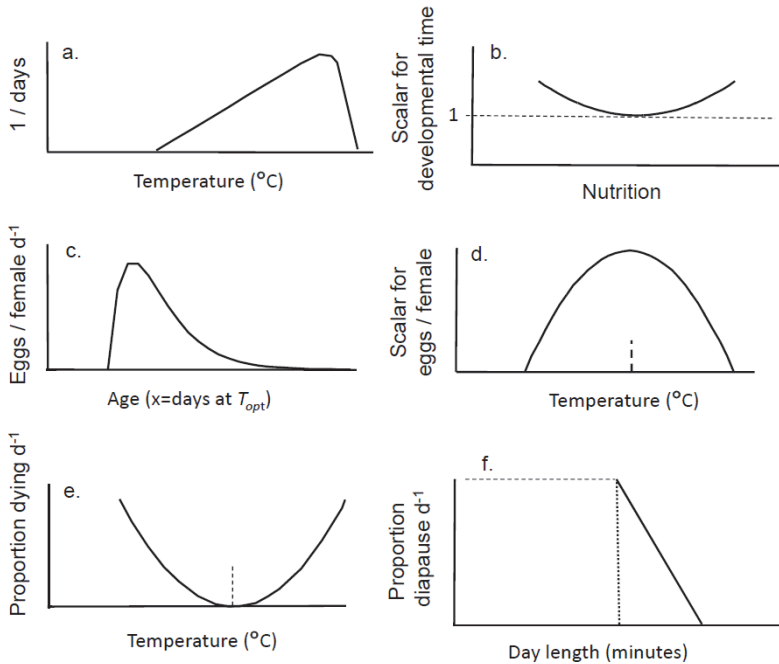


Fig. 1. PBDM sub-models used for all species: (a) the rate of development on temperature (modified from Brière et al., 1999); (b) the effects of say nutrition on developmental time (for example, nutrients in plants may negatively affect developmental time both when in shortfall by acting as a limiting 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). Modified from Gutierrez & Ponti (2013b).

The model is per capita and can be scaled to the individual, population, area or regional level (Fig. 2; Gutierrez et al., 2010). Resource acquisition (i.e. the supply, S) is a search process driven by organism demand (i.e. the sum of all allocations sink rates, D) (Gutierrez et al., 1994), while allocation occurs in priority order to egestion, conversion costs, respiration, and reproduction, growth, and reserves (see also de Wit & Goudriaan, 1978). The ratio $0 \leq S/D < 1$ is due to imperfect consumer search, and in the PBDM scales maximal growth rates of spe-

cies in a time-place varying manner. PBDMs may be used to simulate the age-mass structured population dynamics of plant subunits, of pests and of predators/parasitoids, and may be viewed as time-varying life-tables (*sensu* Gilbert et al., 1976). In practice, the effects of temperature on vital rates of plant/herbivore/carnivore species may be simplified and captured by a normalized concave scalar function that approximates the net of *S* corrected for metabolic costs across temperature (see Gutierrez, 1996). Weather to drive the population dynamics may include, as required, daily maximum and minimum temperatures, solar radiation, precipitation, relative humidity, and wind. The weather data may be derived from ground observations, satellite remote sensing, or climate model simulations (e.g., Gutierrez et al., 2005; Ponti et al., 2009b). Simulation results may be mapped at various levels of spatial and temporal resolution using GIS, and the data used in statistical and economic analyses. In our studies we used the open source GIS GRASS (Geographic Resources Analysis Support System; see <http://grass.osgeo.org/>; Fig 2) for both mapping and further GIS (see Neteler et al., 2012) and statistical analysis (via the interface between GRASS and the free software environment for statistical computing and graphics R; Bivand, 2007).

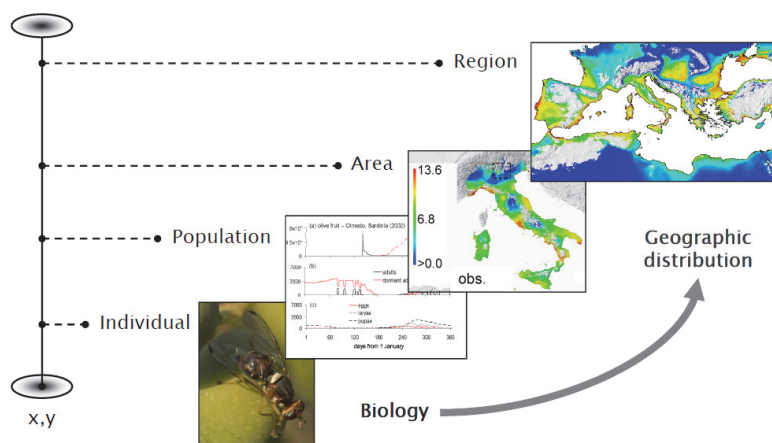


Fig. 2. Levels of PBDMs: individual, population, across ecological zones and across large geographic regions. Letters x,y denote geographic coordinates (longitude and latitude, respectively) used to run PBDMs in a geographic context. Modified from Gutierrez et al. (2010).

3.3. Can ENMs and PBDMs be combined?

Integration of physiological mechanisms and population processes into ENMs has been proposed for climate impact assessments (see Kearney & Porter, 2009). However, the resulting integration is substantially closer to the correlative end of

the process-correlation model continuum (Dormann et al., 2012) and hence should still be considered part of an ENM methodological base. Integration may consist, for example, in superimposing population dynamics layers on correlative approaches (Dullinger et al., 2012). Incorporation of ENMs into PBDMs may be difficult because the two approaches are based on different modeling paradigms (Dormann et al., 2012). Yet good estimate of the native range of a species obtained via ENMs may inform a prospective PBDMs analysis enabling some integration. For example, Kearney & Porter (2009) proposed that mechanistic and correlative models may be combined in three ways: (1) comparing outputs from the two modeling approaches for the same species; (2) using mechanistic models to develop spatial layers for use as additional input to correlative models (see e.g., above reference to Dullinger et al., 2012); and (3) using mechanistic models to define the geographic scope of correlative models, so that for example occurrence records in ephemeral habitats outside of a species' fundamental niche can be identified via mechanistic models and then excluded when developing correlative models. This last item suggests that while factors such as size of the established population, time since establishment, potential lag time, dispersal capability, and isolation of established populations are important for assessing biological invasions, very little information about these factors can be extracted from ENMs because of the lack of explicit population processes inherent in correlative modeling approaches. The low management value of ENMs has been increasingly linked to their inability to provide information on abundance and hence impact of invasive species (Bradley, 2013; Ibáñez et al., 2014).

Below we first review the application of PBDMs to assessing the potential geographic distribution and relative abundance of two fruit flies: Mediterranean fruit fly (medfly) and olive fly in California and Italy (Gutierrez et al., 2008; Gutierrez et al., 2009; Ponti et al., 2009a; Ponti et al., 2009b; Gutierrez & Ponti, 2011, 2013b). Then, using the sub figures in Figure 1 as a guide for assessing the minimum biological information required to formulate a PBDM system, we evaluate the adequacy of the available biological data for developing a PBDM for *T. absoluta* (see Fig. A2 in Gutierrez & Ponti 2013b).

4. Review of PBDMs for medfly and olive fly

The dynamics of the flies are strongly linked to host availability and they do not have a diapause stage, but rather adults females become reproductively quiescent when temperatures are high and/or host fruit populations are scarce. This biology suggests that modeling the plant is necessary for predicting the dynamics of the pests. Furthermore, physical factors have important limiting effects on the host plants and the flies, and are important determinants of their distribution. Sufficient data were available in the literature to parameterize the sub models (Fig. 1) for the two fruit flies

For medfly, the PBDM predicts a restricted distribution of the fly in the USA (potentially near coastal southern California), the wider distribution in Italy, and the infestation of tropical areas of southern Mexico and into Central America (Gutierrez & Ponti, 2011, 2013b). The area predicted for the USA for medfly is considerably smaller than assumed by eradication agencies (Gutierrez & Ponti, 2013b). The PBDM for olive fly predicted the wide distribution of the fly in Italy-Sardinia including microclimate areas south of the colder areas of Garda and Como lakes, and the restriction of the pest by high temperatures in desert areas of California (Gutierrez et al., 2008; Gutierrez et al., 2009; Ponti et al., 2009a; Ponti et al., 2009b; Gutierrez & Ponti, 2013b). The distribution and relative abundance of olive fly across the diverse region of the Mediterranean Basin was also estimated (including the effects of soil water availability; Ponti et al., 2013), with the estimated economic costs of climate change projected for the various sub regions of the Basin (Ponti et al., 2014). The latter study linked crop growth/development and fly dynamics as driven by weather under baseline and warming climate estimated using climate models (see Dell'Aquila et al., 2012). The results showed that there will be economic winners (northward expansion of favorability) and losers (losses in yield in hotter areas) in olive production as a result of climate change. The rich biology that can be embedded in PBDMs for these species enables predictions of not only climate change effects (+,-) on pest distribution and abundance, but also the resulting effects on control costs and profits via changes in pest damage, as well as the associated changes in quality of the olive crop that is mostly used for olive oil production.

A crucial step of practical relevance when developing policy for the management and/or eradication of invasive species is estimating their potential for establishment of measureable self-sustaining population over a period of time corresponding to multiple generations (Blackburn et al., 2011). Medfly, for example, was first detected in California in 1975, but persistent measurable populations of the pest have not been found, and yet a large-scale detection/eradication campaign has since been in place in the absence of sound knowledge of the fly's potential invasiveness and geographic distribution. 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). More recently, an analysis of detection records of fruit flies in California (Papadopoulos et al., 2013) attempted to show the establishment in California of "ultra-low, cryptic" medfly populations below measureable levels, and extended the same methods and assumptions to 17 tropical fruit flies detected in California during 1950-2012 concluding that at least five species including medfly and olive fly are established in the state. However, Papadopoulos et al. (2013) failed to explain why the polyphagous medfly did not develop measureable continuous populations despite more than 35 years of multiple introductions and large numbers of detections, and why in sharp contrast the olive fly quickly spread widely in California (Gutierrez et al., 2014). Papadopoulos et al. (2013) made the simplistic assumption that California is a "fruit-fly-friendly region". To answer such para-

doxes, a mechanistic description of a species' niche for estimating its potential for establishment and population growth in time and place under current and climate change scenarios is required. PBDM analyses of medfly and olive fly provided biological explanations for the lack of persistent measurable population of medfly in California, and for the wide distribution of olive fly in the state (Gutierrez et al., 2014). The contrast between the two species is easily explained using PBDMs. Costs for the eradication program for medfly in California are in excess of 450 million US dollars (Gutierrez & Ponti, 2013b), this despite the fact that much of the state is outside medfly's thermal envelope (Gutierrez & Ponti, 2011).

In general, assessing the regional pest status of a species, be it native or invasive, is the cornerstone of integrated pest management (IPM) as well as of any regional plan to control a species (Kogan, 1998), and should be a prerequisite for establishing a plan for regional control. This important capacity when performed in a GIS context provides the basis for science-based assessment of regional eradication/management programs. Several examples illustrate the utility of PBDMs for appropriate regional management of invasive species. For pink bollworm (PBW, *Pectinophora gossypiella*), a major pest of cotton worldwide that invaded southern Arizona and California about 50 years ago, a PBDM analysis suggested that the ongoing eradication program to keep it from establishing in the Central Valley of California was not needed as the region is already outside the range of year-round persistence of the pest under current climate (Gutierrez et al., 2006). The analysis also suggested that PBW would become a serious economic pest in the Central Valley due to climate warming because the expected increase in average temperatures would greatly enhance winter survival of the pest there (Gutierrez et al., 2006). Were this to occur, the PBDM for cotton/PBW could be used in a GIS context to compare IPM options including the efficacy of short season and transgenic insecticidal cottons – a capacity that is already present in the model.

Another example is that of light brown apple moth (LBAM, *Epiphyas postvittana*). Native to Australia, LBAM was first found in California in 2006 and has thereafter spread to coastal areas of the state causing no economic damage despite its broad host range. In 2007, a controversial eradication program including aerial sprays was begun over urban and suburban areas to eradicate LBAM based on its predicted wide geographic range (including much of Arizona and California and the southern half of the US) and consequent economic losses estimated by the United States Department of Agriculture (USDA; see Fowler et al. 2009). A PBDM developed for LBAM yielded predictions that differed markedly from those made by USDA, and showed that the potential distribution of LBAM in California is, as observed, largely restricted to near coastal areas (Gutierrez et al., 2010). The LBAM eradication program has since been switched to regional containment and quarantine programs (see Gutierrez & Ponti, 2013). In 2009, the polyphagous European grapevine moth (*Lobesia botrana*), the principal native pest of grape berries in the Palearctic region, was found in the major American grape growing region of Napa County, California where it is subject to an ongo-

ing eradication program. A PBDM for *Lobesia* predicts that the species can infest all of the major agricultural areas of the state of California (Gutierrez et al., 2012) and wide areas of the United States and Mexico (Gutierrez & Ponti, 2013). Hence, if eradication fails, *Lobesia* will have to be managed given its high pest status, and the PBDM was used prospectively to analyze the timing of mating disruption pheromone for control of the moth. The PBDM analysis shows that the greatest benefit would accrue by targeting adults emerging from winter diapause pupae and the flight of first summer adults, and that climate warming would not alter this control strategy (Gutierrez et al., 2012).

5. A PBDM for *T. absoluta*

The oligophagous leafminer *T. absoluta* and its primary tomato host are native to South America. The pest also develops on other solanaceous crops such as potato and eggplant (Desneux et al., 2010; Caparros Megido et al., 2013). *T. absoluta* was identified as a potentially serious problem for the Mediterranean tomato industry before it invaded the region (EPPO, 2005). The first Mediterranean record is from Spain in 2006 (Urbaneja et al., 2007), and two years later the leafminer was found in Italy (Tropea Garzia et al., 2009; Viggiani et al., 2009). Population genetics studies suggest that a single genetically-uniform invasive population spread in the Mediterranean Basin (Cifuentes et al., 2011), but this finding is controversial and the invasion pathways are unresolved (Desneux et al., 2011). Invasion of the Mediterranean basin was rapid with *Tuta* spreading about 4,000 km in five years (Desneux et al., 2010; Tropea Garzia et al., 2012), and has now become a major threat to tomato production (Desneux et al., 2011) in Europe, Africa, and Asia. Its range extends North-South from green house in The Netherlands to field in Sudan, Ethiopia and Senegal (see Pfeiffer et al., 2013), and West-East from Portugal to Iran (Tropea Garzia et al., 2012). The invasion history of *T. absoluta* suggests it is able to spread and rapidly colonize new areas without human mediation, and further it is unlikely that current management/quarantine programs will slow or prevent further spread (Desneux et al., 2011). Projecting prospectively the potential distribution and abundance of *T. absoluta* as affected by current weather and climate change using a PBDM would provide important background information for evaluating regional management strategies (see above for other invasive species).

Desneux et al. (2010) used the ENM CLIMEX to project the potential distribution of *T. absoluta* in the Mediterranean Basin, and found that the projections underestimated its observed distribution. Summer warming was particularly intense during the first two years of *T. absoluta* invasion of the Basin (i.e., 2006 and 2007; see Fig. 3), and may in part explain why CLIMEX underestimated climatic suitability for the pest in the region (see Desneux et al., 2010).

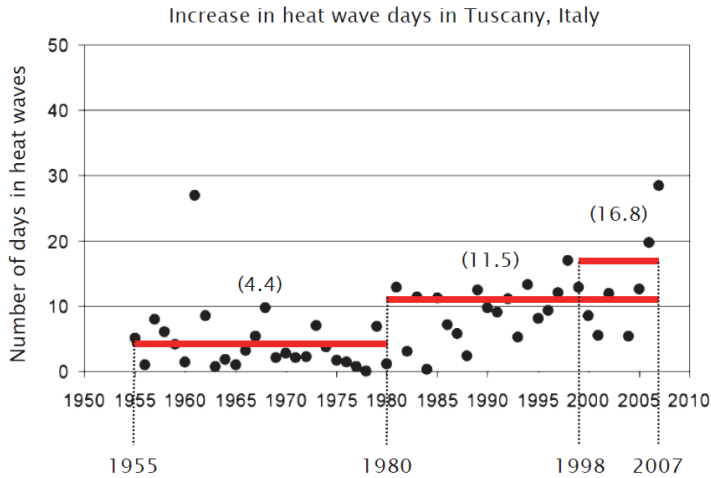


Fig. 3. Mean annual count of Warm Spell Duration Index (WSDI; count of days with at least six consecutive days when maximum temperature exceeds the 90th percentile) during the period 1955-2007. Red horizontal lines spanning 1955-1980, 1981-2007, and 1998-2007 indicate average values for respective periods (numeric values in parentheses). Modified from Bartolini et al. (2012).

6. Biological data on *T. absoluta* relevant to PBDM development

A well parameterized PBDM for *Tuta* could be used to perform a regional level analysis with the goal of developing the components of an ecologically-based management program for the pest. Here we evaluate the available data for *T. absoluta*.

Mechanistic models for tomato growth and development that include dry matter assimilation and partitioning are reported in the literature (Wilson et al., 1987; Heuvelink, 1999), and could be modified for inclusion in our PBDM system. The field and laboratory data on the developmental biology of *T. absoluta* was reviewed by Desneux et al. (2010), Tropea Garzia et al. (2012), and Sannino and Espinosa (2010). In summary, the pest is multivoltine and has a high reproductive rate (Tropea Garzia et al., 2012). Barrientos et al. (1998) reported developmental time and survival of the fly at 14.0, 19.7 and 21.1°C, and estimated the lower thermal threshold for the various life stages. In degree-days (*dd*), approximately 103.8 *dd* above 6.9 °C are required for eggs development, 238.5 *dd* above 7.6 °C for larvae, 117.3 *dd* above 9.2 °C for pupae. Studies by Cuthbertson et al. (2013) had similar data gaps at high and low temperatures. Pereyra and Sánchez (2006) estimated the age-specific survivorship and fecundity, net reproductive rate, and intrinsic rate of increase at 25 °C on both for tomato and potato. Medeiros et al.

(2009b) estimated age-specific survivorship at 25 °C on tomato plants grown in conventional vs. organic greenhouse systems.

Laboratory studies by Sannino and Espinosa (2010) show that adults can live up to six weeks at 15 °C but only a few days (4-5) at 35 °C.; the preoviposition period is about two days, with eggs laid singly or in batches of 2-5, and total fecundity varies considerably (40-262 eggs per female). Sannino and Espinosa (2010) also monitored *T. absoluta* field populations year-round in southern Italy, and estimated the duration of life stages in physiological time units (*dd*).

Using Figure 1 as a guide, the data for developmental rates (Fig. 1a), fecundity (Fig. 1d; one single point for 132.78 eggs per female at 25 °C is provided by Perreyra and Sánchez, 2006, and hence not shown) and mortality (Fig. 1e) on temperature are at best incomplete (Figure 4). The data are insufficient to estimate the limiting effects of temperature extremes, and hence to predict the geographic range and relative abundance over the vast invasive range of *T. absoluta* (see below). Specifically, data on the upper thermal threshold and on diapause are missing and are important for determining the invasiveness of the species.

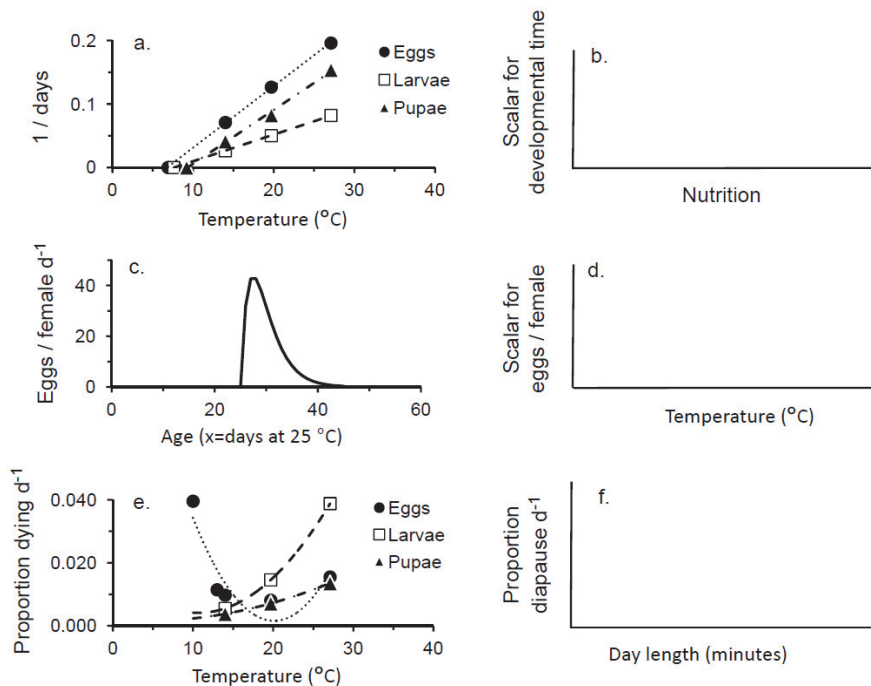


Fig. 4. Knowledge gaps in *T. absoluta* biology that prevent development of a PBDM: only sub-models for developmental times (a) and mortality (e) can be partially parametrized. See Fig. 1 for comparison.

In warmer Mediterranean climates, *Tuta* adults are found throughout the year (Vercher et al., 2010). Field observations show that *Tuta* continues development as host availability and weather allow with up to 12 generations occurring in the warmer areas of its range (Desneux et al., 2010). The species appears to lack a diapause stage, and yet Sannino and Espinosa (2010) report that overwintering pupae take 65.1 days on average to complete development in fall and winter: only one third of the pupae formed in the first half of November develop to adults by the first half of December (i.e., an average of 17.9 days for development), while the remaining pupae (i.e., overwintering pupae) emerge the following January and February. What causes the delayed development in some individuals is unknown, but it could simply be that temperatures are below the threshold for development. In another gelechiid species, the peach twig borer *Anarsia lineatella* (Zeller) (Fam. Gelechiidae), chilling is required by diapause larvae before they complete diapause development in late January-early February (Damos & Savopoulou-Soultani, 2010). Biological and behavioral characteristics such as oviposition preferences and the number and duration of instars are important and must be estimated in developing a PBDM for *T. absoluta* (see EPPO, 2005; Sannino & Espinosa, 2010). While the available data are insufficient, we have identified the data gaps providing guidelines for targeted future research. Considerable progress has been made in the development of control strategies and tactics that in concert with PBDM analysis could provide the basis for the management of this pest.

7. Management options for *T. absoluta*

Management of *T. absoluta* must be holistic with the capacity to predict the season dynamics being a key component in developing IPM practices to manage this invasive pest (Lewis et al., 1997; Kogan, 1998; Ehler, 2006; Tomich et al., 2011). First and foremost, ecologically-based pest management (IPM/agroecology) should foster pest control methods with low dependence on external inputs (Smith & van den Bosch, 1967). Tactics to achieve control include habitat management above-ground (i.e., crop diversification; see Landis et al., 2000) and below-ground (i.e., organic soil enhancement; see Altieri & Nicholls, 2003) and their synergistic interactions, as well as biological control (Huffaker, 1971; van den Bosch & Messenger, 1973), host plant resistance (HPR; Kogan, 1994), mating disruption (Witzgall et al., 2010), and other methods, with chemical control being the option of last resort. We start our review of management practices with the current status of resistance to insecticides in *T. absoluta*.

7.1. Chemical insecticides

Resistance in *T. absoluta* to a wide range of insecticides occurs in South America (Lietti et al., 2005; Silva et al., 2011; Guedes & Siqueira, 2013), with the rapid development of insecticide resistance being of major concern (Cifuentes et al., 2011). In the Mediterranean, populations of this pest have a narrow genetic basis and high levels of insecticide resistance exists (Cifuentes et al., 2011). A high frequency of mutations associated with pyrethroid resistance in *T. absoluta* populations occurs across much of its range, and further supports the hypothesis that insecticide resistance facilitated the rapid invasion of new areas (Haddi et al., 2012). Resistance to organosphosphates, insect growth regulators, spinosad and other insecticides has also been reported (see Guedes & Picanço, 2012; Gontijo et al., 2013). allowing *T. absoluta* to be substantially unconstrained by insecticide-based quarantine measures (Desneux et al., 2011). In addition, the use of pesticides compromises natural enemies further rendering IPM programs on tomato ineffective (e.g., Arnó & Gabarra, 2011; Biondi et al., 2012a; Biondi et al., 2012b; Biondi, 2013). This suggests that insecticides are unlikely to be viable components of management programs for *T. absoluta* in the Mediterranean Basin.

7.2. Habitat management in the native range

Evidence from South America suggests that habitat management is a viable option for regulating *T. absoluta* in tomato. In a field experiment conducted at Embrapa Hortaliças (Brasília, Brazil), Medeiros et al. (2009a) used a randomized block design to compare organically vs. conventionally grown tomato with three levels of crop diversification: tomato monoculture and tomato intercropped with either coriander (*Coriandrum sativum*, Apiaceae) or gallant soldier (*Galinsoga parviflora*, Asteraceae). They observed greater abundance and diversity of predators and reduced density of *T. absoluta* larvae in organic compared to conventional tomato crops (see Drinkwater et al., 1995; Letourneau & Goldstein, 2001). Further intercropping tomato with coriander and gallant soldier had an additional positive effect by impairing host location and providing food sources for natural enemies (Medeiros et al., 2009a). In another experiment, Medeiros et al. (2011) showed higher mortality of *T. absoluta* eggs by parasitoids and generalist predators in organic than in conventional tomato crops (cf. Ponti et al., 2007). However, organic cropping treatments were established in an area with higher vegetation diversity of a nearby riparian forest, polycultures, crop rotations, green manures, hedgerows, and uncultivated areas with spontaneous vegetation that may have influenced both pests and their natural enemies (see Andow, 1991). Medeiros et al. (2009b) conducted an experiment at the same location but in semi-controlled greenhouse conditions where they compared oviposition and mortality of *T. absoluta* on tomato plants potted in soil taken from either organic

or conventional farming systems. Tomato plants were artificially infested and then transferred after 24 hours to another greenhouse to track the fate of cohorts of eggs daily until all individuals completed life cycle or died (Medeiros et al., 2009b). *T. absoluta* oviposition on tomato plants grown in soil from conventional agriculture was twice that on plants grown in soil from organic agriculture (cf. Phelan et al., 1995), suggesting that there was a link between organic soil fertility and the reduced oviposition rates (Medeiros et al., 2009b).

Habitat manipulation has also shown potential for *T. absoluta* management in its invasive range. For example, in a greenhouse cage experiment conducted at Biobest N.V. (Westerlo, Belgium), Balzan and Wäckers (2013) found that floral resources provided by *Lobularia maritima* (Brassicaceae) and *Fagopyrum esculentum* (Polygonaceae) enhanced the efficacy of the indigenous parasitoid *Necremnus arytynes* (Hymenoptera: Eulophidae), an important biological control agent of *T. absoluta* in the Mediterranean region (Desneux et al., 2010; Urbaneja et al., 2012; see section on biological control). Even though *N. arytynes* is the most abundant native parasitoid recovered on *T. absoluta* in Southern Italy and the only species able to build up in tomato greenhouses, relatively low parasitization rates occur in the field (Zappalà et al., 2012a). Hence, improving floral resources to enhance the action of the parasitoid may be an important component in conservation biological control, if the conventional disruptive chemical and mechanical practices are to be replaced (Balzan & Moonen, 2012; Balzan & Wäckers, 2013).

7.3. Natural, classical, and augmentative biological control in invaded areas

Natural control of *T. absoluta* in its native range is not well understood, and would hinder selection of candidate biocontrol agents for introduction into invaded areas (Desneux et al., 2010). Classical biological control would provide a long-term sustainable management of *T. absoluta*. Some caution that the introduction of exotic natural enemies may have unintended effects on non target organisms, but this must be weighed against prospective benefits (see Messing & Wright, 2006; Desneux et al., 2010).

The rich biodiversity found in the Mediterranean region has resulted in efficacious new associations of natural enemies on invasive species (Nicoli & Burgio, 1997; see also Moonen & Bärberi, 2008). Several native predators and parasitoids attack *T. absoluta* in the Mediterranean Basin (natural control), and have probably contributed to the observed decline in pest severity 2-3 years post invasion (Tropea Garzia et al., 2012; Urbaneja et al., 2012; see Zappalà et al., 2013 for a comprehensive review of indigenous natural enemies in the invasive range). Based on a field survey of native parasitoids recruited to *T. absoluta* in southern Italy, Zappalà et al. (2012a) highlight the need to conserve indigenous natural enemies (e.g., via habitat management) as part of an IPM strategy. In a similar

study carried out in the Mediterranean coast of Spain, Gabarra et al. (2013) concluded that non crop habitats may be a source of native larval/pupal parasitoids of *T. absoluta* that may complement current biological control programs based on egg predators. A review of experiments and the extensive literature review show that native agents in Europe contribute to the control of *T. absoluta* (Biondi, 2013). Studies carried out across a North-South gradient in Italy by Ferracini et al. (2012) show that two indigenous parasitoid species of the genus *Necremnus* are good candidates for mass production and augmentative biological control of this pest.

Other successful augmentative control programs have been implemented for *T. absoluta* using native generalist predators such as *Nesidiocoris tenuis* (Hemiptera: Miridae) that also help control whiteflies in tomato (see Calvo et al., 2012). This finding led to a substantial increase in the proportion of the tomato crop area under augmentative biological control, especially in greenhouses of south-eastern Europe and Morocco (Urbaneja et al., 2012). In Spain, native Mirid predators have been shown to integrate well with applications of the biological insecticide *Bacillus thuringiensis* in the greenhouse (González-Cabrera et al., 2011; Mollá et al., 2011). Zappalà et al. (2012b) further showed that Mirid predators can be used with applications of sulphur, an organic insecticide used in tomato crops that is effective against the moth but relatively non toxic to the Mirids. Working in a multi-tunnel greenhouse in Spain, Calvo et al. (2012) tested early augmentative release of *N. tenuis* in tomato transplant trays five days before planting followed by three weekly releases after transplanting, and concluded that this tactic may provide successful biological control of both *T. absoluta* and the whitefly *Bemisia tabaci* without additional input. In Spain, Cabello et al. (2012) carried out a greenhouse experiment where *N. tenuis* was released right before tomato transplanting, and then the crop was artificially infested with *T. absoluta* three weeks later, with release of two parasitoid species (*Trichogramma urquijoi* and *T. achaeae*) occurring each in an isolated compartment of the greenhouse four weeks after transplant. Starting five weeks after transplant, seven weekly samples were taken on tomato leaves, and the model for antagonistic interactions among parasitoids by Mills (2006) was used to explore the resulting experimental data with the goal of understanding interspecific competition among natural enemies released in the experiment. Model simulations indicated that *T. achaeae* was more effective than *T. urquijoi* in controlling *T. absoluta*, and that intraguild competition occurred between *N. tenuis* and the two parasitoid species (Cabello et al., 2012). Calvo et al. (2012) found that at high densities of the Mirid, *T. achaeae* had no effect on the pest.

Given these positive findings in Europe, the native natural enemy complex of *T. absoluta*, including predatory Mirids, is being investigated in its native range (Bueno et al., 2012; Luna et al., 2012). Analyses of natural enemy interactions, HPR and other factors, could be incorporated into PBDMs for evaluating the pest on a regional basis (see Gutierrez & Ponti, 2013a). PBDMs can be easily harnessed to evaluate the potential impacts of coevolved natural enemies of *T. abso-*

luta as candidate species for classical biological control of the pest in its invaded range. Gutierrez et al. (1988, 2011), Neuenschwander et al. (1989), and Gutierrez & Ponti (2013a) provide examples of analyses of the impact of introduced natural enemies that may be performed prospectively for candidate biological control agents given the requisite biological knowledge about the species illustrated above for *T. absoluta*.

7.4. Host plant resistance

Adding HPR in tomato would provide plant bottom-up effects that would augment top-down regulation by natural enemies, and increase the likelihood of regulating pest populations at non economic low levels in an ecologically sound manner. Although commercial tomato hybrids resistant to *T. absoluta* are thought to be easily developed (Maluf et al., 2010b), implementation of HPR in tomato is still not fully utilized. In Brazil, tomato breeding programs have shown that it is possible to introgress resistance from wild taxa of tomato-related *Solanum* spp. into commercial cultivars. This enables tomato to produce allelochemicals such as acylsugars that confer resistance to a broad range of pests including whiteflies, aphids, spider mites, as well as *T. absoluta* and other lepidopteran pests (Maluf et al., 2010a; Maluf et al., 2010b; Oliveira et al., 2012). An explanation for the wide susceptibility of current cultivars to pathogens and pests was provided by Oliveira et al. (2012) who posited that tomato genes related to pest and disease resistance were lost during domestication. HPR would also lessen the development of resistance to insecticides in *T. absoluta* and associated environmental impacts.

7.5. Mating disruption

Pheromone-mediated mating disruption is emerging as an important component of management programs for major insect pests (Witzgall et al., 2010). Early in the invasion of *T. absoluta*, the exceptionally rapid spread and lack of efficient chemical and biological control methods, spurred the development and early implementation of monitoring lures for mass trapping (Witzgall et al., 2010) and later for mating disruption technique. In southwestern Sardinia (Italy), Cocco et al. (2012) showed that mating disruption is an efficient strategy to control *T. absoluta* in greenhouse tomato crops where immigration of mated females into the population is prevented (Vacas et al., 2011). Undermining mating disruption, mass trapping of males, and the sterile insect technique (SIT, see next section) is the discovery that asexual reproduction occurs in *T. absoluta* in the laboratory (Caparros Megido et al., 2012). Asexual reproduction would also increase the spread of insecticide-resistant genotypes (Gontijo et al., 2013).

7.6. Sterile insect technique

Though SIT is normally used in eradication efforts, SIT is being considered as a prospective mean of control of *T. absoluta* (Cagnotti et al., 2012), but no information is available on its potential effectiveness. Likely SIT is not a viable option because of the potential for asexual reproduction, the wide geographic range of the pest, multiplicity of hosts, its apparent high vagility and the high costs of such a program.

8. Conclusions

Recent warming in the Mediterranean Basin (Bartolini et al., 2012) is consistent with climate change projections for the region (Barkhordarian et al., 2011; Diffenbaugh & Giorgi, 2012; Gualdi et al., 2013), and has likely facilitated the establishment and spread of invasive species (Robinet & Roques, 2010) including *T. absoluta*. High vagility and propensity for resistance to insecticides enhanced *T. absoluta* rapid invasion of the Mediterranean Basin (Cifuentes et al., 2011). The invasion of the pest was substantially unconstrained by quarantine measures that relied primarily on insecticides (Desneux et al., 2011). This species is likely to become a major global pest of tomato due to wide spread resistance to insecticides, and will have to be managed using ecologically-based approaches over its large geographic range (Guedes & Siqueira, 2013). The capacity to predict the potential geographic distribution and relative abundance (i.e., the invasiveness) of *T. absoluta* is pivotal to developing sound policy for managing this (or other) invasive species (Gutierrez et al., 2011). PBDMs are physiologically-based weather-driven geospatial modeling tools that could be harnessed to gauge accurately the invasiveness of *T. absoluta*. PBDMs circumvent many of the deficiencies of mainstream assessment methods that are based on essentially correlative, climate envelope assumptions. PBDM analysis would enable capturing the complexity of tomato agroecosystems and enable an interdisciplinary synthesis for holistic management of *T. absoluta*. In a future scenario dominated by climate change and escalating costs of external inputs, PBDM methods would enable addressing the ecological root causes of the *T. absoluta* problem more efficiently (see Altieri, 2012), and serve to increase system stability and resilience across the varied agro-ecological landscape where tomato and other solanaceous crops are grown.

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