

HOLISTIC MANAGEMENT OF INVASIVE SPECIES: THE CASE STUDY OF *TUTA ABSOLUTA* (MEYRICK) (LEPIDOPTERA, GELECHIIDAE)

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Holistic management of invasive species: the case study of Tuta absoluta (Meyrick) (Lepidoptera, Gelechiidae)

The Mediterranean Basin is a climate change and biological invasion hotspot of global relevance where recent warming has likely facilitated the establishment and spread of invasive species. Projecting the potential geographic distribution and relative abundance of species that invade the Basin is pivotal to developing sound policy for their management, and the need for this capacity has increased dramatically in the region. The tomato borer *Tuta absoluta* (Meyrick) recently invaded the Mediterranean Basin from South America and threatens to become a major global pest of tomato. Here the available biological data relevant to the development of a physiologically-based demographic model (PBDM) for *T. absoluta* are summarized, and the components of a prospective ecologically-based management program for the pest are reviewed to lay the ground for assessing the relative importance of the different components at a regional level. We propose that the PBDM approach can be used in a GIS context to develop and implement a holistic analysis of this pest. The complex interactions that underpin scientifically-sound management of invasive species including *T. absoluta* can be captured quantitatively, and the resulting interdisciplinary synthesis can then be used within the conceptual framework of agroecology to help design ecologically-based pest management strategies suited to specific resource and socioeconomic realities.

KEY WORDS: physiologically-based weather-driven demographic models, geographic information systems (GIS), climate change effects, ecologically-based pest management, holistic analysis.

THE MEDITERRANEAN BASIN AS A GLOBAL HOTSPOT FOR BIOLOGICAL INVASION

The Mediterranean Basin is a biodiversity (MYERS *et al.*, 2000) and climate change hotspot (GIORGI, 2006) that is also challenged by biological invasions of exotic species (DRAKE & LODGE, 2004; TATEM, 2009). The area's status as a climate change hotspot is based on a consensus of 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). The Mediterranean Basin and other areas of Europe are at increased risk of exotic species introduction (e.g., pests) because of the high density of airports with high-volume incoming traffic from many regions with similar climates. This combination of factors is anticipated to increase invasive species establishment (TATEM, 2009). In Europe, approaches to pest risk analysis usually follow a

conventional paradigm that involves assessing probability of introduction, probability of establishment, potential economic impact, and options to prevent establishment/economic impact (GIOLLI & BAUMGÄRTNER, 2009; VAN DER STRATEN *et al.*, 2011).

The recent arrival and establishment of several tropical insect species illustrates how the recent warming observed in the Basin is likely to facilitate the establishment and spread of invasive alien species (ROBINET & ROQUES, 2010). Climate mismatches would appear to be the only natural barrier still effective against the global spread of invasive species, as major geographical barriers have been made mostly ineffective by global air and other kinds of commercial traffic (TATEM & HAY, 2007; TATEM, 2009). Invasive species may be of any taxa and cause yearly an estimated trillion US dollars worldwide damage (OERKE & DEHNE, 2004). This figure is nearly an order of magnitude higher than losses to natural disasters (see RICCIARDI *et al.*,

2011). The accidental introductions of exotic insects has resulted in a high number of established species with considerable negative economic impact (PYŠEK *et al.*, 2008). Plants are another major group of invasive organisms, but their introduction has mostly been intentional (PIMENTEL *et al.*, 2005). About one-third of insect pests are alien species (WARD & MASTERS, 2007), whose potential geographic distribution and relative abundance (i.e., measures of invasiveness) are mostly poorly understood, even after costly and long-standing management/eradication programs (GUTIERREZ & PONTI, in press).

The field of agroecology (ALTIERI, 1995; ALTIERI *et al.*, 2003) is a holistic vision of the study and implementation of the agricultural sustainability problem, but the gap between this concept and our capacity to analyze agroecosystems is large. Holistic analyses are often advocated (ZAVALETA *et al.*, 2001; HULME, 2006; SUTHERST & BOURNE, 2009; GILMAN *et al.*, 2010), but rarely implemented – there are simply too many factors, and the best we can currently do is to examine sub sets of the agroecosystem. But even this requires projecting regionally the population dynamics of the sub system as driven by weather and constrained by interactions with other species and all elements of the abiotic environment (GUTIERREZ, 1996). Focusing on invasive species, key issues include predicting their potential distribution and relative abundance, the effects of natural enemies, and assessment of available control methods, with the effects of future climate change being an additional layer of complexity.

In this paper, we summarize available biological data relevant to the development of a physiologically-based demographic model (PBDM) for *Tuta absoluta* (Meyrick) (Lepidoptera, Gelechiidae), and review the components of a prospective ecologically-based management program for the pest to lay the ground for assessing the relative importance of the different components at a regional level. The PBDM approach circumvents long-standing shortcomings of mainstream approaches commonly used to assess exotic species invasiveness, and when used in a holistic interdisciplinary framework may help increase system sustainability and resilience in the face of social, cultural, economic and pending climate change.

PREDICTING THE GEOGRAPHIC DISTRIBUTION AND RELATIVE ABUNDANCE OF PEST SPECIES

Pivotal to developing sound policy for eradication, or control and management of invasive species is the capacity to predict their potential geographic

distribution and relative abundance (i.e., their invasiveness) under current and climate change scenarios (GUTIERREZ *et al.*, 2011). Climate is a highly 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 TYLIANAKIS *et al.*, 2008). Common methods used to predict the geographic distribution of invasive species fall under the ambit of *climate envelope* approaches (i.e., ecological niche models; ENMs hereafter). Distribution records of the species are used to develop ENMs for assessing the species' potential geographic distribution by characterizing climatically the ecological niche of the species. ENMs may be statistical (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 & LEATHWICK (2009). 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 is maintained in both space and time (BEAUMONT *et al.*, 2009). However, because of the correlative nature of ENMs, a number of problems may occur (see also Fig. 1): the difficulty of 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 is often used that miss important short-term weather effects (see Fig. 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). These shortcomings were recognized by the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR4) summarized as including the “inability to account for species interactions, lack of a physiological mechanism, and inability to account for population processes” (FISCHLIN *et al.*, 2007) (Fig. 1).

However, while ENMs are often good at fitting current ranges of species, they are not as good at projecting range shifts due to climate change or the

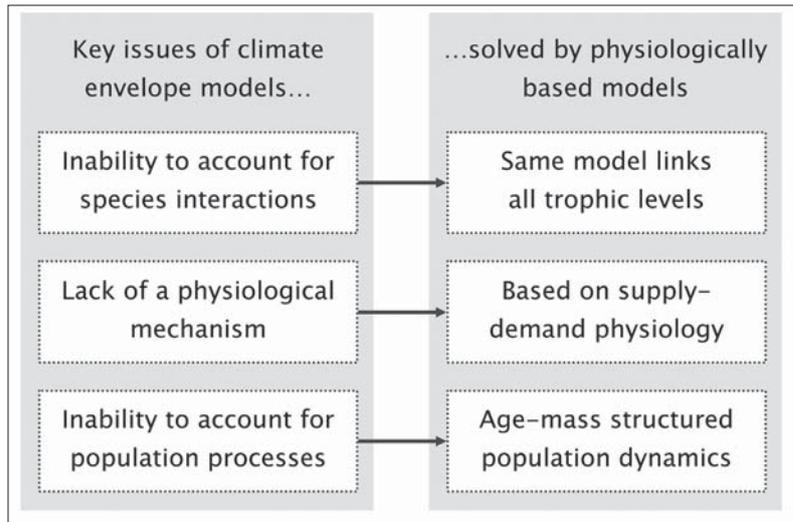


Fig. 1
 Limitations of climate envelope models that were acknowledged in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change and how these limitations are addressed by physiologically-based demographic models.

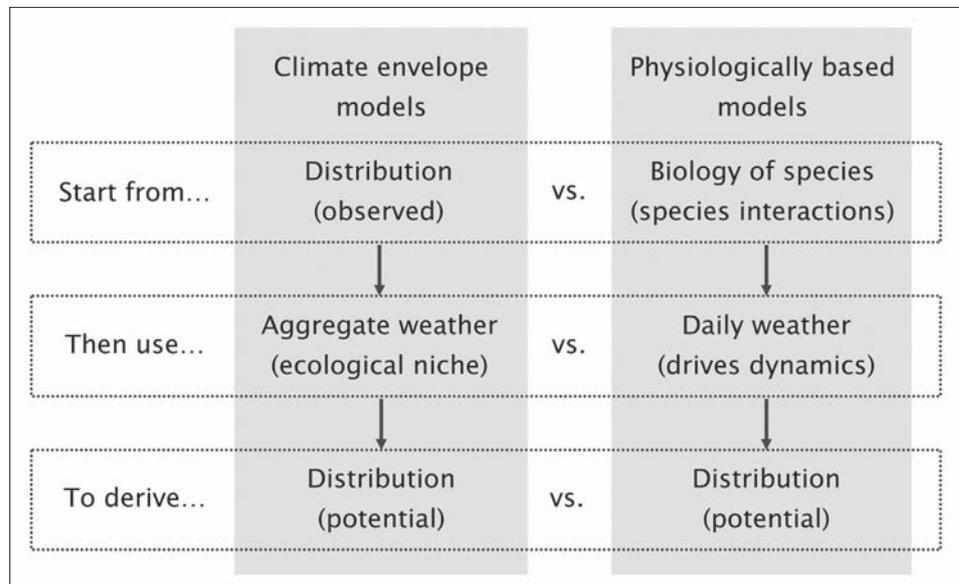


Fig. 2
 Comparison of the climate envelope approach and the physiologically-based demographic modeling approach.

spread of invaders (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 available methods for estimating the ecological niche (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).

PBDMs address these shortcomings by explicitly capturing the mechanistic weather-driven biology of the species and of relevant interacting species in its food chain or web. (The physiological basis of the approach has early roots in the work of DE WIT & GOUDRIAAN, 1978.) Instead of beginning with the assumed native range of an invasive species, PBDMs model the biology of the target species and other species in the same food chain or web (i.e., the system) (Fig. 2), and when the

model is driven by weather predict the phenology, dynamics and distribution of the interacting species across wide geographic areas independent of distribution records (GUTIERREZ *et al.*, 2008; GUTIERREZ & PONTI, in press) (Fig. 1). PBDMs of herbivores may include bottom-up effects of plant growth and development and in some cases the top-down action of natural enemies (see GUTIERREZ & BAUMGÄRTNER, 1984; GUTIERREZ *et al.*, 1994). Because the biology is modeled, the PBDM system can easily deal with the effects of climate change on the species.

The underlying idea of PBDMs is that all organisms are consumers and have similar resource acquisition (inputs) and allocation (outputs) priorities (GUTIERREZ, 1996) (Fig. 3), and the dynamics of all species can be captured using the same resource acquisition and same shape birth-death rates sub-models imbedded in an age-mass struc-

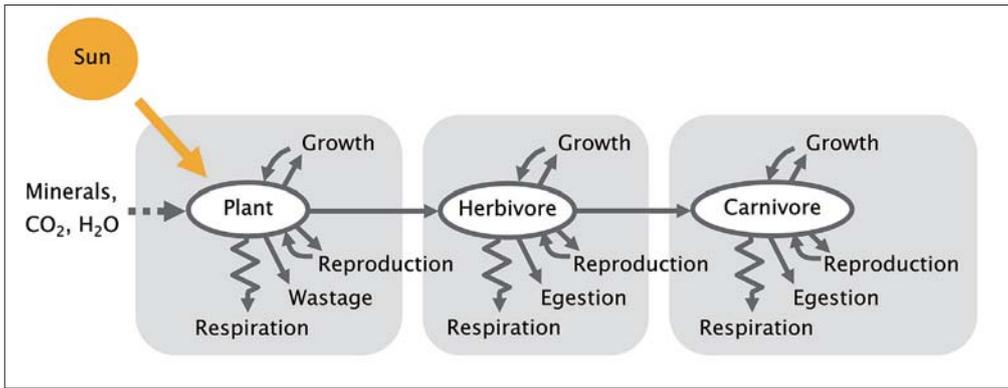


Fig. 3

All organisms show a common pattern of energy acquisition (supply) and allocation (demand) that allows to use the same model to describe the biology of the species in all trophic levels including the economic one (see GUTIERREZ, 1996).

tured population model that capture sub processes such as developmental rates on temperature, age-specific fecundity and mortality as modified by temperature and other factors, diapause and the interaction with resource species and with natural enemies (GUTIERREZ, 1996). The model can be scaled to the individual, population, area or regional level (Fig. 4). Resource acquisition (i.e. the supply, S) is a search process driven by organism demand (D), while allocation occurs in priority order to egestion, conversion costs, respiration, and reproduction, growth, and reserves. The ratio $0 \leq S/D < 1$ is due to imperfect consumer search, and in the PBDM scales maximal growth rates of species in a time-place varying manner. PBDMs simulate the age-mass structured population dynamics of plant subunits and of pest and preda-

tor/parasitoid numbers. Weather is used to drive the population dynamics of the interacting species and may include, as required, daily maximum and minimum temperatures, solar radiation, precipitation, relative humidity, and wind, and may be derived from ground observations, satellite remote sensing, or climate model simulations (e.g., GUTIERREZ *et al.*, 2005; PONTI *et al.*, 2009). The results of the PBDM analyses can be mapped using GIS at various levels of spatial and temporal resolution (e.g., using GRASS GIS, <http://grass.osgeo.org/>). Most important, the results of the modeling/GIS analyses can be compared to field data. The main drawback is that the development of PBDM analyses requires a minimum level of biological information. Here we review the adequacy of the available information for *T. absoluta*.

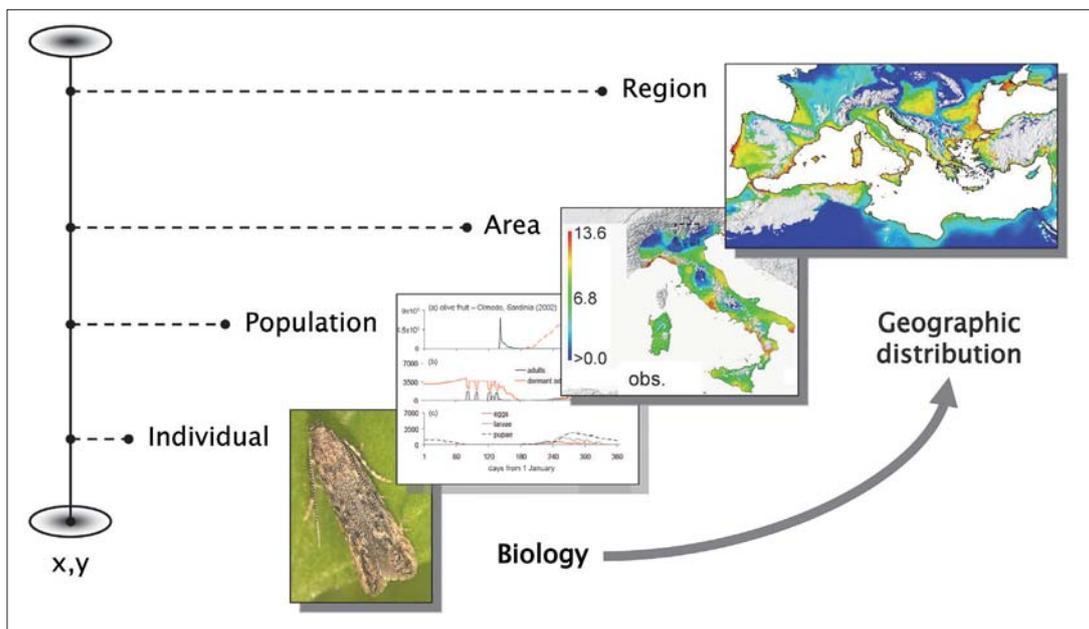


Fig. 4

Levels of physiologically-based models: individual, population, across ecological zones and across large geographic regions (modified from GUTIERREZ *et al.*, 2010).

THE RANGE OF *TUTA ABSOLUTA*

The oligophagous leaf miner *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). This leaf miner was identified as a potentially serious problem for the Mediterranean tomato industry before it invaded the region (EPPO, 2005). The first Mediterranean Basin record is from Spain in 2006 (URBANEJA *et al.*, 2007), and two years later it was also found in Italy (TROPEA GARZIA *et al.*, 2009; VIGGIANI *et al.*, 2009). Population genetics studies suggest that a single genetically-uniform invasive population spread to the Mediterranean Basin (CIFUENTES *et al.*, 2011). Invasion of the Mediterranean Basin was rapid, as *Tuta* traveled about 4,000 km in five years (TROPEA GARZIA *et al.*, 2012) and has now become a major threat to tomato production (DESNEUX *et al.*, 2011) in three continents (Europe, Africa, and Asia). Its range extends North-South from The Netherlands to Sudan, 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 even without human mediation, and hence it is unlikely that current management/quarantine programs will slow or prevent further spread (DESNEUX *et al.*, 2011).

In the Mediterranean Basin, recent climate warming has been concentrated in summer (MARIOTTI & DELL'AQUILA, 2011) especially during the last decade of the twentieth century (BARTOLINI *et al.*, 2012). This recent warming is consistent with climate change projections for the region (BARKHORDARIAN *et al.*, 2011) and stands out from long-term temperature variability spanning the last millennium (GUIOT, 2012; JOËL, 2012). Summer warming was particularly intense in the decade ending with the first two years (2007 and 2008) of recorded invasion of *T. absoluta* in the Basin (decade 1998-2007, Fig. 5), and this may in part explain *T. absoluta* rapid spread.

REVIEW OF *T. ABSOLUTA* BIOLOGY RELEVANT TO PBDM DEVELOPMENT

A mechanistic model for tomato growth and development that includes dry matter assimilation and partitioning is reported in the literature (HEUVELINK, 1999), and may serve as basis for developing a PBDM for the tomato plant to provide the bottom-up dynamics on *T. absoluta*.

T. absoluta is a multivoltine species with high reproductive potential (TROPEA GARZIA *et al.*, 2012). Studies on the moth's development (BARRIENTOS *et al.*, 1998) estimated the lower thermal

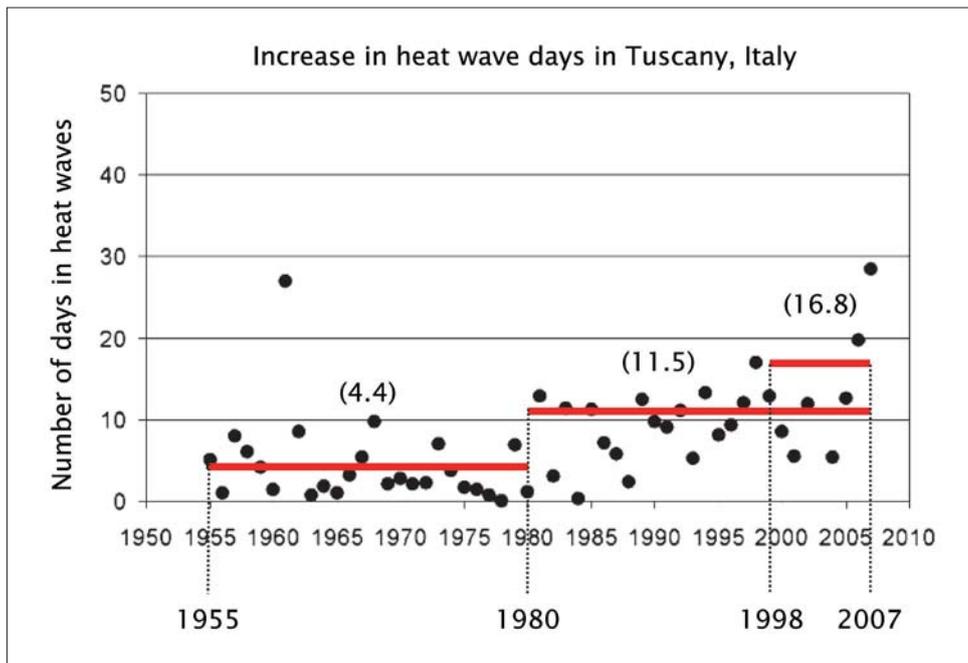


Fig. 5

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) days in 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).

threshold and the duration of the life stages in degree-days (*dd*): eggs (103,8 *dd* above 6.9 °C), larvae (238.5 *dd* above 7.6 °C), and pupae (117.3 *dd* above 9.2 °C). Other data provided by BARRIENTOS *et al.* (1998) could provide information for estimating sub-models for temperature-dependent rate of development (Tab. 1) and for mortality. SANNINO & ESPINOSA (2010) monitored field populations year-round and estimated the duration of life stages in physiological time units (*dd*). These observations may be used as field estimates for inclusion in the developmental rate sub-model. Data from PEREYRA & SÁNCHEZ (2006) on age-specific survivorship and fecundity profiles, net reproductive rate, and intrinsic rate of increase at 25 °C (on both tomato and potato), and data from MEDEIROS *et al.* (2009b) on age-specific survivorship at 25 °C on tomato plants grown in conventional vs. organic systems could be used to develop sub-models for mortality and fecundity.

SANNINO & ESPINOSA (2010) found that adults can live up to six weeks at 15 °C but only a few days (4-5) at 35 °C, information that could help model the effect of temperature on adult longevity. The preoviposition period is about two days with eggs being laid singly or in batches of 2 -5. Total fecundity varies considerably (40-262 eggs per female) in the literature reviewed (SANNINO & ESPINOSA, 2010).

Tuta continues development as food and weather allow (up to 12 generations in the warmer reaches of its native range). It appears not to have a diapause stage, and yet SANNINO & ESPINOSA (2010) at Scafati found that overwintering pupae take 65.1 days on average to complete development with one third of the pupae formed in the first half of November developing to adults by the first half of December (17.9 days on average). The remaining pupae are quiescent during cold months and emerge the following year between January and February. This could indicate that insufficient thermal units accrue or some other factors delay development. For example, termination of diapause in *Anarsia lineatella* (Lepidoptera, Gelechiidae) requires chilling and its larvae complete diapause development in late January-early February

(DAMOS & SAVO-POULOU-SOULTANI, 2010) as occurred for some *Tuta* pupae. This aspect of the biology requires further examination. In Mediterranean climes, adults are found throughout the year (VERCHER *et al.*, 2010).

Other biological and behavioral traits include: adults are nocturnal and usually hide during the day in the canopy; females lay eggs on aerial parts of their host plants, and four larval instars develop; pupation may take place in the soil, on the leaf surface, or within mines (EPPO, 2005; see also SANNINO & ESPINOSA, 2010).

PROSPECTIVE MANAGEMENT OF *T. ABSOLUTA*

An array of management options exist that may be considered as part of a prospective management strategy for *T. absoluta* and include chemical insecticides, habitat management, pheromones, biological control, host plant resistance (HPR) and other methods.

Chemical control

Chemical insecticides use should be considered with care as resistance in *T. absoluta* to common insecticides is widespread in South America (LIETTI *et al.*, 2005; SILVA *et al.*, 2011), and the speed at which insecticide resistance evolved in this species is of major concern (CIFUENTES *et al.*, 2011). The invasive population has been shown to have a narrow genetic basis expressing a high potential for insecticide resistance (CIFUENTES *et al.*, 2011) making it substantially unconstrained by quarantine measures (DESNEUX *et al.*, 2011). Specifically, the high frequency of mutations associated with pyrethroid resistance in *T. absoluta* populations occurs across much of its range and suggests pyrethroids are likely ineffective as means of control, and further supports the hypothesis that insecticide resistance facilitated the rapid expansion of its invasive range (HADDI *et al.*, 2012). Hence, insecticides are unlikely to be viable components of management programs for *T. absoluta* in the Mediterranean Basin.

Table 1 – Summary of data on the thermal biology of *Tuta absoluta* provided by BARRIENTOS *et al.* (1998).

	Average duration in days (Survivorship %)					
	14.0 °C		19.7 °C		27.1 °C	
<i>Eggs</i>	14.1	(86.3)	7.9	(93.6)	5.1	(92.1)
<i>Larvae</i>	38.0	(79.0)	19.9	(71.0)	12.2	(52.7)
<i>Pupae</i>	24.2	(90.8)	12.1	(91.4)	6.5	(91.2)
<i>Total</i>	76.3	(61.9)	39.8	(60.7)	23.8	(44.3)

Non chemical control

First and foremost, ecologically-based pest management should design the agroecosystems to foster pest regulation with low dependence on external inputs (ALTIERI, 1999). Among these options are habitat management above-ground (i.e., crop diversification; see LANDIS *et al.*, 2000; ALTIERI *et al.*, 2003; PONTI *et al.*, 2005; ALTIERI *et al.*, 2009) and below-ground (i.e., organic soil enhancement; see ALTIERI & NICHOLLS, 2003; ALTIERI *et al.*, 2005) and their synergistic interactions (PONTI *et al.*, 2007; ALTIERI *et al.*, 2011) as well as biological and natural control and augmentative releases (VAN DEN BOSCH *et al.*, 1982), HPR (KOGAN, 1994; MALUF *et al.*, 2010b), and mating disruption (WITZGALL *et al.*, 2010).

Habitat management

There is evidence that habitat management is a viable option for regulating *T. absoluta* in tomato cropping systems under Mediterranean conditions. For example, in a comparison of organic vs. conventional tomato agroecosystems in commercial farms in California (USA), DRINKWATER *et al.* (1995) and LETOURNEAU & GOLDSTEIN (2001) could not distinguish between the two production systems based on fruit yields and arthropod pest damage levels, but observed higher levels of associated biodiversity (sensu VANDERMEER & PERFECTO, 1995) of natural enemies that by providing biological control of insect pests would act as a source of biological compensation for the lack of chemical control. Similarly in Brazil, MEDEIROS *et al.* (2009a) observed greater abundance and diversity of predators and reduced density of *T. absoluta* larvae in organic vs. conventional tomato crops, and further that intercropping tomato with coriander (*Coriandrum sativum*, Apiaceae) and gallant soldier (*Galinsoga parviflora*, Asteraceae) had an additional positive effect on reducing pest density and enhancing natural enemies (see PONTI *et al.*, 2007). In another experiment, MEDEIROS *et al.* (2009b) found that tomato plants potted in soil from organic farming systems had half the number of *T. absoluta* eggs when compared to tomato plants grown in soil from conventional systems. MEDEIROS *et al.* (2011) also observed higher *T. absoluta* egg mortality by parasitoids and generalist predators in organic vs. conventional tomato crops (see PONTI *et al.*, 2007). A similar trend was observed in Ohio (USA) by PHELAN *et al.* (1995) in studies of the European corn borer. Implementation of habitat management and/or organic farming may be hindered in intense greenhouse tomato cultivation systems or control may not be sufficient to regulate the pest below economic levels.

Biological and natural control and augmentative releases

Information on biological control of *T. absoluta* in its native range is not comprehensive, and lacks the biology and ecology of natural enemies that would be critical for selecting candidate bio-control agents (DESNEUX *et al.*, 2010). Classical biological control would be a long-term sustainable management strategy for *T. absoluta*, and introduction of exotic natural enemies carries low risk of unintended effects on non-target organisms (e.g., risk of extinction of non target species; see VAN LENTEREN *et al.*, 2006) that must however be weighed against the prospective benefits (see MESSING & WRIGHT, 2006; DESNEUX *et al.*, 2010; BIONDI *et al.*, 2012).

Several species of predators and parasitoids have adapted to *T. absoluta* since its introduction to the Mediterranean Basin (natural control), and this has probably contributed to the observed decline in pest severity 2-3 years after first invasion (TROPEA GARZIA *et al.*, 2012; URBANEJA *et al.*, 2012). Field survey of native parasitoids recruited to *T. absoluta* in southern Italy (ZAPPALÀ *et al.*, 2012a) highlights the need to conserve indigenous natural enemies (e.g., via habitat management) that could be important components of management strategies for the tomato borer in the Mediterranean region. Laboratory assessment of the impact of native parasitoids on larval populations of *T. absoluta* were carried out in several Italian tomato fields located on the North-South gradient (FERRACINI *et al.*, 2012), and found that two species of the genus *Necremnus* were potential candidates for mass production and augmentative release. These findings emphasize the importance of the rich and variegated biodiversity found in the Mediterranean that may result in efficacious new associations of natural enemies with invasive species (see NICOLI & BURGIO, 1997).

The implementation of augmentative releases of natural enemies for control of *T. absoluta* in the Mediterranean Basin was initially constrained by the extensive insecticide use following the introduction of the pest (NANNINI *et al.*, 2012; URBANEJA *et al.*, 2012). However, successful augmentative control programs have been implemented for *T. absoluta* using native generalist predators (Miridae) that at the same time help manage other major tomato pests such as whiteflies. This development led to a substantial increase in the tomato crop area under augmentative biological control, especially in greenhouses of south-eastern Europe and Morocco (URBANEJA *et al.*, 2012). In Spain, control using egg predators such as the

native Mirid *Nesidiocoris tenuis* and application of the insecticidal bacterium *Bacillus thuringiensis* was shown to be highly effective in controlling the tomato borer in the greenhouse (GONZÁLEZ-CABRERA *et al.*, 2011; MOLLÁ *et al.*, 2011). Working at the same Spanish location, ZAPPALÀ *et al.* (2012b) showed that control of *T. absoluta* by *N. tenuis* can also be integrated with careful applications of sulphur (still widely used in organic tomato crops) that is effective on the moth but only moderately to non toxic to the Mirid.

Host plant resistance

Adding HPR would provide plant bottom-up effects to the top-down regulation by natural enemies, thereby increasing the likelihood of regulating pest populations at acceptable low levels in an ecologically sound manner. Commercial tomato hybrids resistant to *T. absoluta* are thought to be easily developed (MALUF *et al.*, 2010b). In Brazil, tomato breeding programs have shown that it is possible to introgress resistance from wild taxa of tomato and related *Solanum* spp. into commercial cultivars to produce allelochemicals such as acyl-sugars that confer resistance to a broad range of tomato pests including whiteflies, aphids, spider mites, as well as *T. absoluta* and other lepidopteran pests (MALUF *et al.*, 2010a, 2010b; OLIVEIRA *et al.*, 2012). Genes lost during the domestication of tomato were principally related to pest and disease resistance, and this may explain the current wide susceptibility of current cultivars to pathogens and pests (OLIVEIRA *et al.*, 2012), and the resulting high pesticide use that ultimately leads to resistance and adverse environmental impacts.

Pheromones

Pheromone-mediated mating disruption is emerging as an important component of management programs for major insect pests (WITZGALL *et al.*, 2010). The pheromone technology initially used against *T. absoluta* was immature, and was used because no alternatives were available to control the insecticide resistant invading populations. The exceptionally rapid invasion and lack of efficient chemical or biological control methods boosted the demand for monitoring lures initially employed for mass trapping (WITZGALL *et al.*, 2010) and that later evolved as a mating disruption technique. In a study carried out in southwestern Sardinia, COCCO *et al.* (2012) showed that mating disruption is an efficient strategy to control *T. absoluta* in greenhouse tomato crops. Mating disruption, however, can only be implemented in high-containment greenhouses that prevent immigration of mated females from surrounding habitats (VACAS *et al.*, 2011).

Sterile insect technology

The sterile insect technology (SIT) is also being considered as prospective mean of control. CAGNOTTI *et al.* (2012) studied the effects of X-rays on *T. absoluta* as a first step to assess the viability of implementing SIT as a control technique for this species, but no information is available on potential effectiveness. Likely, SIT is not a viable option because of the wide range of the pest, multiple hosts and the pest's apparent high vagility, and the high costs of such a program.

CONCLUDING REMARKS

In the Mediterranean Basin, recent warming (BARTOLINI *et al.*, 2012) consistent with climate change projections for the region (BARKHORDARIAN *et al.*, 2011; DIFFENBAUGH & GIORGI, 2012) has likely facilitated the establishment and spread of invasive species (ROBINET & ROQUES, 2010) including *T. absoluta*. High resistance to insecticides removed constraints of normal quarantine measures (CIFUENTES *et al.*, 2011; DESNEUX *et al.*, 2011) and appears to have enhanced *T. absoluta* rapid invasion of wide geographic areas (CIFUENTES *et al.*, 2011). This species is likely to become a major global pest of tomato and it will have to be managed using mainly ecologically-based approaches over the large geographic areas it has or will invade. This makes the capacity to predict the potential geographic distribution and relative abundance (i.e., the invasiveness) of *T. absoluta* pivotal to developing sound policy for managing this (or any other) invasive species (GUTIERREZ *et al.*, 2011). PBDMs are physiologically-based weather-driven geospatial modeling tools that can be harnessed to gauge accurately the invasiveness of pests such as *T. absoluta*, while circumventing many of the deficiencies of mainstream assessment methods based on essentially correlative, climate envelope approaches (ENMs). PBDM analyses are able to capture the complexity of tomato agroecosystems and produce an interdisciplinary synthesis for *T. absoluta* that fits nicely into the conceptual framework of agroecology. A sound scientific basis for understanding *T. absoluta* dynamics will increase our ability to improve system stability and resilience in the face of the varied complexities of agriculture that occurs across the pest's geographic range.

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RIASSUNTO

APPROCCIO OLISTICO ALLA GESTIONE DI SPECIE INVASIVE: IL CASO DI TUTA ABSOLUTA (MEYRICK)

Il Bacino del Mediterraneo è una regione del nostro pianeta particolarmente soggetta a cambiamenti climatici ed invasioni biologiche, nella quale un recente aumento della temperatura ha probabilmente facilitato l'insediamento e la diffusione di specie invasive. Stimare distribuzione geografica ed abbondanza relativa delle specie invasive è fondamentale per approntare politiche utili alla loro gestione, e pertanto la necessità di ottenere tali stime è aumentata sensibilmente nel Bacino del Mediterraneo. La tignola del pomodoro *Tuta absoluta* (Meyrick) ha di recente invaso il Bacino del Mediterraneo dall'America del Sud e minaccia di divenire un fitofago chiave del pomodoro a livello mondiale. Il presente contributo riassume informazioni sulla biologia di *T. absoluta* utili allo sviluppo di un modello demografico con base fisiologica (PBDM, "physiologically-based demographic model"), e passa in rassegna le componenti di un possibile programma di gestione della tignola su base ecologica, con ciò preparando il terreno per una valutazione dell'importanza relativa delle diverse componenti a livello territoriale. L'approccio ai modelli demografici basato sulla fisiologia può infatti essere utilizzato nel contesto di un GIS per sviluppare e realizzare un'analisi olistica di questa specie. Le analisi PBDM consentono di cogliere in maniera quantitativa interazioni complesse che sono imprescindibili per gestire su base scientifica le specie invasive, *T. absoluta* compresa. La sintesi interdisciplinare che da queste analisi deriva può contribuire nel quadro concettuale dell'agroecologia alla messa a punto di strategie di gestione adatte a risorse e realtà socioeconomiche specifiche.

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