



Challenging the status quo in invasive species assessment using mechanistic physiologically based demographic modeling

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Received: 4 July 2022 / Accepted: 24 July 2023
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Abstract

The increased incidence of invasive species introductions is a hallmark of global change, but their associated environmental and economic impacts are vastly underestimated. Assessing and managing the impact of invasive species requires understanding their weather driven dynamics as a basis for predicting their potential geographic distribution and relative abundance. Current *de-facto* standards for invasive species assessment are correlative approaches lacking mechanistic underpinnings, and hence fail to capture the weather driven biology limiting their explanatory and predictive capacity to forewarn policy makers of species invasiveness (i.e., its potential geographic distribution and relative abundance under extant and/or climate change weather). The idiosyncratic time-place nature of biological invasions and the inability of correlative approaches to incorporate biological information call for development of a unifying prospective approach across species. Physiologically based demographic models (PBDMs) provide a holistic basis for assessment of invasive species addressing many limitations of correlative approaches while accommodating higher level of biological complexity using a similar number of parameters. We use the South American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) as a case study in the Palearctic and compare the predictions of our PBDM model to those of three analyses based on the correlative CLIMEX model. The PBDM outperformed CLIMEX with comparable CLIMEX predictions only after the pest had reached its potential geographic distribution (i.e., post hoc), using 6–10 vs. 13 parameters, respectively. We suggest creating dedicated laboratories to gather appropriate biological data and developing generalized software to build mechanistic models for assessing invasive species of any taxa.

Keywords Invasive species assessment · Physiologically based demographic models · GIS · Climate change · Invasive species · Policy-making

1 Introduction

Biological invasions are hallmark indicators of global change and are analogous to natural disasters (Ricciardi et al., 2011), but their occurrence is unpredictable and their potential geographic distribution and relative abundance are poorly understood, even in well-funded programs (Gutierrez & Ponti, 2013b; Gutierrez et al., 2021). The high environmental and economic impacts of invasive species were clearly outlined prospectively by Professor David Pimentel's clarion paper (Pimentel et al., 2000). Estimates of losses likely underestimate worldwide the material losses in agricultural yield and natural resources, and their economic costs (Bradshaw et al., 2016; Diagne et al., 2021). The costs in the European Union are potentially order of magnitudes higher than currently estimated, with only ~1% known invasive species having reported costs (Haubrock et al., 2021; Henry et al., 2023). This indicates an urgent need for both improved impact assessments and redirection of efforts from predominantly biosecurity and prevention actions to the management of established invasive species (Haubrock et al., 2021, 2023).

The various approaches used to assess these invasions were reviewed by Johnston et al. (2019) pointing out their strengths and limitation and illustrating the need for a unified general framework to assess such problems under extant and climate change. De Vries and Caswell (2019) proposed a theoretical matrix mechanistic framework for evaluating such problems including aspects of evolution related to climate change, though the application to field problems remains unclear. The most commonly used assessment methods are ecological niche models, also known as species distribution models, and hereafter collectively referred to as correlative species distribution models (CSDMs) (Elith, 2017; Elith & Leathwick, 2009). CSDMs have become the de facto standard in invasive species assessment used by regional, national, and international institutions because they are relatively easy to implement and allow rapid initial assessments even in the absence of sound biological data. CSDMs approaches correlate averaged (weekly or monthly) weather and other data to species occurrence records and use the model parameters to map the potential geographic range of the species (see Johnston et al., 2019 for limitations). As an alternative, we propose the use of physiologically based demographic models (PBDMs) that capture the (daily) weather (and resource) driven biology of species independent of incidence records, provide considerably greater explanatory insights, and can be used to develop management tactics.

PBDMs simulate biological processes explicitly (i.e., are mechanistic) on a daily time step, and have the potential to dramatically improve our understanding of the mechanisms underpinning the geographic distribution and abundance of species. Furthermore, PBDMs enable explicit modeling of management options providing key management-relevant information often unavailable to decision and policy makers (Briscoe et al., 2019; Johnston et al., 2019; Rangwala et al., 2021). Availability of appropriate weather dependent biological data on pest vital rates and accessibility of methods to integrate the data are barriers posited as restricting the use of mechanistic approaches for assessing invasive species under extant weather and climate change, and more generally for predicting population responses to novel environments (Briscoe et al., 2019; Johnston et al., 2019). We show that the PBDM approach streamlines identification and collection of the required biological data (Gutierrez & Ponti, 2013b; Ponti et al., 2015) as evidenced by a plethora of published tri-trophic examples (Gutierrez & Ponti, 2022). What is lacking is wider accessibility of the methods to researchers through a generalized modeling platform (Ponti et al., 2019).

To illustrate how assessment of invasive species can be improved using process explicit PBDMs, we compare the applications of the CSDM CLIMEX model and a PBDM to the analysis of the invasion of the South American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) across wide areas of the Palearctic (Ponti et al., 2021). We note that the pest has also invaded Asia and Africa, but the same model can be used to evaluate the pest there. The PBDM for this pest was based on biology data summarized in Campos et al. (2021). As preamble, we briefly review the underpinning concepts of major models used to predict species responses to environmental change with focus on methods used to assess invasive species.

2 Predicting population responses to novel environments

Johnston et al., (2019; see also Briscoe et al., 2019) assessed several approaches used to predict species responses to environmental change. They cautioned that both correlative and mechanistic approaches have limitations, stressing that most approaches used are correlative that ignore the individual-level mechanisms underlying population dynamics, and hence cannot reliably extrapolate outside of the observed environmental range (e.g., to novel climates and/or geographic areas). Johnston et al. (2019) concluded that little progress has been made in developing a standardized approach that captures the mechanisms driving population dynamics such as physiology, behavior, and evolution in a spatially explicit way and that is general enough to be applied to all species and environmental scenarios. Johnston et al. (2019) cite the following constraints:

- The limited availability of data to parametrize the model at the individual level and to calibrate and validate models at the population level, with data available being often presence/absence or aggregate animal population dynamics data.
- The need to develop and test quantitative methods for representing individual mechanisms and the interactions between them, and that many competing theoretical approaches with different goals exist that need to be integrated into a single framework.
- The need for realistic and multi-dimensional environmental scenarios that can serve as input to population models and include multiple standardized stressors such as land use, atmospheric CO₂ concentration, and nitrogen availability.

These constraints suggest Johnston et al. (2019) are seeking a generalized one-to-one model of nature.

The recent 6th IPCC Assessment Report (IPCC, 2022) pointed out that:

- “A lack of understanding of physiological constraints and mechanisms remains a barrier to predicting many of the ecological effects of climate change [...].
- Many behavioral, morphological, and physiological responses are highly species- and context-specific, making generalizations difficult. [...]
- Improved understanding of the mechanistic basis for observed geographic patterns in thermal tolerance and plasticity is needed to identify the physiological limits of species [...].”

The unpredictable nature of biological invasions and the inability to incorporate insights gained from CSDMs case studies (Novoa et al., 2020) support the need for a unifying

predictive approach across species (Cuthbert et al., 2019; de Vries & Caswell, 2019; Johnston et al., 2019; Roy et al., 2018).

Johnston et al. (2019) categorized current population modelling approaches according to their ability to describe the individual-level mechanisms (physiology, behavior, and evolution) that drive population responses to environmental changes in spatially explicit landscapes:

- Species distribution models
- Individual-based models
- Demographic models

In Sects. 2.1 to 2.3, we briefly review CSDMs models and other population modeling approaches using these categories and use them in Sect. 2.4 to identify where the PBDM modeling approach fits.

2.1 Correlative species distribution models (CSDMs)

Correlative species distribution models approaches are widely used for assessing invasive species risk (Yates et al., 2018), and predicting the potential range of a species using averaged climatic and other data correlated with occurrence records in the known range that strongly influence the predictions of potential geographic range (Elith, 2017; Elith & Leathwick, 2009). Specifically, the predictive power of CSDMs approaches is potentially lower than simple spatial interpolation as it is largely due to the spatial patterns of environmental variables (e.g., climate data) and species occurrence data, with no underlying functional relationship (Bahn & McGill, 2007). Because they model observed spatial patterns statistically, correlative approaches cannot reliably extrapolate outside of the observed environmental range, and this substantially limits their transferability in space (invasive range expansion) and time (projected climate change) (Evans, 2012; Heikkinen et al., 2012; Liu et al., 2020, 2022; Srivastava et al., 2019; Yates et al., 2018). Further, because CSDMs fail to explicitly model biological and ecological mechanisms underlying species responses to environmental change (Johnston et al., 2019), they have limited ability to explain and hence manage the potential distribution and economic impact of invasive species (Briscoe et al., 2019; see Thompson et al., 2021). To circumvent such limitations requires mechanistic modeling of the processes underlying the spatial patterns of species occurrence (geographic distributions) (Bahn & McGill, 2007), as given its resource base, weather driven vital rates determine the phenology and population dynamics of species, and ultimately their observed (and potential) distribution and relative abundance (Gutierrez, 1996).

Among the CSDMs methods widely used to assess invasive species is the commercially available software CLIMEX (Sutherst & Maywald, 1985). Based on physiological indices, CLIMEX has quasi-mechanistic roots in the assumed normalized concave growth response of species to various factors with minimum and maximum values and an optimum (Gutierrez et al., 2010). Unlike other CSDMs methods, CLIMEX was specifically developed for modelling invasive species (Elith, 2017), and has its roots in the early studies by Fitzpatrick and Nix (1970) on growth indices developed to estimate the climatic limits of Australian grasslands types, and by Gutierrez et al. (1974) and Gutierrez and Yaninek (1983) to capture the climatic limits of aphids in southeastern Australia. Aspects of these growth indices are found in PBDMs (Gutierrez, 1996).

Recently, Barker et al. (2020) proposed Degree-Days, Risk, and Phenological (DDRP) event mapping that is similar to CLIMEX but has a daily rather than weekly time step, is limited to insects, and seeks to predict phenology in addition to climatic suitability.

Integration of physiological mechanisms and population processes into CSDMs has been proposed for climate impact assessments (Kearney & Porter, 2009) including for invasive species (Kearney et al., 2009). To address the shortcomings of correlative approaches, additional processes such as demographic rates, physiological and behavioral constraints to movement, connectivity between suitable patches, and population dynamics have been incorporated in what are now identified as process-based SDMs (Briscoe et al., 2019; Dormann et al., 2012; Kearney & Porter, 2009; Kearney et al., 2008; Rougier et al., 2015; Teal et al., 2012; Thuiller et al., 2013). Dormann et al. (2012) pointed out that the resulting integration is substantially closer to the correlative end of the process-correlation modeling continuum and hence should still be considered part of the CSDMs methodological base. However, CSDMs can provide a reasonable first approximation when only occurrence data are available (Fordham et al., 2018). Further, most CSDMs were not designed to assess invasive species (Elith, 2017) but continue to serve important functions in ecology and evolutionary biology research as they did in their early applications (Elith & Leathwick, 2009).

Dynamic range models (DRMs) have been developed that provide probabilistic forecasts of future dynamics of species ranges under environmental change, using both occurrence and abundance data to statistically infer species niches and spatio-temporal population dynamics (Zurell et al., 2016). Yet, DRMs remain statistical models that use environmental variables as correlates of demographic rates, density dependence, and dispersal rates based on species occurrence and abundance data (Pagel & Schurr, 2012).

2.2 Individual based models (IBMs)

Individual-based models, also called agent-based models (ABMs), simulate populations composed of individual organisms each having a set of state variables or attributes (e.g., spatial location, physiological traits, and behavioral traits) and behaviors (e.g., growth, reproduction, habitat selection, foraging, and dispersal), with population-level dynamics resulting from the interactions among individuals and their abiotic environment (DeAngelis & Grimm, 2014; DeAngelis & Mooij, 2005; Grimm, 1999). However, IBMs/ABMs require individual-level data for parametrization, and hence are not widely used (Johnston et al., 2019). Applications of IBMs/ABMs increasingly include models that describe individual-level mechanisms, thus improving predictions outside of the range of environmental conditions for which they were parametrized. For example, Energy–Environment–Earthworm (EEEworm) is a mechanistic individual-based model of *Lumbricus terrestris* populations developed by Johnston et al. (2018) as a tool for assessing how soil systems respond to combinations of land management and climate change. Extensive validation showed how the EEEworm mechanistic approach can extrapolate across diverse soil, management, and weather conditions. Other applications of IBMs/ABMs include assessments of biodiversity management and policy under environmental change (Stillman et al., 2015) and invasive species assessment (e.g., Coulter et al., 2022; Dominiak & Fanson, 2023; Goslee et al., 2006).

2.3 Demographic models (DM)

Demographic matrix models (DMs) (Leslie, 1945) played an initial role in population ecology, enabling inclusion of intrinsic birth and survivorship rates and population density. Advances in computational and statistical approaches in ecology (Griffith et al., 2016) enabled development of more powerful approaches, such as integral projection DMs that include both mass and life stage for improved representation of population structure (East-erling et al., 2000), and integrated DMs that combine individual- and population-level data to better estimate the influence of individual variation on demographic rates (Schaub & Abadi, 2011). However, these DMs are still based on statistical relationships between demographic rates and observed environmental conditions, and hence are unsuited for predicting population responses to novel environments (i.e., invasive species, climate change), that requires inclusion of mechanisms that underpin demographic rates (Johnston et al., 2019). Despite the increasing combination of integral projection DMs with energy budget models (Smallegange et al., 2017), the model predictions remain informed by the observed population data, limiting predictions of population responses to novel environmental conditions (Johnston et al., 2019).

2.4 Physiologically based demographic models (PBDMs)

PBDMs are time-varying life tables models that can incorporate age, mass, and other attributes of field populations (see Gutierrez, 1996, p. 231). The effects of factors determining the vital rates may be captured using mechanistic weather driven physiology of resource acquisition and allocation (i.e., metabolic pool models, MPMs; e.g., Gutierrez, 1996; Gutierrez & Baumgärtner, 1984) or as biodemographic functions (BDFs) that capture cohort level responses to weather (e.g., Gutierrez et al., 2021). These components are described below with real world applications. PBDMs may also be cast as metapopulation models with movement of pest and natural enemy between plants (see Gutierrez et al., 1999), or as dispersal model estimating the dispersal of the invasive chestnut gall wasp (see Gilioli et al., 2013).

Using Johnston et al. (2019) classification, PBDMs include features of matrix DMs (time-varying life tables), integral projection DMs (include life stages and mass), and integrated DMs (use both individual- and population-level data). Further, PBDMs include per capita mechanistic physiological processes of resource acquisition and allocation in the form of MPMs with dry matter (energy) acquisition, including behavior such as stage preference, and allocation linking trophic levels in an age-stage specific manner. Aspects of growth indices included in the quasi-mechanistic CSDM CLIMEX are also components of PBDM/BDFs. Through more than 40 years of development (see Gutierrez & Baumgärtner, 1984; Gutierrez, 1992, 1996), PBDMs have incorporated a range of population modeling features contributing to basic bioeconomic theory (Regev et al., 1998) and helped solve many applied field problems (e.g., Gilioli et al., 2017, 2022; Gutierrez et al., 2012, 2014). PBDMs bridge the gap between purely theoretical analytic models and overly complicated simulation models. The population dynamics of PBDMs may use a variety of mathematical models to model field populations (Di Cola et al., 1999; Gutierrez, 1996). A known caveat of PBDMs is that they do not model movement explicitly except for background immigration levels. The major area for improvement is the need to make the PBDM methods easier to access and implement by developing a modeling software platform of general

applicability to any invasive taxa by unifying the wide variety of modeling features for examining field problems that PBDMs have addressed over more than 40 years of development (see Gutierrez & Ponti, 2022).

2.4.1 Population dynamics models

A mathematical model that captures the distribution of maturation times of age-stage structured populations is the distributed delay models (DDMs) (Abkin & Wolf, 1976; Manetsch, 1976; Vansickle, 1977) (Fig. 1, see supplemental materials). A mathematically more nuanced dynamics model is the forward Kolmogorov model (Buffoni & Pasquali, 2007), that for the same biology would yield similar results to that of DDMs.

Specifically, absent mortality, if the mean developmental time of cohort individuals is del with variance var , the maturation times of a cohort members in a DDM are characterized by Erlang distribution captured using $k = del^2/var$ age classes (Fig. 1a). Note that the larger the value of k , the narrower is the Erlang distribution of developmental times (Fig. 1b). In the model, time and age are in physiological time units (proportion development or degree days, see below). The DDM captures the flow (aging) between age classes within and between stages (Fig. 1a) in a time-temperature-resource dependent manner. While Fig. 1 illustrates the development of an insect, the same model has been used to model the population dynamics of whole plant or plant sub units like buds (or any other organ) through flowering and maturity (see Gutierrez, 1996 for references).

Two approaches have been used to parameterize PBDMs:

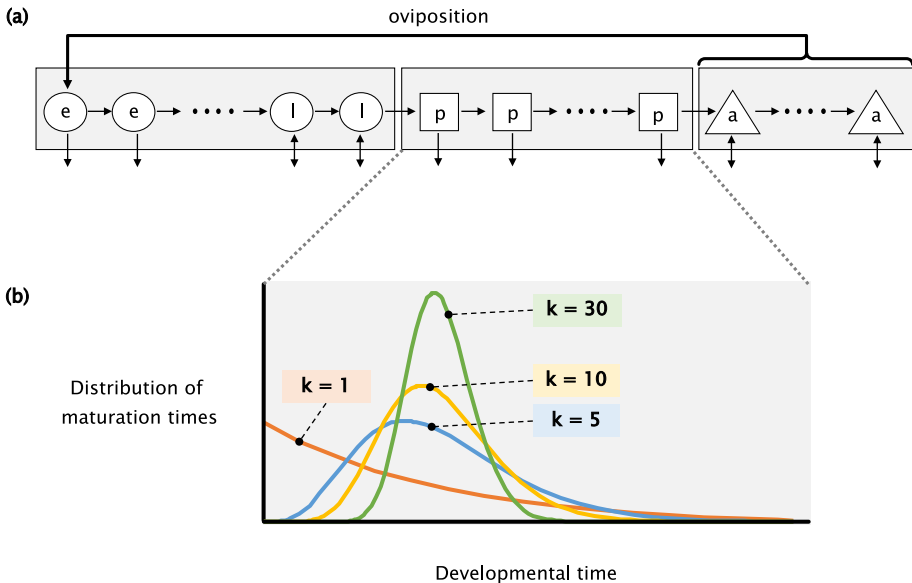


Fig. 1 Population dynamics: **a** an age structured model for the dynamics for the egg (circle with letter e), larval (circle with letter l), pupal (square), and adult (triangle) stages of an insect species, with arrows indicating flows (aging) between age classes and stages, and double arrows in some stages indicating the net age-specific mortality; and **b** the distribution of developmental times based on the number of age cohorts (Erlang parameter $k = del^2/var$) in sub figure **a** (see Severini et al., 2005)

1. mechanistic models of energy/dry matter acquisition and allocation (metabolic pool models, MPMs) and
2. biodemographic functions (BDFs) that summarize the effects of various factors (e.g., temperature) on the species vital rates.

Attributes such as mass, sex, dormancy, and other factors can be easily incorporated (Gutierrez, 1996), as well as microclimate effects such as that of solar irradiance on temperature in the leaf mine microclimate (Ponti et al., 2021). Because the BDFs are the resultant of resource acquisition and allocation under different biotic and abiotic conditions, both MPMs and BDFs paths lead to PBDMs that are time varying life tables (sensu Gilbert et al., 1976).

2.4.2 Mechanistic metabolic pool models (PBDM/MPMs)

The underpinning basis of this approach is that all organisms are consumers and all have similar resource acquisition (supply) functions and allocation (demand) priorities; a notion that allows use of the same resource acquisition model and birth–death dynamics models to describe explicitly the biology of heterotherm species across trophic levels (see Gutierrez & Baumgärtner, 1984; Gutierrez, 1992, 1996), including the economic level (Regev et al., 1998) (Fig. 2). The inflow and outflow processes are analogous across species and have similar shapes. Resource acquisition (i.e., the supply, S) is a search driven functional response process driven by organism demand (D) for resources under current biotic and abiotic conditions, with allocation occurring in priority order to egestion, conversion costs, respiration, and reproduction, growth, and reserves (see Fig. 2). The ratio $0 \leq S/D < 1$ occurs because of imperfect search for resources and serves to scale vital rates from the genetic maximum (Gutierrez, 1992, 1996). A wide range of real-world ecosystem-level problems driven by global change have been analyzed using this unifying supply/demand (i.e., $0 \leq S/D < 1$) approach based on the paradigm of ecological analogies (see <http://www.casasglobal.org>). This approach is highly suitable for modeling the dynamics of plant population and for herbivores consuming plant subunits. An important drawback is that appropriate data are rarely available, but are not difficult to assemble (e.g., Gutierrez & Baumgärtner, 1984).

2.4.3 The biodemographic functions approach (PBDM/BDFs)

An alternate modeling path that streamlines implementation of PBDM development is the use of biodemographic functions (BDFs) (see Fig. 3; Gutierrez & Ponti, 2013b; Gutierrez et al., 2021) that capture the resultant resource driven effects on the species vital rates (i.e., Fig. 2, MPMs). BDFs capture the resultant effects of temperature and resource-based effects on species birth, death, and developmental rates common to all species using a modest number of measurable parameters. Specifically, similar shaped birth–death rates sub-models are fitted to data and embedded in age (mass) structured population dynamics models (i.e., DDMs) that are forced principally by temperature and resource levels, but other factors can be easily added as identified (Fig. 3). Among the BDFs are temperature-dependent developmental rates, age-specific fecundity, and mortality and other factors such as diapause (see Fig. 3; modified from Gutierrez & Ponti, 2013b). The BDFs capture analogous processes in the life histories of species across trophic levels enabling establishing the relationships between resource and consumer species. These analogous BDFs simplify parameter estimation and provide significant

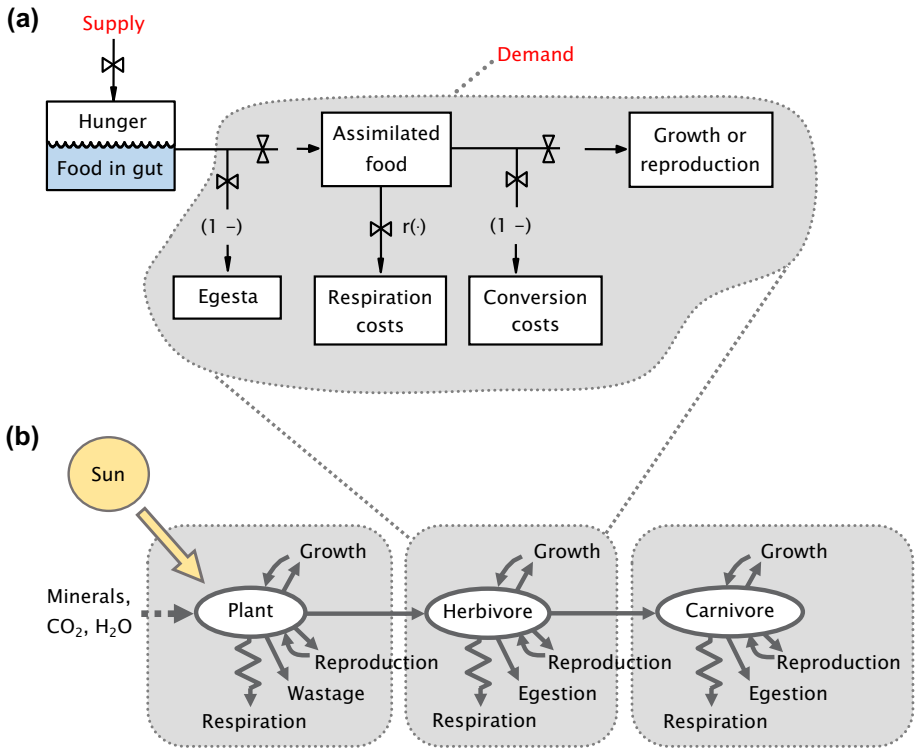


Fig. 2 The physiological basis of PBDMs. All organisms have common patterns of energy acquisition (supply) and allocation (demand) (a), and this allows the use of the same modeling paradigm to describe the biology of the species in all trophic levels (b) (see Gutierrez, 1996). Development of PBDMs with a metabolic pool model (MPM) approach entails describing the energy (dry matter) acquisition and allocation functions

guidance in reviewing the literature for relevant biological data required to parameterize PBDMs for any trophic level. The resulting advantages are:

- Easier harvesting, organization, standardization, and integration of data.
- Guidance for identification of data gaps and discrepancies in extant biological data when plotted on the same scale of a putative BDF.
- Identification of experiments needed to address data gaps and discrepancies.

The BDF path has been used in numerous PBDM analyses (Gutierrez & Ponti, 2013a; Gilioli et al., 2016, 2021, 2022; see Table 15.1 in Gutierrez & Ponti, 2022). In this paper, we review the PBDM analysis of the tomato pinworm *T. absoluta* as our foil (Ponti et al., 2021).

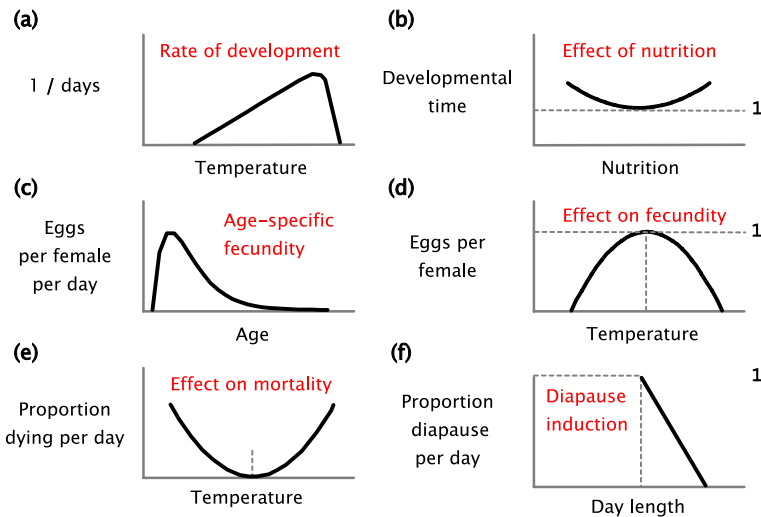


Fig. 3 PBDM biodemographic functions (BDFs, modified from Gutierrez & Ponti, 2013b; Gutierrez et al., 2021). **a** The rate of development on temperature (e.g., Brière et al., 1999). **b** The effects of nutrition and other factors on developmental time may also be included (e.g., nutrition affects developmental time as a limiting factor when shortfalls or excesses are toxic). **c** The per capita fecundity profile on female age (e.g., 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 daily mortality at different temperatures (Gutierrez, 1996). **f** The proportion diapause induction as a function of day length (e.g., grapevine moth, Gutierrez et al., 2012), but it could also be due to the interaction with temperature (see pink bollworm; Gutierrez et al., 1981) and other factors

3 Methods

3.1 The PBDM/BDF for *Tuta absoluta*

The PBDM for *T. absoluta* is based on BDFs (Fig. 4) that were parameterized largely using the biology and data summarized in Campos et al. (2021) and additional data in the scientific literature (see Gutierrez & Ponti, 2013b, 2022). For *T. absoluta*, the parameters include developmental times in physiological time for each stage, and the constants for the fitted BDFs for developmental rate, fecundity as a function of age and temperature, and temperature-dependent mortality (Fig. 4). As illustrated by Table 2 in Gutierrez et al. (2021), a set of analogous BDF parameters can be developed to describes the biology of any species, with the BDF parameters of six fruit fly species discriminating their weather driven geographic distribution and relative abundance. Historically, occurrence records have been used to assess invasiveness of the tropical fruit flies, with vague concepts such as “fruit fly-friendly regions” used to declare establishment (Carey et al., 2017; Papadopoulos et al., 2013). The BDFs that describe the biology *T. absoluta* and of the fruit flies in Gutierrez et al. (2021) are the same mathematical forms fitted to different datasets of the species’ vital rates. Knowing the shape of the BDFs provides significant guidance in reviewing the literature for relevant biological data (e.g., Fig. 4). As noted, BDFs guide identification of data gaps and discrepancies when available biological data from the same or different sources are plotted on the same scale of the putative BDF, so that missing biological data can be collected efficiently. The number of BDF parameters for the *T. absoluta* PBDM

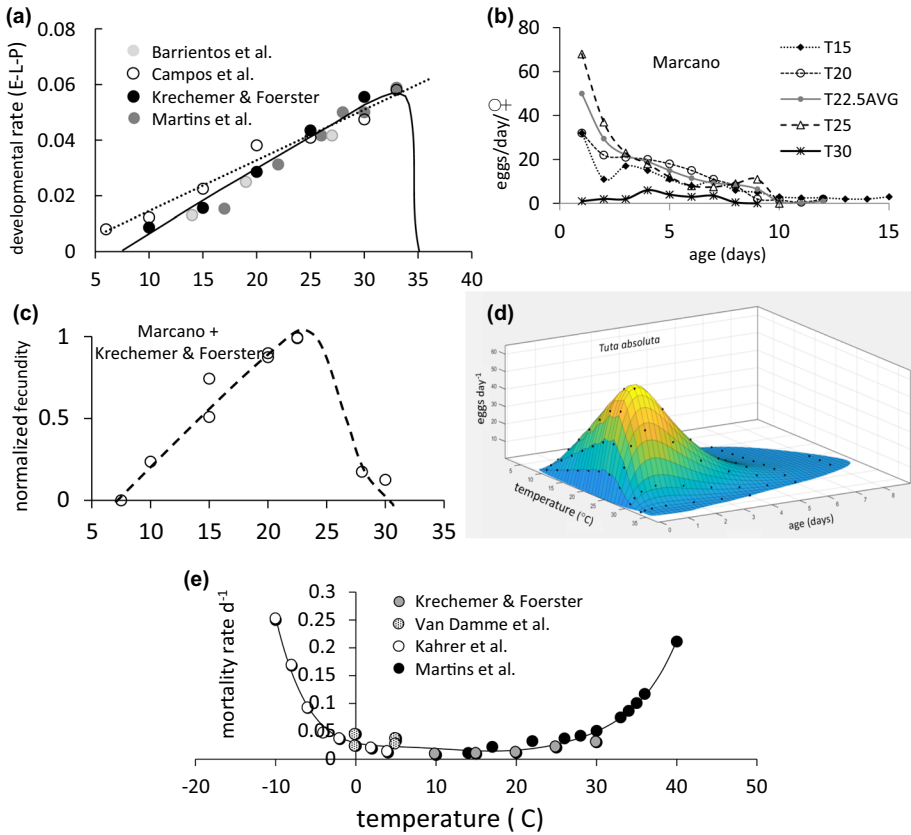


Fig. 4 Thermal biology of *Tuta absoluta* summarized as biodemographic functions (BDFs): development, reproduction, and mortality as a function of temperature. **a** Developmental rate as a function of temperature (data from Barrientos et al., 1998; Krechemer & Foerster, 2015; Martins et al., 2016; Campos et al., 2021). **b** Age-specific fecundity (data from Marciano, 1995). **c** Normalized gross fecundity as a function of temperature (data from Marciano, 1995; Krechemer & Foerster, 2015). **d** Oviposition per female as a function of age and temperature (Eq. 8). **e** Temperature-dependent mortality (data from Van Damme et al., 2015; Krechemer & Foerster, 2015; Martins et al., 2016; Kahrer et al., 2019) with the line indicating the fitted polynomial function used in the model. From Ponti et al. (2021)

was six parameters fitted to three BDFs in addition to a polynomial fit of temperature-dependent mortality (Fig. 4e) that replaced a simpler BDF (Fig. 3e) for higher accuracy. The PBDM also enabled modeling the effects of altered temperatures experienced by *T. absoluta* larvae and pupae in leaf mines using data from Pincebourde and Casas (2006).

3.2 Comparison of PBDM predictions with CLIMEX assessments

PBDM/BDF projections of the geographic distribution and relative abundance of *T. absoluta* made for the Palearctic (Ponti et al., 2021) were compared to projections of CLIMEX ecoclimatic indices (EI) of favorability for the same region (Desneux et al., 2010; Han et al., 2019; Santana et al., 2019). The CLIMEX EI is scaled from 0 to 100, with 0 indicating climatically unsuitable locations and 100 indicating highly suitable locations. The open

source geographic information system (GIS) GRASS (see <http://grass.osgeo.org>) originally developed by the United States Army Corps of Engineers (GRASS Development Team, 2022) was used for geospatial data management and the comparative analysis of *T. absoluta* geographic distribution. PBDM output was mapped using bicubic spline interpolation on a 3-km raster grid. The same grid was used to compare PBDM and CLIMEX maps. The maps of three CLIMEX studies (Desneux et al., 2010; Han et al., 2019; Santana et al., 2019) were imported as raster maps from the PDFs of the published papers to GRASS GIS using the *r.import* module, and then orthorectified using the *g.gui.gcp* module. Relevant vector data in imported raster maps, such as locations of species occurrence (vector points) in maps from Desneux et al. (2010) or areas of favorability (vector polygons) from Santana et al. (2019) and Han et al. (2019) were manually digitized using the *g.gui.vdigit* module. Raster and vector maps digitized from the CLIMEX studies were then converted to the Albers Equal Area projection used in the PBDM study to enable the PBDM-CLIMEX comparisons (Neteler et al., 2012).

Specifically, geographic locations of *T. absoluta* first occurrence during 2006–2010 in Fig. 1 of Desneux et al. (2010) (see Fig. 5, square symbols) were used:

- to identify the closest CLIMEX EI point estimate from Fig. 2 of Desneux et al. (2010) (see Fig. 5, circle symbols) using the *v.distance* GRASS module;
- to sample the corresponding raster values of CLIMEX EI in Fig. 1 of Han et al. (2019) and Fig. 3a of Santana et al. (2019), and PBDM relative abundance in Fig. 4a in Ponti et al. (2021) (see Fig. 6) using the *v.what.rast* module.

The results of the *v.distance* and *v.what.rast* analysis at locations of known *T. absoluta* occurrence were then checked manually for consistency with the published CLIMEX maps, to detect errors introduced by the differing spatial resolution of the digitized maps or by the digitization process. This allowed comparison of CLIMEX EI predictions of climate suitability (Desneux et al., 2010; Han et al., 2019; Santana et al., 2019), and PBDM-based predictions (Ponti et al., 2021) in the absence of the original CLIMEX data.

4 Results

4.1 Comparison of CLIMEX and PBDM at locations of known species occurrence

The predictions of climate suitability of the three CLIMEX analyses are compared with PBDM-based predictions of invasiveness at 56 specific latitude and longitude locations where *T. absoluta* was present in 2010 (see Fig. 5, square symbols; Desneux et al., 2010), with results for each location reported in supplementary Table S1. Prediction error occurs when CLIMEX and/or PBDM predict a specific location is unsuitable for *T. absoluta* but the species was detected there by national plant protection services. Desneux et al. (2010) predicted unsuitable climate at 16 of 56 locations where *T. absoluta* was present (error = 29%); Han et al. (2019) at 15 of 56 (error = 27%); Santana et al. (2019) at 10 of 56 (error = 18%); and the Ponti et al. (2021) PBDM analysis at 2 of 56 (error = 4%). Compared to the PBDM analysis, the CLIMEX predictions were problematic in non-Mediterranean Basin European countries and colder areas of Northern Italy (see supplementary Table S1) because the CLIMEX analyses lacked information on cold tolerance and facultative

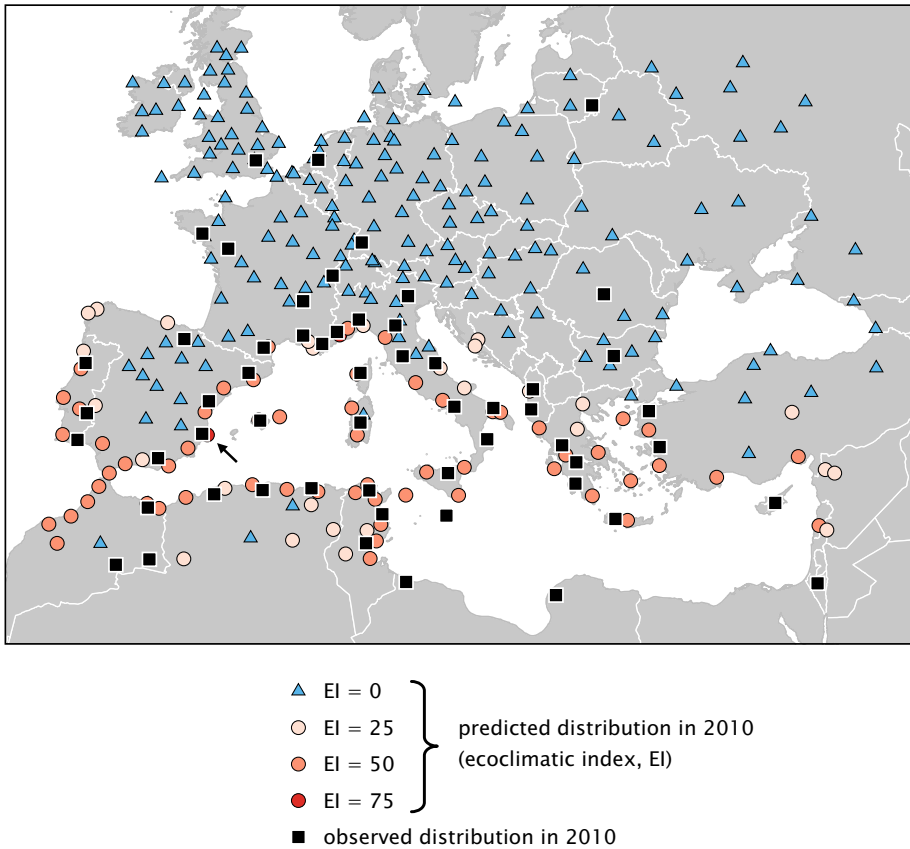


Fig. 5 Predicted and observed geographic distribution of *Tuta absoluta* in the Palearctic region as reported in the first CLIMEX study on the species by Desneux et al. (2010). Predicted distribution is shown using the CLIMEX ecoclimatic index (EI) of favorability that ranges from 0 to 100, with EI=0 indicating climatically unsuitable locations shown as blue triangles and increasing values of EI>0 indicating locations of increasing suitability shown as circles of darker shades of orange. Only one red circle with the maximum EI=75 is indicated by an arrow. Locations of first occurrence of *T. absoluta* in 2006–2010 are indicated as black squares. Geospatial data on *T. absoluta* presence and CLIMEX EI were digitized from Desneux et al. (2010) using GRASS GIS (see Ponti et al., 2021; GRASS Development Team, 2022)

diapause in *T. absoluta*. Further, CLIMEX predictions are given as wide intervals making comparison with PBDM predictions problematic. Supplementary Table 1 provides a partial comparison of CLIMEX vs. PBDM in terms of species presence-absence only.

4.2 Comparing mapped predictions of CLIMEX and PBDM

Figure 6 compares visually the predictions of the two most recent CLIMEX analyses (Han et al., 2019; Santana et al., 2019) to those of the PBDM (Ponti et al., 2021) for the western Palearctic, Nearctic, and Mexico. Note the PBDM simulates the daily dynamics of *T. absoluta* life stages for each of the ~33,000 lattice cells in the mapped regions (e.g., Fig. 6g for Sacramento, California, USA during years 2009 and 2010; Ponti et al., 2021), while

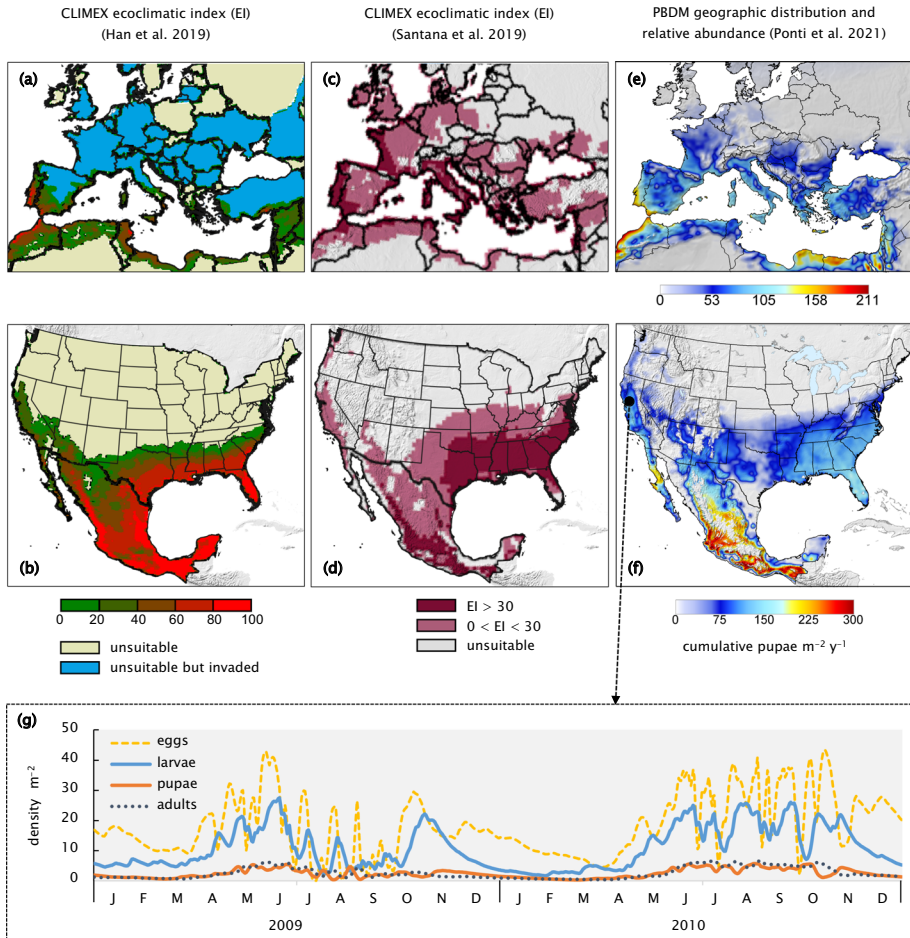


Fig. 6 Comparison of invasion risk for *Tuta absoluta* as predicted by two recent CLIMEX assessments (Han et al., 2019; Santana et al., 2019) and the PBDM (Ponti et al., 2021). The geographic distribution in the Euro-Mediterranean region (a, c, e) and in the USA and Mexico (b, d, f) of the CLIMEX ecoclimatic index (EI) from Han et al. (2019) (a, b) and from Santana et al. (2019) (c, d) are compared to the prospective average geographic distribution and relative abundance (i.e., invasiveness) predicted by the PBDM (e, f). Simulated daily PBDM population dynamics of *T. absoluta* life stages during 2009 and 2010 in Sacramento, California (USA) (g). The location of Sacramento is shown in (f) as a dot symbol connected to (g) by a dashed arrow. Increasing EI values indicate increasing climate suitability for *T. absoluta* in all CLIMEX studies. Geospatial data in (a–d) were digitized from Han et al. (2019) and from Santana et al. (2019) using GRASS GIS (see Ponti et al., 2021; GRASS Development Team, 2022)

the cumulative number of pupae produced per square meter per year is used as a metric of climatic suitability/invasiveness in each lattice cell in tomato-growing areas of the western Palearctic (Fig. 6e), and the Nearctic (United States and Mexico) where the pest has not invaded (Fig. 6f). Values above the midpoint of the color legend (i.e., 150 pupae) are increasing levels of favorability and vice versa.

Only the results of Santana et al. (2019) are comparable to the PBDM predictions that explained the biological bases for the invasiveness of *T. absoluta* across the regions (Ponti

et al., 2021): namely, the moth has a modest low developmental threshold (7.9 °C) and a facultative diapause (Campos et al., 2021), that combined with its high degree of cold hardiness (Kahrer et al., 2019) enabled its northward range expansion. The northward limits can be defined by the cumulative yearly mortality rates of 3.5 at temperatures below 7.9 °C, and southward by high temperatures that adversely affect reproduction and survival rates, particularly in hot-dry desert areas of North Africa, USA, and Mexico.

Had the data illustrated in Fig. 4 been available before 2006 and incorporated in a PBDM, the analysis would have accurately identified the pest's high invasive potential, its current distribution, and would have triggered global quarantine measures that could have prevented its invasion. In contrast, correlative methods (e.g., Santana et al., 2019) could make similar projections only after the invasion had occurred over the full area.

5 Discussion

Tuta absoluta is a native insect pest of tomato in South America (Desneux et al., 2010) that was not identified as a serious threat by the European Union, the USA, or other tomato-growing areas until it invaded Spain in 2006, from where it spread rapidly across Europe, Africa, and Asia (Biondi et al., 2018; Han et al., 2019; Pratt et al., 2017). Before invading the Euro-Mediterranean region, *T. absoluta* was not a regulated quarantine pest in the European Union and the United States (Biondi et al., 2018). The failure to recognize its invasive potential was due in large measure because correlative methods were used to assess the invasive potential of the pest in the Palearctic.

Three CLIMEX studies of *T. absoluta* invasiveness were conducted during the period 2010–2019 after the initial 2006 detection (Desneux et al., 2010; Han et al., 2019; Santana et al., 2019). The first study (Desneux et al., 2010; Fig. 5) projected that only coastal southern Europe would be favorable, this despite the pest having been recorded from central Europe in 2009–2010. This result was predicted because the known range expansion of *T. absoluta* is from South America and its first reported range expansion was to tomato in areas of Brazil with warm climates similar to coastal areas of the Mediterranean. Furthermore, data on its thermal biology (Fig. 7) were available only in the range of favorable temperatures above 12 °C, and did not accommodate the fact the pest putatively originated from the cold semi-arid climate of the Andean highlands (Biondi et al., 2018).

The second CLIMEX assessment in 2019 (Han et al., 2019) also failed to predict fully the areas of Europe invaded by the pest for similar reasons (Fig. 6a). The third CLIMEX assessment (Santana et al., 2019) provided good predictions for the Euro-Mediterranean region because it used occurrence data from the larger invaded Palearctic region, a lower thermal threshold, and a wider thermal range for development. This, however, was a post hoc assessment after the pest's widespread invasion of Europe and the Mediterranean Basin (Fig. 6c).

The development of the PBDM was also hampered by gaps in knowledge of the thermal biology of *T. absoluta* at low temperatures—data filled in piecemeal fashion over 13 years after the species was first recorded in Spain in 2006 (Fig. 7). Studies on the thermal biology below 12 °C became available only in 2015 (Van Damme et al., 2015; Krechmer & Foerster, 2015; Martins et al., 2016), after the invasion of central Europe made the overwintering potential of the species evident. Kahrer et al. (2019) estimated *T. absoluta* survival below 0 °C (Fig. 7) and Campos et al. (2021) explored survival at low temperatures and the development of facultative diapause. Had the BDF research path suggested in Fig. 3

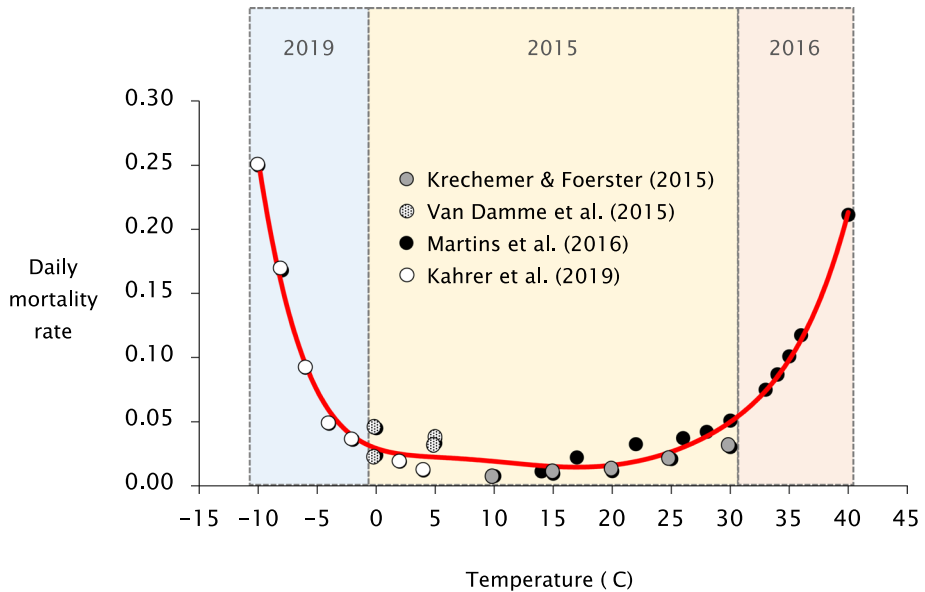


Fig. 7 Temperature-dependent mortality rate of *Tuta absoluta* (data from Van Damme et al., 2015; Krechmer & Foerster, 2015; Martins et al., 2016; Kahrer et al., 2019) with the red line being the fitted polynomial function used in the PBDM model (Ponti et al., 2021). Colored regions indicate when (i.e., year) the mortality data became available in the literature. Modified from Ponti et al. (2021)

been implemented proactively before the pest's invasion of Europe, its potential geographic distribution could have been assessed using PBDMs (see Fig. 6) that explain the biological bases for *T. absoluta*'s prospective geographic distribution and relative abundance (i.e., invasiveness) in the European Mediterranean region (see Fig. 6e, f, and g). Furthermore, because the PBDM/BDF for *T. absoluta* captures its weather driven biology, the model was transferable to the analysis of its invasive potential in the USA, and Mexico/Central America and more recently Africa (unpublished). Lastly, given the availability of appropriate weather data, the analysis of other regions is possible, as well as analyses of climate change effects on range expansion/contraction (see climate change analysis in Ponti et al., 2021).

6 Final remarks

David Pimentel foresight analyses brought into focus the “uncomfortable knowledge” of the impact of invasive species for policy makers whose agencies are responsible for pest risk assessment, quarantine and control/eradication efforts, and who increasingly need updated information to deal with a complex and changing world of global change (Elliott et al., 2021; Roy et al., 2018). However, while holistic analyses are often advocated (e.g., Gill et al., 2021; Gilman et al., 2010; Hulme, 2006; Pullin et al., 2009; Simberloff et al., 2013; Sutherst & Bourne, 2009; Zavaleta et al., 2001), such analyses are rarely conducted because they are thought to be too complicated, that there are simply too many factors (Barlow, 1999). Pest risk assessments that go beyond opinion and verbal

summaries of the literature are only now being adopted; methods that enable effective management of real-world problems.

Currently, correlative species distribution models (CSDMs) are the de facto standard commonly used in invasive species risk assessment to infer the invasive potential as correlates of aggregate weather data at locations of species occurrence records. Unfortunately, as indicated here for *T. absoluta*, accurate assessment of invasion risk using correlative CSDM methods may accrue as post hoc analysis after the pest's invasion of its potential range. A recent study on *T. absoluta* using the most widely used CSDM (Qazi et al., 2022; Yan et al., 2021) Maxent (Phillips et al., 2006) confirms that CSDMs require constant updating with occurrence records in new areas to generate useful invasion risk assessments (Marchioro & Krechmer, 2023). This paradox was illustrated using *T. absoluta* where well-organized plant quarantine systems underestimated the invasion risk posed, allowing a pest of South American tomato crops to become a global food security threat to solanaceous crops. As outlined herein, mechanistic physiologically based demographic models (PBDMs) can circumvent many of the limitations of correlative CSDM approaches without additional parameters or complexity. For example, the PBDM of *T. absoluta* included 6 to 10 parameters to fit BDFs of the vital rate data (Fig. 4), while the CLIMEX models required 13 parameters (see Santana et al., 2019) fitted statistically to monthly average weather and other factors correlated with species distribution data without biological underpinnings. The identification of data needs using BDFs (see Fig. 3) simplifies the process (see Campos et al., 2021) and enables rapid development of the model for projection of the population dynamics and the resultant prospective distribution and relative abundance of a species as driven by weather (Ponti et al., 2021). More nuanced models of trophic interactions and the added complexity of the introduction of natural enemies for biological control can be added seamlessly (see Gutierrez & Ponti, 2022). Most important, because PBDMs capture the weather driven biology, they are not time-place specific and may be transferred to other regions, with the capacity to assess the effects of future climate change on the systems (e.g., Fig. 7). Lastly, marginal analysis of PBDM results allow examination of the target system from many perspectives (see Gutierrez & Ponti, 2022), helping to develop increased system sustainability and resilience in the face of social, cultural, economic, and climate change.

The PBDM approach has been used in many holistic analyses that challenged politically sensitive environmental issues such as questioning the fallacy of an eradication program in central California where the pest could not establish (Gutierrez & Ponti, 2013b), and the dystopic Indian hybrid Bt cotton system (Gutierrez et al., 2020). The PBDM approach can help bridge the pervasive gap between advocacy for, and successful implementation of, holistic solutions to invasive species and related environmental problems worldwide.

While the PBDM/GIS approach has an extensive record of success (see <http://www.casasglobal.org>) and has been proposed as an alternative to CSDMs at national and international scientific fora, adoption has been low because off-the-self software to develop PBDMs by scientists globally is currently unavailable. Hence, a clarion call is made for the development of dedicated laboratories to assemble the appropriate biological data (e.g., Fig. 3) required to build mechanistic models, and a generalized software system for developing PBDMs, enabling researchers globally to develop risk assessment models for invasive species of any taxa.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10668-023-03698-9>.

Acknowledgments The study was supported by the Center for the Analysis of Sustainable Agricultural Systems Global (CASAS Global, <http://www.casasglobal.org/>), Agenzia nazionale per le nuove tecnologie, l'energia e lo sviluppo economico sostenibile (ENEA), Rome, Italy, by project MED-GOLD funded by the European Union's Horizon 2020 research and innovation programme under grant agreement No. 776467, and project TEBAKA (project ID: ARS01_00815) co-funded by the European Union—European Regional Development Fund and European Social Fund, “PON Ricerca e Innovazione 2014-2020”.

Funding Open access funding provided by Ente per le Nuove Tecnologie, l'Energia e l'Ambiente within the CRUI-CARE Agreement.

Data availability statement The data generated during the current study are available in supplementary Table S1. These were generated by analyzing data from Ponti et al. (2021) that are available from the corresponding authors on reasonable request.

Declarations

Conflict of interest The authors declare no conflicts of interests.

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