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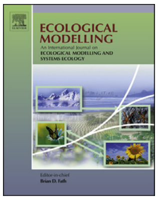

Modeling insect population fluctuations with satellite land surface temperature

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ABSTRACT

The simulation of insect pest populations in agricultural and forest ecosystems is an important and useful tool for integrated pest management (IPM). Insect population models are mainly driven by environmental temperature data, which are usually collected from agrometeorological stations or derived from geographic statistical extrapolations. The present study describes the modeling of olive fly (*Bactrocera oleae*) populations in the Eastern Mediterranean region using the MODIS (Moderate Resolution Image Spectro Radiometer) land surface temperature (LST) product from NASA TERRA satellite. These data, together with in situ temperature data, were used to estimate the tree-canopy temperatures at the pixel resolution (1 km). The estimated canopy temperature was used as input for the olive fly population model. Our main aim was to demonstrate the use of satellite-acquired information for modelling biological and ecological phenomena. Eleven years (2001–2012) of olive fly population fluctuations were simulated for three different geographic locations, representing different geo-climatic conditions. The model successfully simulated the seasonal population fluctuations throughout the 11-year period and did a good job of connecting all of the life stages of the insect. To evaluate the validity of these findings, we compared them with adult olive-fly trapping data. We observed a high degree of correlation between the trapping data and our model's predictions. Here, we demonstrate that satellite thermal data can be used to predict insect pest population fluctuations for IPM purposes. The study also advances some new modelling concepts, such as the "window of opportunity" which links physiological development with chronological age.

1. Introduction

Population modeling and epidemiological forecast models have traditionally been driven by temperature indices derived from meteorological stations and/or in situ data-loggers (Olatinwo and Hogenboom, 2014). For large geographic areas, temperature data from meteorological stations (usually separated by more than 10 km) are interpolated to create meaningful and useful spatial databases that can provide reliable topographic temperature data sets (Logan et al., 2004). Accuracy in temperature measurements is important for applying integrated pest management (IPM) in both forest and agricultural settings (e.g., Fand et al., 2014; Faye et al., 2014), for exploring the possible effects of global warming on ecosystems and organisms (e.g., Logan et al., 2004; Gutierrez et al., 2009; Ponti et al., 2009) and for developing strategies for the management of vector-borne diseases of humans and animals over large geographic areas (e.g., Rogers et al., 1996; Gilioli and Mariani, 2011; Amek et al., 2012; Chen and Hsieh, 2012). Recently, land surface temperature (LST) data derived from satellites have been proposed as a possible source of temperature data to be fed into insect population models and used to explore ecological and environmental questions (Carbajal de la Fuente et al., 2009; Coops et al., 2009; Chuang et al., 2012; Lensky and Dayan, 2011; Morag et al., 2012; Steinman et al., 2012; Blum et al., 2013; Aharonson-Raz et al., 2014). Lensky and Dayan (2011) used LST data to investigate the variability in the developmental rate of an agricultural pest (*Heliothis* sp.) found in a relatively small geographic area. They showed that differences (resulting from the local topography) in climatic conditions between fields separated by only few kilometers might be responsible for a three-week delay in the emergence of adult moths in the field.

The present study demonstrates the utilization of the estimated olive-tree canopy temperature derived from retrieved satellite data as input for a deterministic model of olive fly populations (Gutierrez

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Table 1
The five life stages of the olive fruit fly, their developmental time (*del*) in degree days (DD), temperature threshold for development (T_c) and the maximum chronological time (i.e., window of opportunity) for each developmental stage (in days). The window of opportunity provides the maximum theoretical time-period (based on laboratory and field for adults, survival curves) that the organism can stay in a specific stage before dying. If the organism is unable to accumulate the required energy (*del*) within the survival-derived time period, its probability of moving into the next developmental stage drastically decreases.

	Stage	*Del* [DD]	T_c [°C]	Window of opportunity [days]
1	Eggs	56	6.3	18
2	Larvae	187	6.3	40
3	Pupae	248	8	52
4	Adults	82	8	30
5	Reproductive adults	630	8	30

et al., 2009). Canopy temperature in olive trees (*Olea europaea* L.) is one of the main variables driving the developmental rate of the olive fruit fly immature stages, as well as the adult fly's reproductive maturation rate and behavioral patterns. Blum et al. (2013) derived a function to estimate olive grove canopy temperature from satellite data and demonstrated that this function provides estimates that are more accurate than those based on the interpolation of data from meteorological stations. Our main aim was, thus, to demonstrate the utilization of satellite-generated data sets as a source of information to run theoretical functions that "model" ecological and biological phenomena. We used the olive fly (*Bactrocera oleae*) as our model insect.

The female olive fruit fly usually lays a single egg in each olive fruit. However, under heavy population pressure, more than one egg can be found in a single olive fruit (Tzanakakis, 2003). After a few days and the accumulation of enough thermal energy, measured in degree days (DD; Allen, 1976; Ratte, 1984), the larvae hatch and start to feed on the mesocarp, inducing heavy economic damage due to early fruit-drop and low oil quality (Neuenschwander and Michelakis, 1978; Michelakis and Neuenschwander, 1983). Third instar larvae pupate in the fruit or soil and, after the accumulation of enough thermal energy, adult flies emerge. The emerging adults reach sexual maturity after accumulating at least 80 DD. Mature flies mate starting a new generation (Tzanakakis, 2003). Development at every stage depends on the environmental temperature sensed by the organism (i.e., accumulated DD; Allen, 1976):

$$DD = 0.5\,(T_{\max} + T_{\min}) - T_c \tag{1}$$

where $T_{\max}$ and $T_{\min}$ are the maximum and minimum temperatures during the day and T_c is the critical temperature for the development for each stage (see Table 1). The optimal temperature range for the development and activity of the olive fly is 23 to 29 °C. At higher temperatures, the probability of mortality increases for all stages and, at lower temperatures, reproduction and flight activity are reduced (Avidov, 1954). Population growth is also affected by the availability of the olive host (Tzanakakis, 2003). Thus, from the time the trees begin to bloom (spring), at which point all of the fruits from the previous year drop, until the new olive fruit reaches a certain size and maturity, these flies do not reproduce and lay eggs (Fletcher et al., 1978). In the Eastern Mediterranean, this period lasts from March to mid-June (Engelhard, 2012). The fly completes 4–5 generations in this area (Avidov, 1954).

The model simulations were performed for specific geographic locations in the Eastern Mediterranean for which we have field trapping data useful to validate and explore the ability of the system to predict population trends. We specifically asked if historical LST data can be used to simulate relatively long periods of population fluctuations of the olive fly in three geographic locations differing in their climatic profile. In addition, we explored the ability of the LST-population modeling system to predict population fluctuations by comparing predicted olive fly patterns with observed original trapping data. We hypothesized that the predicted adult olive fly population fluctuations during the summer and fall of the investigated years follow a similar, relative, increase pattern to the observed population fluctuations derived from adult trapping data.

2. Data and methods

2.1. Olive fly population modeling

2.1.1. The physiologically based demographic model (PBDM)

We used a continuous time-age olive fly population model in which the per capita age-structured dynamics of growth, development, reproduction and behavior are seen as driven by the environmental temperature (see Appendix 1 in Gutierrez et al., 2009 and Gutierrez, 1996 for a full description of the model). In this model, the population at each life stage (i.e., egg, larvae, pupae, non-reproductive adults and sexually mature adults) is described by the partial differential equation:

$$\frac{dN_i(t)}{dt} = \frac{k}{\text{del}}\left[N_{i-1}(t) - N_i(t)\right] - \mu_i(t)N_i(t) \tag{2}$$

in which $i = 1\ldots5$ is the developmental stage, t is the time, $N(t)$ is the (time-dependent) population density, del is the reference developmental time in DD (values in Table 1), $k = 40$ is the number of steps at each stage and $\mu_i(t)$ is the attrition or mortality rate (i.e., mortality/DD, see Section 2.1.3).

Since both independent variables (time and age) are in DD, each stage equation can be presented as a set of k (=40) ordinary differential equations for each cohort (i.e., 40 equal developmental age group, or bins, within each insect stage) in the form:

$$\frac{dr_i(t)}{dt} = \frac{k}{\text{del}}\left\{r_{i-1}(t) - \left[1 + \mu(t)\,\frac{\text{del}}{k}\right] r_i(t)\right\} \tag{3}$$

where r is the output flux from the kth cohort, defined as: $r = \frac{k \times N_i(t)}{\text{del}}$

The reference developmental time (del), which is the total amount of DD that are needed for the organism to complete each developmental stage, was assumed to be constant (see Table 1).

2.1.2. Attrition

The attrition rate, μ(t), sums all the processes that remove organisms from the population (e.g., death due to high temperature, killing by natural enemies and migration). In the present study, we included only the first of these processes. The mortality rate (attrition) at each stage was calculated by building a continuous temperature-dependent function based on data obtained in laboratory experiments and published by Pappas et al. (2011) (see our Appendix A).

2.1.3. Windows of opportunity

In the population model, we assume that movement from one stage to the next is dictated by physiological age (i.e., accumulation of DD). The time required to accumulate DD is usually shorter than the maximal time that the organism can survive in the given stage. However, if DD accumulation proceeds slowly due to low environmental temperatures, the organism may die from "uncompleted development." We refer to the probability of successfully moving from one stage to the other as the "window of opportunity." Using data presented by Tsitsipis (1980), continuous linear associations between survival/day vs. time (days) were calculated for egg, larvae and pupae. These linear associations provide the maximal possible period an individual insect can survive at each stage (i.e., the window of opportunity). The windows of opportunity for sexually immature adults and reproductive adults were derived from Yokoyama (2012) (see our Table 1 and Appendix A for details).