FORUM

Ecological Modeling and Pest Population Management: a Possible and Necessary Connection in a Changing World

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Modelagem Ecológica e Manejo de Populações de Pragas: Uma Conexão Possível e Necessária para um Mundo em Transformação

RESUMO - A modelagem ecológica é uma ferramenta importante para a investigação de padrões de comportamento dinâmico em populações, interações tróficas e também em ecologia comportamental. Contudo, os padrões ecológicos que refletem tendências de oscilação populacional muitas vezes não são claramente visíveis sem instrumentos analíticos, como os modelos ecológicos. Dessa forma, a modelagem ecológica exerce papel fundamental na descrição de processos demográficos importantes para a dinâmica populacional. Os modelos ecológicos, além de tornarem possível a visualização de padrões ecológicos, podem também revelar padrões de persistência populacional nos diversos sistemas tróficos, incluindo as relações presa-predador ou hospedeiro-parasitóide, interações comumente presentes em programas de manejo integrado de pragas. Neste fórum apresentamos os principais aspectos ecológicos importantes para a construção de modelos e implementação de programa de manejo de pragas em insetos. Em particular, analisamos a combinação entre modelos hospedeiro-parasitóide e o conceito de nível de dano em escala espaço-temporal. Como conclusão sobre a combinação de modelos, evidencia-se que a estrutura espacial é essencial para modelos desta natureza, já que sua introdução no sistema altera significativamente os valores de nível de dano econômico.

PALAVRAS-CHAVE: Ecologia teórica, manejo integrado de pragas, modelo matemático

ABSTRACT - Ecological modeling is an important tool for investigating dynamic behavior patterns in populations, trophic interactions, and behavioral ecology. However, the ecological patterns that reflect population oscillation trends are often not clearly visible without analytical instruments such as ecological models. Thus, ecological modeling plays a fundamental role in describing demographic processes that are important for population dynamics. Ecological models, besides making possible the visualization of ecological patterns, may also reveal patterns of population persistence in many trophic systems, including prey-predator or host-parasitoid relationships, interactions that are commonly present in integrated pest management programs. In this forum, we present the main ecological aspects important for model building and implementation of integrated pest management programs for insects. Particularly, in this study, we analyze the combination between host-parasitoid models and the concept of economic threshold level on a spatio-temporal scale. As a conclusion about the model combination, spatial structure is essential for models of this nature, since its introduction into the system significantly alters the economic threshold-level values.

KEY WORDS: Theoretical ecology, integrated pest management, mathematical model

Why Combine Ecological Modeling with Pest Population Management?

Many textbooks, reviews, and scientific papers mention the importance of the connection between population theory and laboratory experiments or field data (Kareiva 1989, Kot 2001). At the same time, increasing numbers of articles have been published in order to convince theoretical ecologists and entomologists to work together as multidisciplinary teams in order to discover or improve the comprehension of

ecological patterns and population trends including cycles, peaks, or crashes (Kareiva 1989, Costantino *et al* 1995, 1997, Cushing *et al* 2003, Hilker & Westerhoff 2007). Generally, these patterns are strongly associated with endogenous and/ or exogenous forces (Gotelli 2008). For this reason, the relationship or correlation of these factors with population abundance have been intensely explored in recent decades. In addition, the terrestrial biome has undergone intense and rapid changes, mainly since the past century, probably resulting in new ecological patterns as a result of the pressure exerted by these changes on the organisms (Memmott *et al* 2007, Gillman 2009).

The expression "changing world" is present or implied in many papers, magazines, newspapers, or even titles of scientific meetings. Particularly, in entomology there is an increasing concern about the changing world associated with pest outbreaks, environmental noise, biological invasions, and the establishment of exotic species in new areas (Hengeveld 1989, Cushing *et al* 2003, Hilker & Westerhoff 2007). The reason for this concern stems from the role of insects as pests in agriculture and animal and human health, and at the same time as essential integrants of biodiversity. Finally, the effects of a changing world are essentially reflected in the temporal and spatial dynamics of the populations. However, to investigate rapid transformations with a high level of complexity is not a trivial exercise, at least to understand them in their totality (Hastings 1997).

The best approach for analyzing such complex systems could be simplification (Gotelli 2008). A mathematical model is essentially a caricature of a system and may function as an important prototype to be investigated, mainly because of its simple structure (Hastings 1997). Therefore, to model systems could be a first step to understand partially complex systems, mainly because an important characteristic of models is their flexibility, which allows a gradual introduction of complexity. Our intention in this forum is to show, first, what are the major points currently listed by ecologists and entomologists, that may impede the comprehension of insect population behavior and consequently the implementation of Integrated Pest Management (IPM). Secondly, we would like to show the most important ecological aspects for a management program, and finally, to give some examples of how management and theoretical ecology can be combined to improve the comprehension of essential patterns or trends in an IPM context.

Food Supply and Insects

Food production around the world is a constant and challenging human task, which requires rapid and practical responses, mainly with respect to pest control (Berryman 2002). However, history shows that rapid solutions for this problem may dramatically affect the environment, fauna, and flora, and also the quality of human life. For example, the discovery of DDT in 1939 brought a rapid solution for the pest problem at that time, but the residual damage to the terrestrial biome by the indiscriminate use of this substance is probably incalculable.

Eleven years ago, Yudelman *et al* (1998) stated that the food supply in developing countries needed to rise 70% by 2020 to keep pace with the growth of human populations, requiring both a sustained increase in food resources and a significant reduction in losses due to pests in these areas. There are also an increasing number of malnourished people worldwide, which requires an increase of the current levels of food production (Kindall & Pimentel 1994).

Malthus was the first to project the insufficiency of food supply for humanity, and unfortunately his predictions are being confirmed, in spite of the optimism produced by the good agricultural performance exhibited by some countries in recent years (Kindall & Pimentel 1994). New technology and agricultural practices have substantially contributed to increase the agronomic potential of plants by using recombinant DNA techniques, and new varieties of cultivars have been developed, employing genes from wild varieties to improve disease resistance (Thompson & Head 2001). However, the demand for food seems always below the real requirements of humanity, resulting in negative prospects for the future. If we associate this demand with factors that limit food distribution, as for example the damages caused by insect pests, we will really have pessimistic projections for the future.

Pesticides and IPM

Two points affecting insect pests have been discussed in recent years: the use of pesticides and IPM strategies (Ferron & Deguine 2005). Even with the implementation of intense efforts to control insects, pest management persists as a significant challenge for this century (Ferron & Deguine 2005). The use of pesticides has been increasing in many parts of the world, and their excessive application contaminates foods, the environment, and growers, besides killing the natural enemies of pests (Altieri 1999).

Future developments with IPM involve a blend of different techniques (Metcalf & Luckmann 1994, Thacker 2002) including cultural techniques and agronomic practices such as resistant varieties, crop rotation, tillage, fertilization, sanitation, trap crops, pruning, etc. As mechanical techniques we can list hand destruction, trapping devices, and pest exclusion. Certainly, physical and chemical techniques including heat, cold, humidity, sound, irradiation, pheromones, sterilants, growth inhibitors, and pesticides will be among the usual control mechanisms (Thacker 2002).

Regulatory methods such as quarantine, eradication, and legislation will comprise part of the blend of practices. Finally, biological methods, which have received increasing attention in recent years, will also be among the most commonly used methods. They include classical biological control, conservation, augmentation, and inundation with predators, parasitoids, and/or pathogens (Thacker 2002). In particular, genetic techniques such as sterile insect release and engineered organisms are under intense development for immediate application. Although the importance of this new scenario is generally recognized, the available scientific and economic information does not accurately project the possible effects of the use of modern pesticides and/or the

above-mentioned control methods on insect pests, as well as on human health and on the environment (Thacker 2002, Ferron & Deguine 2005).

Global Warming and Insects

The earth's surface is predicted to warm by approximately 1.5°C to 6°C by 2100 (Kiritani 2006). Global warming associated with greenhouse gases is expected to affect insect populations by changing their host plants in quantity and quality (Scriber & Slansky 1981). Global warming will also influence the distribution of species, magnitude of demographic parameters, seasonality, number of annual generations, and time synchronization between insects and plants or their natural enemies (Kritani 2006, Feehan *et al* 2009). This emerging scenario has important consequences for humanity, with real implications for the population dynamics of pest insects, food production, and epidemiology of diseases (Ferron & Deguine 2005, Andrew & Huges 2007). Losses caused by insects under the global-warming effect are estimated at between 25% and 100% depending on the crop (Pimentel 1993). Massive degradation of forests in response to global warming has also been reported from many parts of the world (Uniyal & Uniyal 2009). The consequences of these changes may be attributed not only to the high temperatures, but perhaps to the rate of population increase (Root & Schneider 1993), changes in mortality rates, shortening of seasons, and a consequent increase of annual generations (Kiritani 2006).

Recently Kearney *et al* (2009) investigated key factors affecting the dynamics of the mosquito dengue vector *Aedes aegypti* (L.), showing that climate changes in Australia may allow the expansion of mosquitoes into many regions of the continent. The spatial distribution of malaria vectors depends on the latitude, altitude, and temperature. With the recent climate changes, the boundaries of malaria-transmission regions may be changing in response to increasing temperatures (Patz & Lindsay 1999). As an example, Europe has experienced the introduction of vector-borne diseases from tropical areas, for example Africa (Takken & Knols 2007), and two cases of dengue were notified in Florida in 2009 (http://www.keysmosquito.org/dengue_fever.html). In addition, the potential risk of a dengue outbreak has been assessed in North Central Texas in response to three imported dengue cases (Lee *et al* 2009a, b). This kind of prediction supported by clear notifications leads to important discussions about the epidemiology of diseases transmitted by insect vectors in new areas.

Scenarios, Ecological Theory, and IPM

Scientific actions are often theoretically minded (Berryman 2002) and commonly focused on understanding how systems work. Jointly, the complexity of nature is an attractive scenario for applying complex reasoning and sophisticated analytical tools (Cushing *et al* 2003). The puzzle naturally emerging from this ambiguous scenario is how to connect theoretical science with experimental designs to measure and improve systems production without causing environmental damage. This point has been a growing challenge for scientists, production managers, growers, ecologists, and entomologists.

The scenarios described in the previous paragraphs give us an opportunity to reflect about the efficiency of the analytical tools available to monitor and control pests, mainly in developing countries. Ecological theory is certainly an important ingredient of research programs concerned with monitoring and pest control (Berryman 2002). The ecological bases are always expected to be connected to pest-control programs (Kogan & Jepson 2007). Among the most important aspects of ecological theory from the viewpoint of the Integrated Pest Management (IPM), we can mention the temporal course of insect populations (Kogan & Jepson 2007).

The time trajectory of insect populations can exhibit ecological patterns which may describe important trends that can indicate susceptibility to crashes or outbreaks (Kogan & Jepson 2007). Another relevant question in this context concerns the fluctuation of insects over time and space. Unfortunately, this is not an easy question to answer, but understanding insect fluctuation in ecological patterns and predicting outbreaks are essential ingredients to support appropriate management decisions (Pedigo & Zeiss 1996). For example, nonlinear dynamics is a prevalent aspect of animal populations, including insects (Cushing *et al* 2003), and it has been mentioned as an ecological pattern associated with a high probability of extinction (Belovsky *et al* 1999). Nonlinear dynamics may also be associated with the presence of recurrent peaks in population numbers (Berryman 1987, Dwyer *et al* 2004). The prevention of insect outbreaks has been a constant concern for entomologists for many years (Berryman 1987), and modern IPM takes into account important ecological aspects involved in insect pests in an attempt to provide alternative strategies to monitor and control pest populations (Tang & Cheke 2008).

Currently, the use of traditional pesticides is partially controlled in order to ensure human and environmental safety and contain the development of insect resistance (Thompson & Head 2001). Insect pest population management programs have been implemented for decades in an attempt to control pests (Yuldeman *et al* 1998). Nevertheless, in practice, rarely do the programs incorporate all the components that are necessary to periodically evaluate the status of pests.

Monitoring is essentially a quantitative tool that provides information about the status of a pest (Pedigo & Zeiss 1996). Nevertheless, monitoring abundance also means to investigate trends in time and space (Bart *et al* 1998). Management of pest species also implies the analysis of ecological patterns by investigating the distribution frequency of insects in order to evaluate the spatial dispersal pattern and to develop standard sequential decision plans (Pedigo & Zeiss 1996). Plans for sampling insect populations have been regularly implemented for the purpose of IPM decision-making, taking into account at least three components: pest population density, economic threshold, and the phenological forecast (Binns & Nyrop 1992, Heong *et al* 2002, Arnaldo & Torres 2005, Spencer *et al* 2009).

Ecological and Intuitive Bases for Modeling and Pest Management Integration

An ecological model can be considered as a caricature or perhaps a simplification of a system (Kot 2001). However, in spite of its limitations, modeling is viewed as an important step toward better understanding and improved decision making, mainly in the context of dynamic systems as observed in pest populations (Hastings 1997, Roughgarden 1998). The use of models as an attempt to understand interactions, for example the prey-predator system, was initially suggested by Vito Volterra in the first years of the 20th century (Volterra 1926). The motivation was the oscillation commonly observed in Adriatic fisheries, which was described theoretically by formulating differential equations in order to show how the interaction between predator and prey could drive sustained oscillations (Volterra 1926). Hence, mathematical ecology emerged as an interesting and intriguing area designed to capture the essence of the interactive systems. Almost simultaneously, another mathematical ecologist, Alfred Lotka, developed similar equations in an attempt to model ecological problems (Lotka 1925). Other famous scientists in this era, Nicholson and Bailey, also proposed models for predator-prey interactions (Nicholson & Bailey 1935).

Thanks to these scientists, ecological modeling nowadays has an important role in determining the most important processes in biological systems. Ecological modeling can be comprehended essentially as the art of capturing the essence of biological systems in order to investigate their dynamics based on specific parameters, which lend realism to the system if they originate from or reproduce the real data. The most important ability of a modeler is to correctly decide on a suitable level of complexity to be applied in a system. The abstraction is the first step to construct a new model (Hannon & Ruth 1997, Roughgarden 1998). Abstractions consist of focusing on the main points of a system and in capturing its essence, building the best caricature. The subsequent steps consist of describing the system by mathematical equations based on assumptions that are capable of well representing the system.

Insect biological control theory has a history associated with theoretical ecology, with emphasis on interactions between a host and a parasitoid (Hassell 1978, Mills & Getz 1996, Hochberg & Ives 2000). The basic framework for parasitoid-host models can be written as a generalized predator-prey model (Nicholson & Bailey 1935) of the form

Host$_{t+1}$ = (net rate of increase) Host$_t$ (host survival with respect to parasitoid and host densities)
Parasitoid$_{t+1}$ = Host$_t$ [1- (host survival with respect to parasitoid and host densities)].
or

$$H_{t+1} = rH_t f\left(H_t, P_t\right) \tag{1}$$

$$P_{t+1} = H_t \left[1 - f\left(H_t, P_t\right)\right] \tag{2}$$

Assuming $f(H_t, P_t) = exp(-aP_t)$, where a is the parasitoid's area of discovery, a searching efficiency, this model is suitable to describe the host-parasitoid interaction in a very simple way (Hassell 1978), and is analogous to the Lotka-Volterra Prey-Predator model except for the discrete time formulation. The density-dependence has a stabilizing effect on the dynamics of this model by introducing the term *H/K* into the host equation (Beddington *et al* 1975)

$$H_{t+1} = rH_t \exp\left[r\left(1 - \frac{H}{K}\right) - aP_t\right] \tag{3}$$

$$P_{t+1} = H_t \left[1 - \exp\left(-aP_t\right)\right] \tag{4}$$

This formulation does not take into account the handling time spent by the parasitoid on the host during the attack period. To do this, it is necessary to consider the functional response, i. e., an increase of the number of hosts parasitized per parasitoid in response to the increase of host density. The most common type of functional response observed in insects is Type II (Holling 1959), where the consumption or the parasitism rises asymptotically to saturation. The Type II functional response can be expressed by introducing the handling time term into the equation (4). In this case, the function $f(H_t, P_t)$ can be written as

$$f\left(H_t, P_t\right) = \exp\left(\frac{-aTP_t}{1 + aT_h H_t}\right)$$

where T is the constant searching time available and T_h the handling time required for a parasitoid to oviposit on each host. Including these constants, the equations (3) and (4) are described by

$$H_{t+1} = rH_t \exp\left(\frac{-aTP_t}{1 + aT_h H_t}\right) \tag{5}$$

$$P_{t+1} = H_t \left[1 - \exp\left(\frac{-aTP_t}{1 + aT_h H_t}\right)\right] \tag{6}$$

Ecological Host-Parasitoid Model and the Economic Threshold

Recently, Tang & Cheke (2008) extended the classical host-parasitoid model, including the Integrated Pest Management (IPM) control program in order to consider the economic threshold as a component of the formulation. The results found in this study suggest that it is possible to maintain the host level below the economic threshold (ET), avoiding the economic injury level (EIL). In addition, they showed that a high initial density of parasitoids, as well as high parasitoid inter-generational survival may significantly influence the ecological pattern of the time series (Tang & Cheke 2008).

The interactive dynamics of host and parasitoid investigated by Tang & Cheke (2008) is based on the Nicholson & Bailey (1935) formalism. Thus, the dynamics of interaction between parasitoid and host with discrete generations is given by

$$H_{t+1} = f\left(H_t\right)H_t g\left(H_t, P_t\right) \tag{7}$$

$$P_{t+1} = \gamma H_t \left[1 - g(H_t, P_t)\right] + \delta P_t \qquad (8)$$

where H and P are the host and parasitoid densities respectively, in successive generations t and $t+1$, $f(H)$ is the growth function of the non-parasitized host, $g(H,P)$ is the fraction of the host escaping parasitism (one minus this term gives the fraction of hosts parasitized), γ is the mean number of female parasitoids emerging from a host (usually $\gamma \leq 1$ due to egg mortality and the fact that only one parasitoid can emerge from each host) and δ is the density-independent parasitoid survival. The Tang & Cheke model assumes a logistic population growth for hosts and a Type II functional response for parasitoids, given by

$$f(H_t) = \exp\left[r\left(1 - \frac{H_t}{K}\right)\right] \text{ and } g(H_t, P_t) = \exp\left(\frac{-\alpha T P_t}{1 + \alpha T_h H_t}\right)$$

where r is the growth rate, K is the carrying capacity, α is the chance of encounter between host and parasitoids, T is the total time available for host searching, and T_h is the host handling time.

In IPM programs, usually both pesticide spraying and parasitoid release take place when the population density of the host reaches the economic threshold. To be clearer, Fig 1 shows the population dynamics of a pest with an oscillatory dynamics and the respective economic threshold (ET) and economic injury level (EIL). When the density of the hosts reaches the *ET* level, control methods such as pesticide or parasitoid release are applied (intervention) in order to keep the host density below the *EIL*. The incorporation of this strategy into the model suggests that equations (7) and (8) should be written as

$$\left.\begin{array}{l} H_{t+1} = f(H_t) H_t g(H_t, P_t), \\ P_{t+1} = \gamma H_t \left[1 - g(H_t, P_t)\right] + \delta P_t \end{array}\right\} if \quad f(H_t) H_t g(H_t, P_t) \leq ET, \qquad (9)$$

$$\left.\begin{array}{l} H_{t+1^+} = ET, \\ P_{t+1^+} = P_{t+1} + \tau \end{array}\right\} if \quad f(H_t) H_t g(H_t, P_t) > ET, \qquad (10)$$

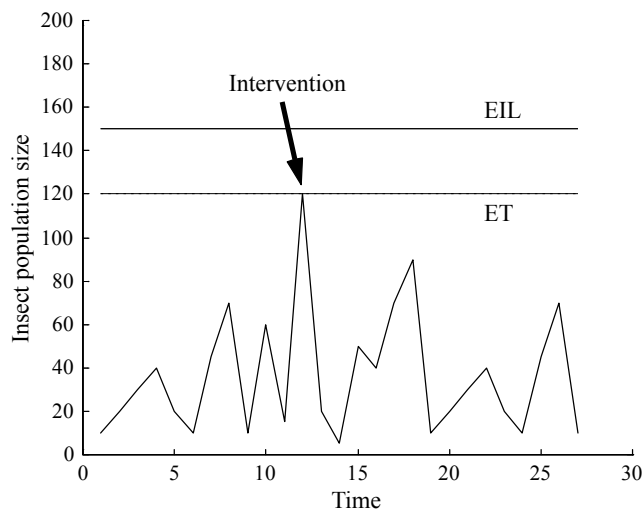$$H_{0^+} = H_0 < ET, \quad P_{0^+} = P_0 \qquad (11)$$

Fig 1 Dynamics of the insect population, showing the economic injury level (EIL) and economic threshold (ET).

Therefore, equations (9) describe the dynamics of hosts and parasitoids when the host density does not reach the economic threshold, and equations (10) are designed to show the dynamics of hosts after the control actions at time *t*. The number of parasitoids released at time *t* is given by τ. Assuming that the initial density of the host is always less than *ET*, the instantaneous mortality rate in response to the pesticide may be estimated as

$$T_t^d = \begin{cases} 1 - \dfrac{ET}{f(H_t) H_t g(H_t, P_t)}, & if \quad f(H_t) H_t g(H_t, P_t) > ET, \\ \qquad\qquad 0, & otherwise. \end{cases}$$

Ecological Host-Parasitoid Model with Economic Threshold and Spatial Structure

The spatial structure can be added to equations (9) and (10) using the formalism of coupled map lattices, based on the spatial dynamics theory (Bascompte & Solé 1994, Bonsall & Hassell 2000). Space is introduced as a discrete lattice, with the host and parasitoid population arranged on each site (patch) of the lattice. Further, populations belonging to different patches are linked with dispersal to the nearest neighbor. In the simulations, we used a square lattice with 101×101 sites, reflective boundary condition (the cyclic boundary condition was also implemented, and gave the same qualitative results), and synchronous updating.

For each generation, the dynamics consist of two phases: dispersion phase and reproduction-parasitism phase. The diffusion processes can be modeled in several ways, and we chose two to explore: (1) Type I diffusion: the diffusion is density-independent, and therefore, in each generation, a fixed proportion of individuals (μ_H for host and μ_P for parasitoid) leave the original patch and colonize, in equal proportions, the eight neighboring patches (Moore neighborhood of radius one) (Hassell *et al* 1994, Comins & Hassell 1996); (2) Type II diffusion: in each patch the host population size is measured. If $H_t \geq Dif_{min}$, where Dif_{min} is the minimum host population size necessary for diffusion, the host population searches in the neighborhood for a patch with lower host density. Similarly, the parasitoid population chooses a neighborhood patch with the highest host abundance. In other words, hosts search for sites with low host density in order to minimize the effects of competition, and parasitoids search for places with a high abundance of hosts to assure effective parasitism. Finally, during the reproduction-parasitism phase, the dynamics of the host and parasitoid populations are governed by equations (9) and (10).

Simulations started with $H_0 = 10$ (host population), $P_0 = 1$ (parasitoid population) in the center of the lattice, and all other patches empty.

Host-Parasitoid Spatial Dynamics with *ET*

In the simulation we assumed a specialist parasitoid ($\delta = 0$) and $\gamma = 0.6$. The result for the non-spatial and non-ET model (equation 9) is a two-point limit cycle, which defines host and parasitoid populations oscillating between two

equilibrium points (Fig 2). The other parameters are *r = 0.9, K = 150, α = 0.001, T = 100* and T_h *= 1*.

Fig 3 shows the temporal evolution of the host and parasitoid population when an IPM program is in progress. The economic injury level was defined as *EIL= 45* and the system dynamics was managed to allow the host density to fall below the *EIL* level. In order to achieve our goal, we must consider the economic threshold as *ET = 30*. Using this strategy, the temporal evolution of the coupled population is also a cycle; however, the host populations are maintained below *EIL = 45* and the frequency of oscillation is higher than that observed in Fig 2.

The instantaneous mortality rate (equation 11) in response to the pesticide can be estimated, and adding it to the previous case can improve IPM strategies by determining both the optimum period of applications and the percentage of pests that need to be eliminated with pesticides. For this set of parameters, the IPM should be applied at intervals of five generations and the pesticide should kill approximately 18% of the population (Fig 4). As a result, we can develop an IPM program without needing to periodically measure pest density.

Now considering the spatial dynamics discussed previously, the dispersal rate for the host population as μ_H *= 0.25*, for the parasitoid population as μ_P *= 0.2* and Type I diffusion, Fig 5 shows that the spatial structure negatively affects the efficacy of the IPM strategies. Observe that the density of the host population is above the *EIL* and consequently, the *ET* level should be lower when spatial structure is considered, to assure that the host density remains below the *EIL* level. The pattern generated by this kind of diffusion is a symmetrical wave front of highest host density, dispersing from the center to the lattice to the border (Fig 6). The same result related to a decrease in the efficacy of the IPM strategy is observed, changing from Type I to Type II diffusion (Fig 7). The main difference is that now we have a random distribution pattern instead of a wave pattern. Therefore, when spatial structure is considered, in order to achieve an efficient IPM strategy, the economic injury
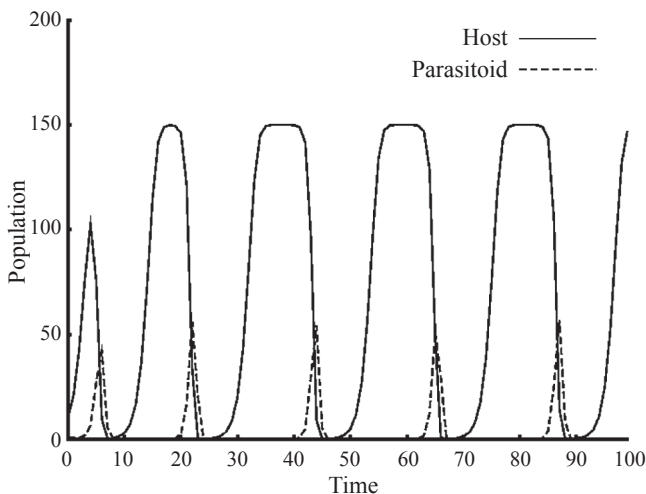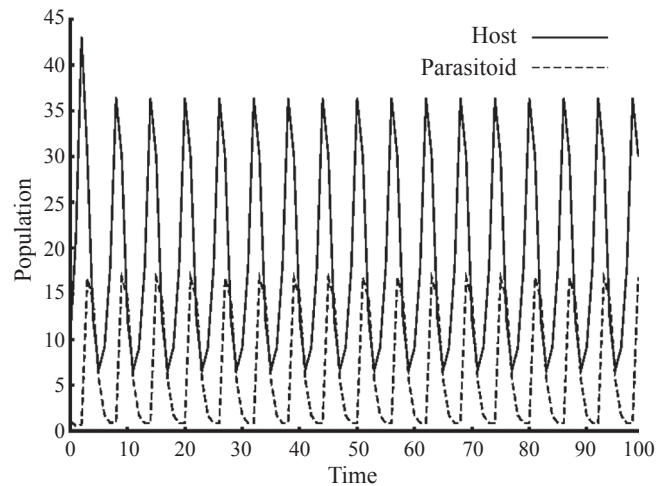

Fig 3 Population dynamics of host (solid line) and parasitoid (dashed line) as a function of time with IPM strategies and without spatial structure.

from the pest should be studied as a function of the applied *ET* levels. Fig 8 shows the economic injury normalized as a function of the maximum value of injury for different *ET* levels. We can observe that, in order to assure that the host density does not cause loss of production, the ET should be lower than *ET = 22*.

In this study, we showed a theoretical case of pest population involving IPM strategies, with the addition of spatio-temporal scales and ecological assumptions to illustrate how the combination of theoretical ecology and pest management can provide interesting and important results. The results shown here suggest that for the success of IPM strategies, the spatial structure of the systems should be taken into account in pest control programs, because migration among local populations may cancel the effect produced by the *ET*. There is no systematic study exploring the connection between IPM strategies and spatial structure. Those studies focused on spatial structure in insect population have emphasized more the spatial synchrony and enemy-victim interactions, showing that dispersal may attenuate the

Fig 2 Population dynamics of host (solid line) and parasitoid (dashed line) as a function of time without IPM strategies or spatial structure.
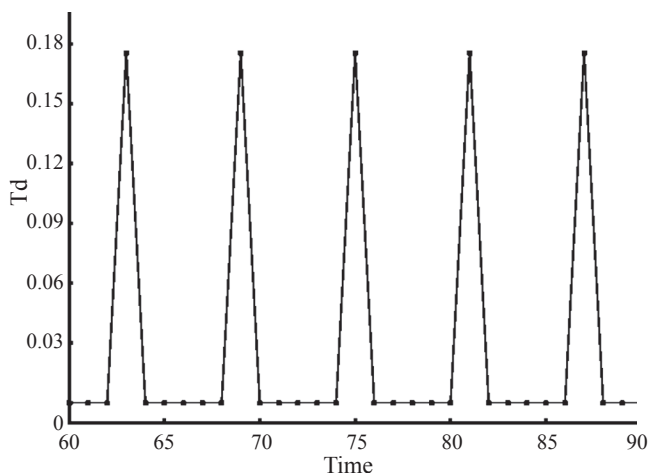

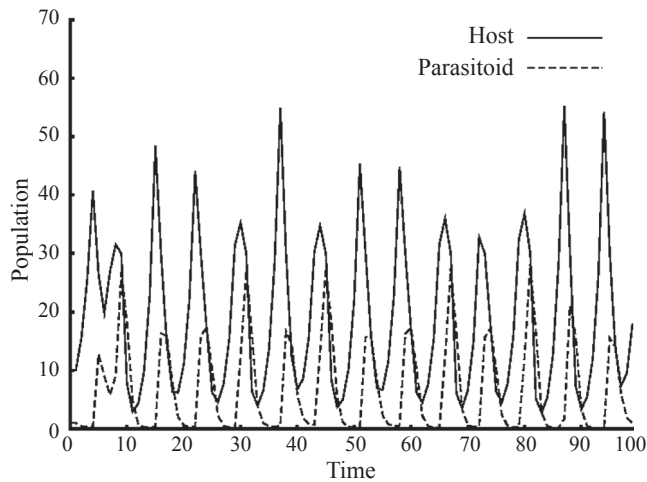Fig 4 Instantaneous mortality rate as a function of time.

Fig 5 Population dynamics of host (solid line) and parasitoid (dashed line) as a function of time with IPM strategies and spatial structure. The results are shown for the central site in the lattice.

local extinction among coupled populations (Taylor 1990, Bonsall & Hassell 2000).

In a previous study, Hassell *et al* (1991) proposed a cellular automata model to investigate how the movement among patches may help the persistence of hosts and parasitoids. They observed that spatial dynamics in parasitoid-host systems depends essentially on the fractions of hosts and parasitoids dispersing among patches, with low rates of host dispersal leading to chaotic oscillations (Comins *et al* 1992). Chaotic patterns in insect populations indicate unpredictable trajectories, which may be important for IPM strategies, since they may suggest the occurrence of outbreaks or crashes (Tang & Cheke 2008). However, spatial structure plays an important
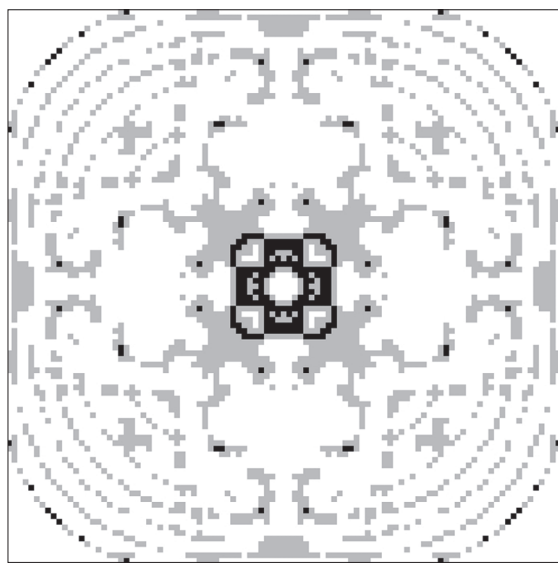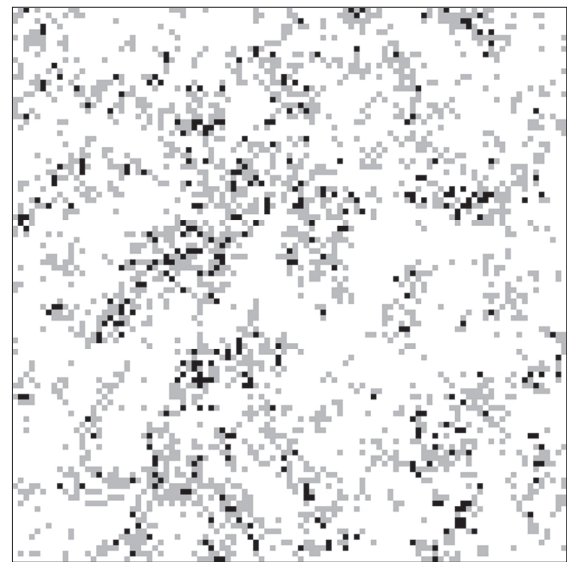

Fig 7 Spatial distribution of population density for Type II diffusion. Different levels of shading represent different densities of the host, respectively, H < ET (white), ET ≤ H <EIL (gray), H ≥ EIL (black).

role in dynamic systems such as parasitoid and hosts (Hassell *et al* 1991, Comins *et al* 1992, Hassell *et al* 1994, Comins & Hassell 1996). Habitats certainly vary considerably from each other, and this variability affects the demographic rates of local populations (Hanski 1999). Heterogeneity has been considered as crucial to host-parasitoid persistence (Cronin 2003). The risk of parasitism is an evident point which is strongly related to density-dependent aggregation in patches of high density of hosts (Comins & Hassell 1996).The comprehension of processes such as this has been a major concern of theorists. The integration of population theory and experimentation is also necessary for a better comprehension of these interactions, considering the spatial scale (Cronin 2003). Particularly, the connection between dynamic models with IPM strategies and the spatial structure has not been investigated systematically with an emphasis on pest insects.
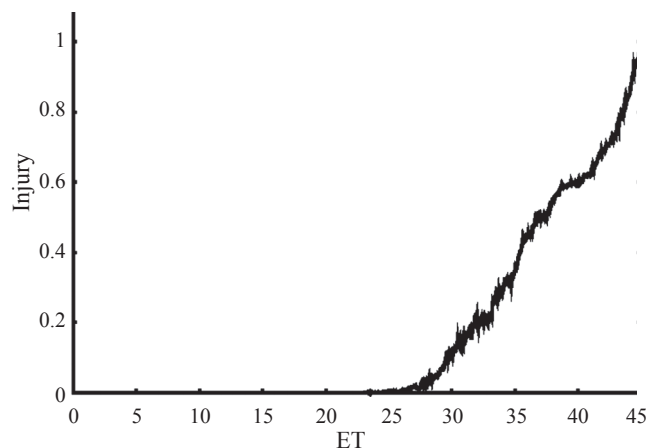

Fig 6 Spatial distribution of population density for Type I diffusion. Different levels of shading represent different densities of the host, respectively, *H < ET* (white), *ET ≤ H <EIL* (gray), *H ≥ EIL* (black).

Fig 8 Injury caused by the host density as a function of different *ET* levels.

However, the first studies have provided theoretical insights, which are helpful to create an initial perspective of IPM combined with ecological theory.

Acknowledgments

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