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A Theoretical Approach to Analyze the Parametric Influence on Spatial Patterns of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) Populations

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Abstract

Studies of the influence of biological parameters on the spatial distribution of lepidopteran insects can provide useful information for managing agricultural pests, since the larvae of many species cause serious impacts on crops. Computational models to simulate the spatial dynamics of insect populations are increasingly used, because of their efficiency in representing insect movement. In this study, we used a cellular automata model to explore different patterns of population distribution of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), when the values of two biological parameters that are able to influence the spatial pattern (larval viability and adult longevity) are varied. We mapped the spatial patterns observed as the parameters varied. Additionally, by using population data for *S. frugiperda* obtained in different hosts under laboratory conditions, we were able to describe the expected spatial patterns occurring in corn, cotton, millet, and soybean crops based on the parameters varied. The results are discussed from the perspective of insect ecology and pest management. We concluded that computational approaches can be important tools to study the relationship between the biological parameters and spatial distributions of lepidopteran insect pests.

Introduction

The order Lepidoptera comprises many insect pests, such as *Helicoverpa armigera* (Hubner), *Helicoverpa zea* (Boddie), and *Anticarsia gemmatalis* (Hubner), whose larval stages cause damage to crops (Mironidis & Savopoulou-Soultani 2008, Milano *et al*. 2010, Reigada *et al* 2016). One of the most important lepidopteran pests is the fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), a polyphagous pest widely distributed in North and South America, which attacks several crops including corn (maize), cotton, and soybean (Barros *et al* 2010).

Understanding the relationship between biological parameters and spatial patterns of insect pest populations in agricultural landscapes may provide useful information for the implementation of integrated pest-management programs (IPM), since it can indicate the invasion potential of a pest (Deffontaines *et al* 1995, Steingrover *et al* 2010). One possible approach to study spatial patterns is the use of computational models.

Spatial models have been widely used to study patterns of insect distribution. Hassel *et al* (1991) found different patterns of host-parasitoid dynamics, such as spiral waves, by altering the parameter values of a Nicholson-Bailey model projected on a lattice of cells. Petrovskii *et al* (2014) reviewed ways to use spatial models to estimate insect density in IPM programs, discussing mathematical approaches at the spatial scale, including random walks and networks. Cerda & Wright (2004) developed a model to test the impact of different refuge sizes and configurations in an agricultural landscape composed of transgenic and non-transgenic crops (refugia) on the evolution of insect resistance to transgenic crops.

Garcia *et al* (2014) presented a computational model to simulate the dynamics of *Diabrotica speciosa* (Germar) (Coleoptera: Chrysomelidae) over different intercropping landscapes, and concluded that intercropping systems composed of corn and soybean were the most efficient in reducing populations of this beetle.

The growing interest in theoretical studies has led ecologists to use spatially structured models such as cellular automata (CA), which allow one to detail the spatial traits of a system (Garcia *et al* 2014). CA are discrete, dynamic systems, in which the space is represented as a grid of cells that assume different states along the time steps. Cell states can change over time by means of transition rules that can represent stochastic or deterministic processes. Therefore, one of the greatest advantages of using CA is the possibility of describing different stages of insect development, by using discrete cell states that can change by means of rules based on insect biology (Hiebeler 2005).

In this theoretical study, we present a cellular automata model to describe the spatial distribution of *S. frugiperda* populations. Our main goal was to investigate different spatial patterns that may develop when larval mortality and adult longevity are varied. We decided to develop a model based on these two parameters because they indicate the survival of two insect stages that are important for pest management. Most control strategies focus on reducing the viability of larvae within the period when the insect feeds on plants. On the other hand, the length of the adult stage is directly related to the period when the insect is reproducing and laying eggs. In order to represent the species in our CA, we designed the transition rules and defined the interval of parameter values based on population data from *S. frugiperda* populations studied in laboratory conditions.

Some investigators have focused on studying spatial patterns of *S. frugiperda* in agricultural contexts, such as Carroll *et al* (2012), who developed a spatial model to study the spatial dynamics of *S. frugiperda* in *Bt* and non-*Bt* maize. Our study used a different approach, focusing on studying the influence of biological parameters on population spatial patterns, rather than the influence of landscape configuration and composition. We intended to use the computational model to study theoretically the influence of these parameter variations on the spatial patterns of an important lepidopteran pest, discussing the possible factors that can lead to these patterns in agricultural systems. We also determined the expected spatial patterns of population distribution in corn, millet, soybean, and cotton fields (the main crops attacked by this pest) by using parameter values obtained in the laboratory when *S. frugiperda* was reared on these hosts. The information from this study is especially applicable to homogeneous landscapes, such as large corn and soybean fields.

Material and Methods

Cellular automata

We developed a system of cellular automata in the C programming language in order to represent the life cycle of holometabolous insects, i.e., we represented the immature and adult insect stages differently. We chose this approach because lepidopteran insects are holometabolous. We also assumed that only adults could move along the landscape and lay eggs (flying stage). In order to represent the two stages, we constructed two stochastic cellular automata, CA-1 and CA-2, respectively, for immatures (larvae and pupae) and female adults, each with 600 × 600 sites. We decided to include only females in CA-2 because they are responsible for laying eggs, connecting CA-1 and CA-2. In CA-1, a cell could be empty (0) or occupied by only one larva. This assumption was based on the horizontal distribution of *S. frugiperda* larvae (mean number of larvae per corn plant), according to Farias *et al* (2001). Only one larva per plant is observed in farm fields because this species is highly cannibalistic, which reduces the number of individuals. Therefore, in our simulations, we simplified the system, assuming one larva per plant as observed in the field.

In CA-2, a cell could be empty (0) or occupied by a number of adults <10. We also used a parallel update with fixed boundary conditions, which means that the first and last rows and columns of cells in the lattice remained unaltered and were equal to 0 (absence of individuals). Each time step, t, corresponded to 1 day, and each cell of the CA represented 1 × 1 m of the crop system. An age-counter was associated with each insect in order to indicate its age (i for immature period and a for adult period). The following rules describe the dynamics of holometabolous insects used in our approach (Garcia *et al* 2014, Garcia *et al* 2016):

1.   CA-1 larvae/pupae population dynamics

   a.   A cell occupied by a larva or pupa could become empty with probability $\theta (i) + \delta (i)$ due to mortality or adult emergence, respectively.
   b.   An empty cell could become occupied by a larva if an adult (in a Moore neighborhood of radius 2) lays eggs in it with probability $\tau (a)$ corresponding to the per-capita oviposition.

2.   CA-2 adult population dynamics

   a.   A cell occupied by an adult female could become empty with probability $\mu (a)$ due to female mortality.
   b.   An empty cell could be occupied with a metamorphosis probability $\delta(i)/2$ if a pupa in the corresponding cell in CA-1 develops into a female adult. The fraction $1/2$ was related to the sex ratio.

In order to perform the simulations, we defined the set of probability functions θ(i), δ (i), τ (a) and μ(a) described in our transition rules. They were based on general trends observed in population data for *S. frugiperda* (Barros *et al* 2010) (Eqs. 1–4). Equations 1 to 4 describe the probability functions $\vartheta(i)$, $\delta(i)$, $\mu(a)$, and $\tau(a)$ as part of these transition rules (Garcia *et al* 2016). They represent the probability of occurrence of each event on each day. In order to run the simulations, we varied adult longevity (*AL*) from 8 to 20 days and larval viability (*LV*) from 0 to 1. The range of *AL* was determined on the basis of the values of adult longevity found by Barros *et al* (2010), studying *S. frugiperda* populations in different hosts. Based on the population data for *S. frugiperda* collected by Barros *et al* (2010), we were also able to simulate the expected spatial patterns observed in corn, millet, soybean, and cotton fields (Table 1).

$$\begin{cases} \vartheta(i) = 1 - \sqrt[15]{LV} \ \text{if } 0 < i \leq 15 \ (\text{larval stage}) \\ \vartheta(i) = 0.04 \ \text{if } 15 < i \leq 25 \ (\text{pupal stage}) \end{cases} \quad (1)$$

$$\begin{cases} \delta(i) = 0 \ \text{if } i < 25 \\ \delta(i) = 1 \ \text{if } i = 25 \end{cases} \quad (2)$$

$$\begin{cases} \mu(a) = 0 \ \text{if } a \leq AL - 5 \\ \mu(a) = 0.1(a - AL - 5) + 0.5 \ \text{if } AL - 5 < a \leq AL + 5 \\ \mu(a) = 1 \ \text{if } a > AL + 5 \end{cases} \quad (3)$$

$$\begin{cases} \tau(a) = 0 \ \text{if } a \leq 3 \\ \tau(a) = 0.7 \log\left(\left(\frac{1}{e^{0.3 \ (a-1)} - 0.3}\right) - \left(\frac{1}{e^{0.3 \ a} - 0.3}\right)\right) \ \text{if } 3 < a < AL + 5, \end{cases} \quad (4)$$

where *LV* is larval viability and *AL* is adult longevity.

We assumed no preferential direction of adult dispersal, i.e., the adults moved randomly. In each time step, we assumed that each adult female could move to any cell randomly chosen by the computer within a radius of 35 cells from the initial cell. We defined this radius by considering the maximum distance reached by adult females of *S. frugiperda* in cornfields per day (Vilarinho *et al* 2011).

Table 1 Adult longevity (AL) and larval viability (LV) values for *Spodoptera frugiperda* populations in different hosts under laboratory conditions, found by Barros *et al* (2010).

Parameters	Corn	Millet	Cotton	Soybean
AL (days)	16	14	15	13
LV	0.98	0.94	0.9	0.82

The initial population (*t* = 0) was composed of 1600 adult insects released in the center of the lattice in 40 × 40 cells (one adult per cell). Simulations were run during 300 time steps, and the spatial patterns of insect distribution (only adults) at *t* = 300 were classified by using the Morisita index of dispersion. We chose 300 time steps because there was a transient and unstable period before this time, since the population was still too small and was becoming established in the field. From this time forward, we could observe a clearer and more stable pattern of distribution, resulting from the initial conditions defined in our simulations (Garcia *et al* 2016).

Morisita index of dispersion

In order to quantify the degree of spatial dispersion of *S. frugiperda* observed in each simulation, the Morisita index of dispersion was calculated for each combination of the two parameters. This tool is often used to evaluate the spatial patterns of biological species (Amaral *et al* 2015). According to Rossi & Higuchi (1998), a low sensitivity to the size of the sampling unit is the main reason to make use of this index. In order to calculate the Morisita index of dispersion (*I_d*), initially the lattice was divided into 100 plots of the same size (60 × 60 cells), recording the number of individuals in the cells per plot. The index is defined as (5), according to Krebs (1999):

$$I_d = q \left(\frac{\sum_{i=1}^{q} x^2 - \sum_{i=1}^{q} x}{\left(\sum_{i=1}^{q} x\right)^2 - \sum_{i=1}^{q} x} \right), \quad (5)$$

where *q* is the number of plots and *x* is the number of individuals in each plot. The values of $I_d = 1$ indicate a random pattern, values of $I_d < 1$ indicate a uniform pattern, and values of $I_d > 1$ indicate an aggregated pattern. However, it is essential to apply a statistical test to verify if the index value is significantly different from 1 (randomness). The statistics for the Morisita index of dispersion (chi square distribution) is given by (6).

$$\chi^2 = n \frac{\sum_{i=1}^{q} x^2}{\sum_{i=1}^{q} x} - \sum_{i=1}^{q} x. \quad (\text{d.f.} = n - 1) \quad (6)$$

If the calculated χ^2 is higher than the critical value (*p* = 0.05), then I_d is significantly different from 1 and the population has either a uniform or an aggregated distribution.

Results and Discussion

Varying the proposed parameter set (larval viability and adult longevity), the Morisita index of dispersion indicated two different spatial patterns (random and aggregated) as

illustrated in Fig 1. The spatial patterns obtained in the parameter space tested are represented in Fig 2.

The aggregated pattern (Fig 1b) is the most common one described in the literature (Zillio & He 2010) and is characterized by the aggregation of individuals in some locales. We observed that a Morisita index higher than 1 (aggregated pattern) is highly dependent on higher values of larval viability and adult longevity, and only extremely low larval viabilities (less than 0.1) would prevent the formation of the pattern when adult longevity exceeds 17 days (complete parameter space in Fig 2). In our case, the highest abundance of individuals is located in the cells of the initial infestation. According to Molles (2009), this pattern is observed when individuals are attracted to a common resource. However, since we are working with a homogeneous area, the main reason that this pattern appeared in our simulations is the high values of the parameters being varied, which maintains a high number of adults in the cells where the population starts to spread over a homogeneous space, allowing the formation of rings with different population densities around this point (Gaussian behavior). Higher rates of larval viability provide large numbers of adults to the population, while increased adult longevities allow large numbers of adults to remain in the field. At first concentrated in the cells of the initial infestation, they start to disperse, creating rings with progressively lower densities of adults. Petrovskii et al. (2014) offered the same explanation for aggregated patterns. They also noted that this behavior is characterized as a swarm and is important for agricultural systems, because early detection of the initial point (termed "point-source release") may improve pest monitoring and control, since control measures can be focused on the initial point. This pattern was observed in all host crops simulated (corn, millet, cotton, and soybean) (Fig 2). Aggregated patterns are commonly reported for *S. frugiperda* larvae, although studies on local movements
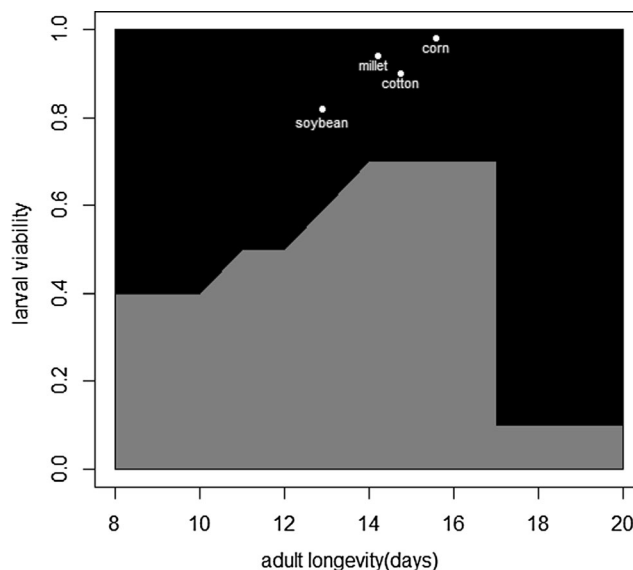

Fig 2 Diagram indicating the parameter values (larval viability and adult longevity) for which the spatial patterns are observed. The four host crops simulated are indicated in *white*. *Gray* indicates random ($I_d = 1$) and *black* indicates aggregated ($I_d > 1$).

of adults have been limited (Vilarinho *et al* 2011). The pattern was observed for *S. frugiperda* larvae in cornfields by Farias *et al* (2001) and Elmo *et al* (2006), when population density was high, as we found in our simulations. In cotton fields, aggregated patterns were documented by Fernandes et al. (2002).

An aggregated pattern indicates that the colonization of the area proceeds from points of aggregation. This is essential information for the development of site-specific IPM strategies. Following the principles of precision agriculture, these strategies are based on maps showing the pest distribution in order to minimize the measures needed for direct control (Brenner *et al* 1998). However, one of the main
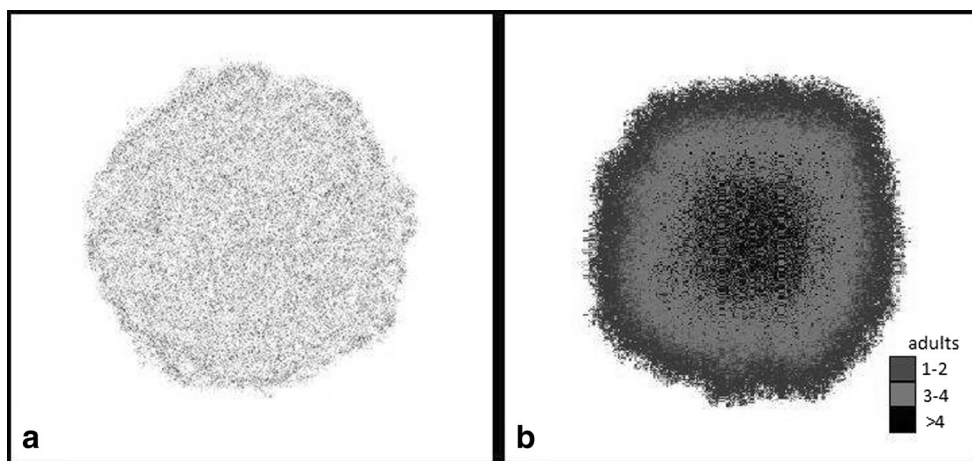

Fig 1 Spatial patterns of insect distribution (adults) observed in our simulation when values of the proposed parameter set were varied. **a** Random (*AL* = 16, *LV* = 0.4, and I_d = 1.02, χ^2 = 40.5, d.f. = 99). **b** Aggregated (*AL* = 20, *LV* = 0.8, and I_d = 2.67, χ^2 = 145.6, d.f. = 99).

requirements for the application of site-specific IPM strategies is an aggregated distribution of the target population (Sciaretta & Trematerra 2014). These strategies have yielded effective results in study cases involving lepidopteran insects reported in the literature. Sciaretta *et al* (2011) identified the source of infestation in aggregated distributions of *Lobesia boltrana* (Lepidoptera: Tortricidae). By identifying these points, they were able to adopt two different control measures: the establishment of a pheromone-trap barrier to prevent the males from moving, and a reduction in the amount of insecticides, focusing their efforts on the highest concentrations of *L. boltrana.* In addition to reducing the amount of insecticides needed, this treatment was more economical and more efficient. Since *S. frugiperda* occurs mainly in aggregations in all of its host crops, similar pest-management strategies can be applied, resulting in more efficient pest control. Finding the epicenter of the aggregated distribution may allow farmers to focus their control efforts, disrupting the wave of the pest outbreak (Johnson *et al* 2006).

Another factor is that an aggregated distribution is composed of concentric rings, and the population density decreases progressively from the inner to the outer rings. Therefore, in the case of biological control by means of introducing either a predator or a parasitoid, it would be necessary to consider these different densities along the rings. According to Bjørnstad & Bascompte (2001), a highly mobile parasitoid/predator can be a good choice to maintain a high within-patch synchrony of the dynamics of the two species. In this context, spatial synchrony refers to coincident changes in abundance in both populations (Liebhold *et al* 2004).

The Morisita index was not significantly different from 1 (random distribution) when larval viability was low enough to allow rapid changes along the cells. The amplitude of larval viability values that correspond to this pattern increased as adult longevity increased from 8 to 17 days (see the parameter space in Fig 2). For smaller larval viabilities, many larvae die over the time steps, leaving more empty cells to be colonized by new individuals, which prevents intraspecific competition and the aggregation of many adults in each cell. This pattern is caused by higher values of adult longevity (although less than or equal to 17 days), which also prevents aggregation in the cells by allowing adults to disperse over greater distances, moving away from the initial center of infestation and avoiding intraspecific competition. According to Molles (2009), random distributions are observed when individuals in a population have an equal chance of living anywhere within an area and do not affect each other. This pattern was observed for *S. frugiperda* larvae in cornfields in Brazil by Elmo *et al* (2006). They attributed the random pattern to low infestation levels that keep the population small and reduce intraspecific competition. This pattern was also observed by Mazza *et al* (2014) in cotton fields, due to low captures in the winter. Therefore, it should be taken into consideration that changes in the weather may decrease larval viability, transforming an aggregated pattern to a random pattern. As seen in Fig 2, a decrease in larval viability may change the aggregated patterns observed in the four host crops to a random pattern. With this in mind, it is not recommended to apply site-specific IPM strategies during colder weather.

According to Elmo *et al* (2006), the random pattern may change to a uniform distribution if the insects start to avoid each other, competing for resources (Elmo *et al* 2006). Uniform patterns were not observed in our simulations, since the maximum number of adults defined in CA-2 was observed in only a few cells, preventing a competition situation. Additionally, we investigated a population of adults, which do not compete intensely for resources as do larvae, since adults are able to fly and to better exploit the space, reducing the chance of a uniform distribution.

Conclusion

Morisita's index of dispersion indicated two different spatial patterns for the parameter space based on data from *S. frugiperda* populations. Lower larval viabilities combined with higher adult longevities (but less than or equal to 17 days) prevented the aggregation of more than one adult per cell, resulting in a random pattern. Random distributions can be observed in the field, in cases of low levels of intraspecific competition or in unfavorable weather conditions.

For higher values of larval viability and adult longevity, an aggregated pattern occurred, in which the number of adults decreased progressively from the inner to the outer rings. This pattern is related to high population densities in the field, and it is required for the application of site-specific IPM strategies that can lead to a more efficient and sustainable pest management. Detection of the epicenter of the aggregated distribution may allow farmers to focus their control efforts. Additionally, when the insect pest shows an aggregated distribution, for effective biological control it is important to consider the pest's spatial synchrony with the parasitoid or the predator used.

The model developed here can potentially be used by entomologists to predict the spatial distribution of *S. frugiperda* populations in the field, proposing control strategies based on the predicted pattern. It would only be necessary to estimate the values of the biological parameters, which can be obtained in the laboratory by using a sample taken from the population studied. Although this approach is theoretical, it may support monitoring studies that aim to observe the same patterns in the field. The model can be easily altered to study other lepidopteran pests, by changing the defined equations in the transition rules.

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