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RESEARCH ARTICLE

A mathematical approach to simulate spatio-temporal patterns of an insect-pest, the corn rootworm *Diabrotica speciosa* (Coleoptera: Chrysomelidae) in intercropping systems

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Abstract We report on the use of a spatially explicit model and clustering analysis in order to investigate habitat manipulation as a strategy to regulate natural population densities of the insect-pest *Diabrotica speciosa*. Habitat manipulation involved four major agricultural plants used as hosts by this herbivore to compose intercropping landscapes. Available biological parameters for *D. speciosa* on bean, soybean, potato and corn obtained under laboratory conditions were used to group the homogeneous landscapes, composed by each host plant, by a similarity measure of host suitability either for larval survival and development, and adult survival and fecundity. The results pointed corn as the most dissimilar culture. Therefore, intercropping corn with any other crop system tested could reduce insect spread through landscape. This was proved using a cellular automata model which simulate the physiological and behavioural traits of this insect, and also different spatial configurations of the intercropping. Spatio-temporal patterns obtained by simulations demonstrated that the availability of corn bordering the field edge, which are areas more likely to invasion, is key for insect population control.

Keywords Cellular automata · Clustering algorithm · Nutritional ecology · Agricultural landscapes

Introduction

Landscape ecology plays an important role in agricultural systems since it allows a holistic management approach of farming systems (Deffontaines et al. 1995; Steingröver et al. 2010). Although habitat spatial structure has been shown to affect insect population structure, it has been often neglected in agricultural activities. However, the growing concern about the impact of extensive use of chemicals on the environment and human health, and the increase of insect resistance to pesticides have motivated the search for alternative control methods to reduce insect pest populations. In this context, achieving a sustainable agriculture by using landscape elements management to increase natural predators and parasites to promote pest control without chemical pesticides is encouraging and challenging (Steingröver et al. 2010).

Moreover, by increasing environmental heterogeneity to control agricultural pests instead of chemicals, land system management can create micro-habitats, simulating a healthier landscape. Such approach

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supports ecosystem services by maintaining ecological processes and can benefit biodiversity, avoiding the negative impacts of chemical pesticides on animals and plants (Scheer and McNeely 2008). Beyond that, the optimal shape and distribution of the habitats is a key stone in developing landscape management (Landis et al. 2000).

Habitat management characterized by crop spatial arrangement, such as intercropping systems, may be viewed as an alternative tool for enhancing biological control, which can be associated to other control methods (Diekotter and Crist 2003; Song et al. 2010; Skirvin et al. 2011; Yao et al. 2012). For instance, field experiment where either wheat or a mix of plants between corn rows were used to protect it from *Agriotes* wireworms was conducted. In this case, plant protection occurred due to a behavioural mechanism represented by a switch in larval feeding from the major crop as a host to the associated plants (Staudacher et al. 2013a, b).

Furthermore, it has been shown that crop heterogeneity is a possible solution to the vulnerability of monocultures to disease. As an example, the rice blast disease can be controlled without fungicides if mixed fields with glutinous and hybrid rice varieties are sown. Several mechanisms can be related to this success, like the increased distance between plant genotypes, the existence of microenvironments in such mixture, and the induced resistance in plants. Also, this approach has the benefit to slow down the mechanisms of pathogen adaptation (Zhu et al. 2000).

The development of mathematical models that include spatial heterogeneity and host suitability impact on the fitness of insect herbivores could provide insights on how to exploit habitat manipulation to manage pest population densities in the field. The growing interest in theoretical studies for problems of this nature stimulates the use of spatially structured mathematical models such as cellular automata (CA). These models are an interesting choice to study habitat manipulation because all spatial traits of the crop can be detailed. Furthermore, it is possible to use discrete cell states to represent the presence or the absence of the different stages of the insect pest at a given space location. These states can change over time through simple stochastic rules that mimic insect life cycle. Finally, insect movement in the landscape is easily added using this approach (Hiebeler 2004).

In this context, very little if any has been made on habitat manipulation for pest population management taking into consideration insect nutritional ecology and its fitness on different host plants, particularly for species in which the immature and adult stages are differentially affected from host to host, such as the polyphagous corn rootworm *Diabrotica speciosa* (Polis et al. 1997; Macfadyen et al. 2011; Panizzi and Parra 2012). This beetle develops on a wide range of host plants, including common beans, soybean and corn, among others. However, larva feeding on C4 host plants (corn) has a better performance, while adult feeding on C3 host plants (bean and soybean) increases its survival and fertility (Ávila and Parra 2002, 2003; Walsh 2003).

Therefore, the core question addressed here is: could the differences in the nutritional ecology of each stage of development of insects with life histories similar to *Diabrotica speciosa* be exploited for habitat manipulation as an alternative strategy for insect pest population management? With this purpose, a CA model was developed to analyse the effects of habitat manipulation on the population growth and spread of *D. speciosa* by alternating mosaic patterns of an agricultural landscape as food availability and suitability are known to influence insect physiology and behaviour (Scriber and Slansky 1981). Four different types of host plants that are commonly attacked by this insect pest (bean, soybean, potato, and corn) were selected, and different spatial combinations of intercropping were proposed to analyse the insect spatio-temporal patterns resulting from these agricultural landscapes. A similar measure was used to group the homogeneous crop systems. The hypothesis was that intercropping between the most different crop system with the others, where the difference is related to the host suitability, could reduce insect spread through the landscape.

Furthermore, simulations with different proportions of row intercropping combinations were accomplished to compare insect dispersion velocity and to relate it with the spatial heterogeneity. Finally, the CA was used to perform a sensitivity analysis, i.e., to determine which parameters most influence the model results, and to determine the best location in the field for the least suitable host plant, i.e., the one that causes the major decrease in insect pest population, and also reduces insect spread.

Methodology

Cellular automata

Immature and adult stages of *D. speciosa* do not compete for space or nutritional resources since larvae feed on roots and adults feed on leaves. Moreover, host suitability is different for each stage of development of *D. speciosa* (larva and adult). Thus, we constructed two stochastic cellular automata, CA-1 and CA-2 (respectively for larva and adult), each one with 256 × 256 sites. For CA-1, a cell can be either empty or occupied by a larva. For CA-2, a cell can be either empty or occupied by an adult female. The automata are connected by adult emergence and oviposition. Both automata have the same habitat type in each site, which determines the landscape explored by the insect. Furthermore, we assumed that insect biological parameters such as mortality, development and oviposition rate are dependent on host plant, and feeding resources are unlimited. We used parallel update with fixed boundary conditions. Each time step, t, corresponded to one day, and each cell of the CA represents 10×10 m^2 of the crop system. Finally, insect population change at each cell according to the following rules (Ferreira et al. 2014):

(1) *CA-1* larva population dynamics

  (a) a cell occupied by a larva can become empty with probability $\mu + \sigma$ due to larval mortality or adult emergence, respectively;

  (b) an empty cell can become occupied by a larva if an adult (in a Moore neighborhood of radius two plus the central cell in CA-2) lays eggs on it. Per-capita oviposition probability is ϕ, and neighborhood size (the Moore neighborhood of radius two comprises the twenty four cells surronding the central cell in a two dimension square lattice) was chosen based on the maximum per-capita oviposition rate observed on potato plants;

(2) *CA-2* adult population dynamics

  (a) a cell occupied by an adult female can become empty with probability γ due to adult mortality;

  (b) an empty cell can be occupied with probability $\sigma/2$ if a larva in the correspondent cell in CA-1 turns into a female adult. The fraction $1/2$ is related to sex ratio.

Table 1 Biological parameters values estimated from laboratory experiments with *D. speciosa* in four host crops (Ávila and Parra 2002)

Host plant	ϕ (day^{-1})	μ (day^{-1})	σ(day^{-1})	γ (days^{-1})
Potato	0.379	0.005	0.027	0.020
Bean	0.394	0.085	0.036	0.020
Corn	0.011	0.011	0.040	0.031
Soybean	0.056	0.045	0.037	0.020

The parameters used in the model were: oviposition rate (ϕ), larval mortality rate (μ), larva-adult development rate (σ), and adult mortality rate (γ)

Based on data from the literature, we estimated a set of parameters related to physiology and behaviour of *D. speciosa* to be used in the simulations (see Table 1). Dispersion occurs between each time step, and the daily capacity of adults to disperse is 6–17 m (Spencer et al. 2009). To simplify we assume that dispersion in all direction is equally probable, therefore, adult insects in CA-2 can move to any empty cell in its neighborhood. Increasing the number of adult insects that are able to disperse accelerates insect dispersion in the lattice.

To compare the effect of different intercropping on insect dynamics, the simulations started by constructing the agricultural landscape by altering different crop systems. The size of the areas occupied by each crop was defined previously, and only strip intercropping were designed. Therefore, each cell of the lattice received a label indicating the crop that was available in this position of the CA. After that, an individual adult was added to the center of the lattice chosen to be an interface between two crop systems. It simulates the arrival of an insect adult in the field bordering. Finally, the CA rules that mimic insect life cycle and also insect movement are applied. Because the time scale of insect dispersion is smaller than the time scale of insect life cycle, one time step of the automata corresponds to one update of the insect cycle and five update of insect dispersion.

To analyse spatial and temporal patterns of the insect pest population, the density of individuals in each strip, and the average distance of the spatial spread of the insect population, that is an indirect measure of the insect velocity of spread, were evaluated. The average distance was measured at each day, and the values presented were the average of twenty simulations. It is defined as the average mean-square distance over which the insects have spread. Plotting it as a function of time, the derivative of the curve is proportional to the velocity of the insect spread over the landscape (Ferreira and Fontanari 2002). All simulations ran until $t = 150$ days. This value of time was chosen to avoid boundary effects related to the finite size of the lattice.

To study the effect of spatial heterogeneities on insect dispersion, the automata was constructed with different proportion of two arbitrary crops. Starting with a single host plant (bean), we systematically inserted rows of a different host plant (corn) until the proportion between the two crops equaled one. At the beginning of each simulation of the CA, an insect adult was added to the center of the lattice. The CA rules were applied, and the temporal evolution of the average distance of the spatial spread of the insect population measured in each spatial configuration allowed us to infer about the effect of spatial structure on insect dispersion.

Clustering algorithm

Given n types of hosts used by the insect pest *D. speciosa*, the number k of different combinations between these hosts that we could accomplish in field resulting in different intercropping is given by:

$$C_k^n = \binom{n}{k} = \frac{n!}{k!(n-k)!}.$$

For instance, if $n = 4$ and $k = 2$, we would have six possible combinations of host plants. Increasing the number of hosts and adding spatial structure, the number of simulations to be evaluated would make impracticable the proposed study. Therefore, we used a hierarchical clustering technique to identify similarities between host plants, where similar hosts were clustered based on the biological parameters described in Table 1. We chose the Canberra distance as a metric, since our data presented values close to zero, and we had no access to the data variability since they were taken from the literature that provide only the mean values and standart deviation (Ávila and Parra 2002). Now, suppose we have two p-dimensional vectors, $\mathbf{x}' = [x_1, x_2 ..., x_p]$ and $\mathbf{y}' = [y_1, y_2, ..., y_p]$. The Canberra distance between these vectors is given by

$$d(\mathbf{x}, \mathbf{y}) = \sum_{i=1}^{p} \frac{|(x_i - y_i)|}{x_i + y_i}, \tag{1}$$

and it is defined only for non-negative values of x_i and y_i (Johnson and Wichern 2007).

In order to assemble clusters by using the Canberra distance, we used a hierarchical agglomerative clustering method (Tryfos 1998). Since our aim was to create clusters based on the proximity among tested host plants, we chose the single linkage method, which is based on the minimum distance or nearest neighbour. For this algorithm, we started by constructing the symmetric $p \times p$ matrix of distances (or similarities) $\mathbf{D} = \{d(\mathbf{x}, \mathbf{y})\}$, where distances are obtained from Eq. (1). Then, the smallest distance in $\mathbf{D}$ was found and the corresponding elements $\mathbf{x}$ and $\mathbf{y}$ were merged to get the cluster $\mathbf{xy}$. Afterwards, the distance between $\mathbf{xy}$ and the other element $\mathbf{z}$ was define as:

$$d(\mathbf{xy}, \mathbf{z}) = min\{d(\mathbf{x}, \mathbf{z}), d(\mathbf{y}, \mathbf{z})\}, \tag{2}$$

where $d(\mathbf{x}, \mathbf{z})$ and $d(\mathbf{y}, \mathbf{z})$ are the distances between elements $\mathbf{x}$ and $\mathbf{z}$ and between elements $\mathbf{y}$ and $\mathbf{z}$, respectively (Sibson 1972). Therefore, the most similar elements were first clustered and the remaining elements were clustered according to their similarities, graphically represented in a dendrogram.

Sensitivity analysis

The cellular automata model has four parameters, ϕ, μ, γ and σ, which are related to the oviposition rate, larva and adult mortality rate, and larva development rate. By fixing three of these parameters and varying the remainder, we could measure how pest population reacts to it, i.e., the sensitivity of the model output, such population density and average distance, for each one of its parameters (Saltelli et al. 2004). The conclusion was obtained from the variance of these variables measured at the end of the simulation chosen as $t = 150$. For each parameter set we carried out 20 simulations in a homogeneuos landscape constituted by corn. This process was repeated to each parameter,

(i)

–	P	B	C	S
P	0			
B	1.051	0		
C	1.668	1.926	0	
S	1.706	1.084	1.516	0

(ii)

–	PB	C	S
PB	0		
C	1.668	0	
S	1.084	1.516	0

(iii)

–	PBS	C
PBS	0	
C	1.516	0

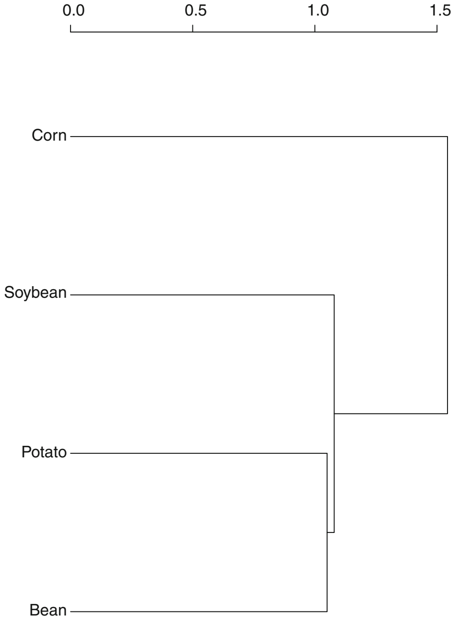


Fig. 1 Distance matrix calculated at each *time step* of the clustering algorithm, represented by **i–iii**, and the resulting dendrogram. The letters *P*, *B*, *C*, *S* represent, respectively, potato, bean, corn and soybean crops

being carefully to vary them in the same scale avoiding biased results.

Results and discussion

The results obtained by the clustering analysis earlier described are shown in Fig. 1. We can see the distance matrix calculated at each time step of the algorithm and the dendogram, which illustrate clusters and the distance between them. Each matrix element was obtained through Eq. (1) with x_i and y_i being the values of each parameter i in distinct host plants, such as oviposition rate in potato and bean. For instance, using the data from Table 1, the Canberra distance between potato (P) and bean (B) is given by

$$\begin{aligned} d(P,B) = {} & \frac{|0.51-0.53|}{0.51+0.53} + \frac{|0.005-0.086|}{0.005+0.086} \\ & + \frac{|0.027-0.036|}{0.027+0.036} + \frac{|0.027-0.027)|}{0.027+0.027} \\ & = 1.051. \end{aligned}$$

Since (P) and (B) were the host plants to yield the most similar fitness parameters for *D. speciosa*, representing the smallest matrix element, they constituted the first cluster (PB), which was followed closely by soybean (S) with

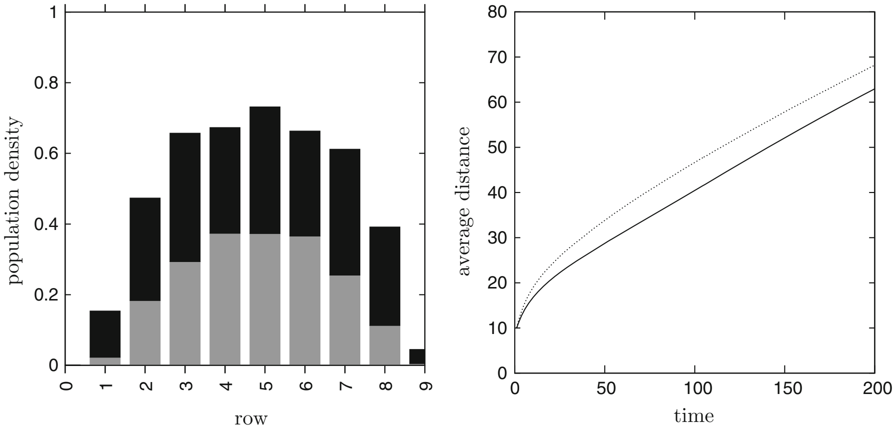
$$\begin{aligned} d(PB,S) &= min\{d(P,S), d(B,S)\} \\ &= min\{1.706, 1.084\} = 1.084. \end{aligned}$$

Corn (C) yielded quite diverse fitness attributes as compared to the remaining tested host plants, and therefore, it is the last element to be clustered with

$$\begin{aligned} d(PBS,C) &= min\{d(P,C), d(B,C), d(S,C)\} \\ &= min\{1.668, 1.926, 1.516\} = 1.516. \end{aligned}$$

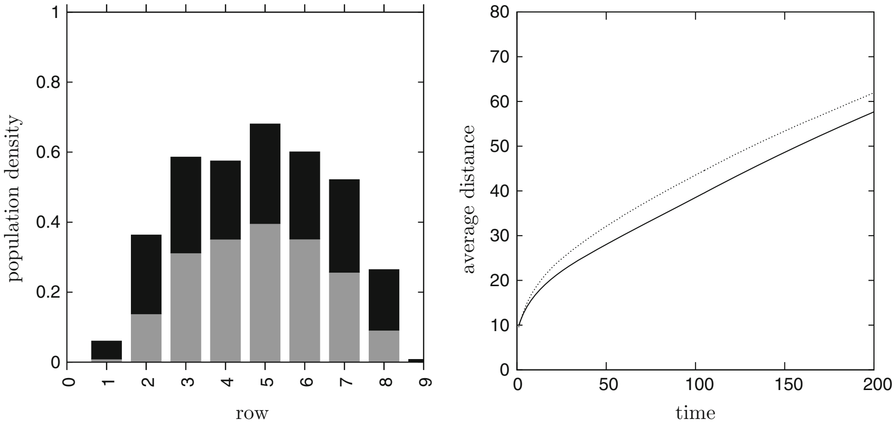
This analysis motivated us to explore the combination between corn and other host plants in an attempt to manipulate the insect habitat in order to affect insect population growth in the field. Although the analysis previously described did not consider the spatial arrangement of the host plants, we could couple it with insect dynamics described by the CA, and use this powerful method to study habitat structure on insect population growth considering how host suitability influence insect physiology and behaviour.

The spatio-temporal patterns of the intercropping systems composed by bean and potato, soybean and bean, and corn and bean are given, respectively, in Figs. 2, 3 and 4. In all spatial configurations, rows have the same width and height, respectively 10×256 that represents a field of $100 \times 2,560$ m^2. To measure spatial pattern distribution, we estimated the average



(a) spatial distribution **(b)** time evolution

Fig. 2 Spatial (**a**) and temporal (**b**) patterns for bean and potato intercropping. Odd numbers correspond to bean crops and even number correspond to potato crops. In **a** is plotted the insect density measured at time $t = 150$ from one simulation for each strip crop. In **b** is plotted the average distance of the spatial spread of the insect population measured at each day. The values are the average of twenty simulations. The *gray color* and *dashed line* counts for adult, and the *black color* and continuous line for larva

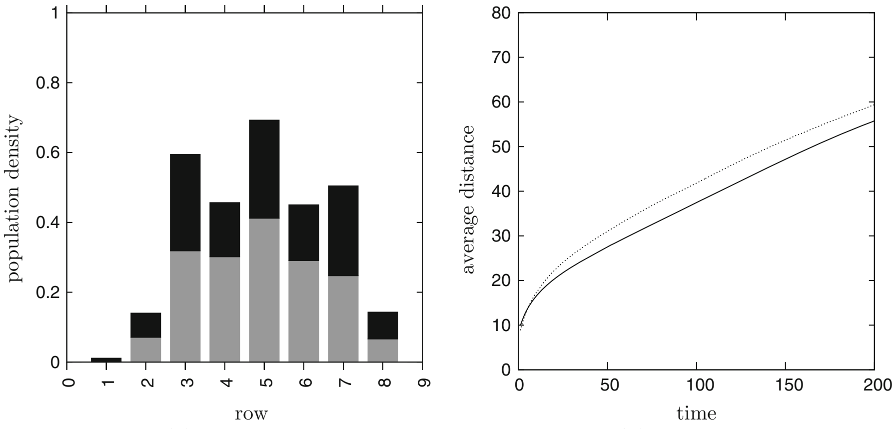


(a) spatial distribution **(b)** time evolution

Fig. 3 Spatial (**a**) and temporal (**b**) patterns for soybean and bean intercropping. Odd numbers correspond to bean crops and even number correspond to soyabean crops. In **a** is plotted the insect density measured at time $t = 150$ from one simulation for each strip crop. In **b** is plotted the average distance of the spatial spread of the insect population measured at each day. The values are the average of twenty simulations. The *gray color* and *dashed line* counts for adult, and the *black color* and continuous line for larva

population density value in each row (Figs. 2a, 3a and 4a). We also calculated the distance over which insect population has spread (Figs. 2b, 3b and 4b).

Our clustering analysis (Fig. 1) together with the CA results (Figs. 2a, 3a and 4a) clearly demonstrated a direct effect between host plant similarity and population density in intercropping systems. As observed, the bigger the difference in host suitability, the greater the difference between insect population density in each strip that compose the agricultural landscape. That is, the intercropping system with corn and beans yielded higher differences in population density at each strip crop, than the intercropping system with beans and potatoes. This occurs as a result of changes in the nutritional conditions when the insect population moves from a host plant to another. Since bean



(a) spatial distribution **(b)** time evolution

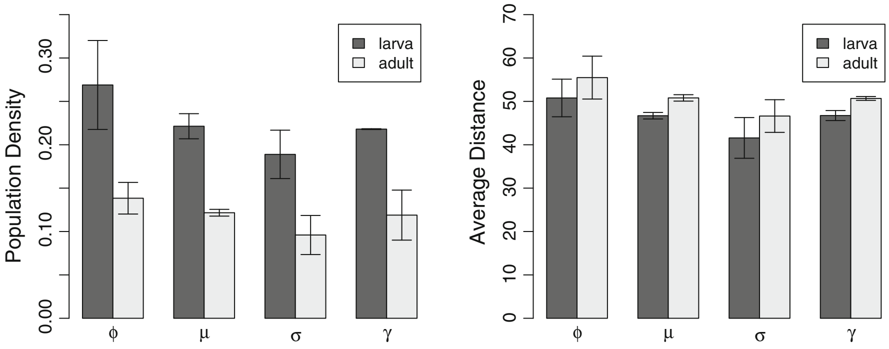
Fig. 4 Spatial (**a**) and temporal (**b**) patterns for corn and bean intercropping. Odd numbers correspond to bean crops and even number correspond to corn crops. In **a** is plotted the insect density measured at time $t = 150$ from one simulation for each strip crop. In **b** is plotted the average distance of the spatial spread of the insect population measured at each day. The values are the average of twenty simulations. The *gray color* and *dashed line* counts for adult, and the *black color* and continuous line for larva

and potato are very similar, as pointed by the clustering analysis, population density is practically equall over the landscape, similarly to a landscape constituted by a single host plant (homogeneous landscape) (Bjorkman et al. 2010). Of course, if simulations were ran for a long time, insect density at same strip crop would be the same. The advantage in using a diversified landscape is based on the combined use of host plants that work synergistically to affect pest fitness, either through reduced host suitability or female reproduction. Furthermore, in an intercropping system, insects may experience difficulty in locating and remaining in favourable rows since microclimatic conditions are highly fractionated (Altieri and Letourneau 1982).

The average distance (Figs. 2b, 3b and 4b) indicates which intercropping system most reduces the pest population ability to disperse through the landscape. Insect population dispersion is slower in corn and soybean intercropping, and faster in bean and potato intercropping. To understand why, we accomplished a sensitivity analysis to verify which parameter most influences the pest population in the model. This approach was required because matrix elements obtained by clustering were not so different from each other. The sensitivity analysis demonstrated that the main parameters that influence population density and dispersion speed were the oviposition rate and the development rate (Fig. 5). The conclusion was obtained from the variance of population density, and the variance of the average distance measured at the end of the simulation (Saltelli et al. 2004).

The sensitivity of population density and average distance to the development rate occurs because this parameter is the only one that connects both population stages, larva and adult. This connection implies that any variation in the larva population is reflected on the adult population and vice-versa. On the other hand, the sensitivity of population density and average distance to the oviposition rate occurs because of the survival strategy adopted by the population. Since we considered resources to be unlimited, and we are studying insect pest colonization and persistence, the population is limited by the reproduction rate. Populations that follow this strategy are called r-strategists as opposed to the k-strategists that are limited by the carrying capacity (MacArthur and Wilson 1967). Furthermore, relating to the mortality rates, the population density in each stage was more affected by its own survival. Observe that, for the range of values used in the simulations ($\phi \in [0.1, 0.4]$, and μ, σ and $\gamma \in [0.01, 0.04]$), the average distance was not affected by the mortality rates.

In summary, the results obtained from simulations suggested that intercropping with corn is the best way to manage population growth of *D. speciosa* as corn negatively affected the speed of dispersion and the population density of the insect in all intercropping



(a) sensitivity analysis **(b)** sensitivity analysis

Fig. 5 In **a** and **b** are plotted, respectively, the mean and the standard deviation of insect population density, and the mean and the standard deviation of average distance of the spatial spread of the insect population, both measured at $t = 150$. The sensitivity was measured for the parameter that appears at the horizontal axis. The input landscape corresponds to a homogeneuos crop chose to be corn, and the values are the average of twenty simulations

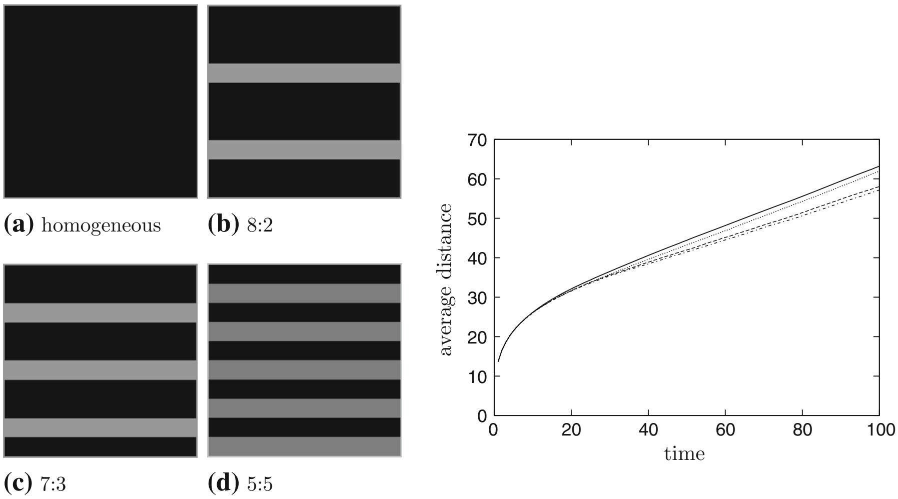
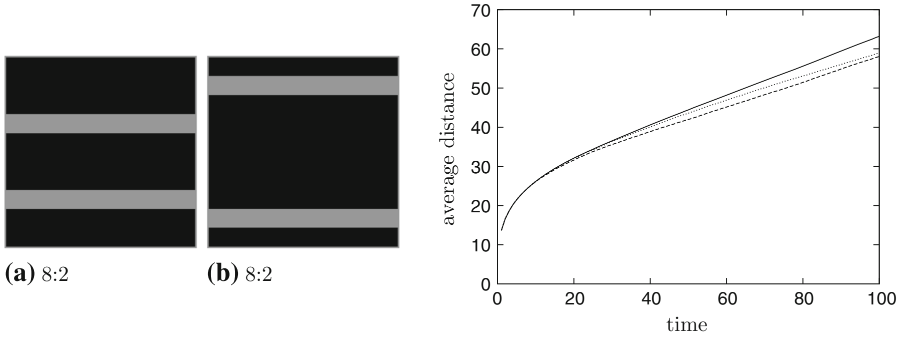


Fig. 6 At *left*, several simulated landscape arrangements indicated as **a**–**d**; and at *right* the temporal evolution of average distance of the spatial spread of the insect population measured for different proportions of the inserted crop (*gray*). *Black color* represents bean crop and *gray color* the corn crop. *Solid line* for **a**, *dotted line* for **b** *dashed line* for **c**, and *dot dashed* line for **d**. The values are the average of twenty simulations

systems tested. These results were expected since insects feeding on corn and soybean present the smallest oviposition rates, which was the parameter, revealed by the sensitive analysis, that most influenced the population dynamics. The reduced fecundity of female feeding on corn and soybean occurs because their leaves have low quantities of nitrogen, which affect negatively the oviposition by providing few nutrients to the oogenesis process (Ávila and Parra 2002). Moreover, the intercropping of corn and soybean was the most efficient to control *D. speciosa* population when compared to the others. It was reported that for the closely-related species *Diabrotica virgifera*, adult emergence and injury level were reduced when this insect was exposed to an intercropping system with soybean and corn as compared to a one-crop system (Ellsbury and Exner 1999). Moreover, predator abundance and diversity is also increased by using corn in intercroppings (Cividanes 2002; Yao et al. 2012).

Some spatial arrangements of the host plants used in the simulations can be seen in Fig. 6. As a rule, insect pest spread decreases as spatial heterogeneity increases. It can be seen by plotting the average distance as a function of time for each spatial intercropping proposed. The results were observed for an intercropping of bean and corn. The same results, but less pronounced, were obtained for others intercropping, since corn and bean are the most dissimilar cultures for host suitability.

Finally, we measured the temporal evolution of the average distance for two intercropping systems with



(a) 8:2 **(b)** 8:2

Fig. 7 At *left*, two simulated landscape arrangements indicate as **a**, **b**; and at *right*, the temporal evolution of average distance of the spatial spread of the insect population measured for different position of the inserted crop (*gray*). *Black color* represents bean crop and *gray color* the corn crop. *Solid line* for individual crop, *dotted line* for **a**, and *dashed line* for **b**. The values are the average of twenty simulations

the same proportion of crops, but alternating in each one the distance of the inserted crop in relation to the initial point of dispersion in the lattice (Fig. 7). As the proportion of the inserted crop in an intercropping system becomes reduced, the curve obtained for the temporal evolution of the average distance gets more similar to that one obtained for a landscape occupied by a single host plant. This is clearly observed when host plants are represented in a ratio of 4:1, which yielded average distances very similar to those obtained in single plant landscape. Also, two intercropping simulations with the same proportion of inserted rows can present different patterns if the position of the inserted rows in relation to the initial point of dispersion is different. Thus, besides the proportion between the intercropped host plants, their positions in the lattice are also an important variable to study (Hiebeler 2000; Parsa et al. 2011; Yao et al. 2012; Ferreira et al. 2014).

In all simulations adult dispersion was modelled as a diffusion process. Preferential direction for dispersion as result of seeking for suitable host for development and oviposition is expected in insect population. This behavior can make insect-pest control harder and it has to be addressed in any technique proposed to control insect population. Therefore, a future direction of this study can be to address a more realistic insect movement, and also the evolution of resistance in insect pests populations to insecticidal proteins from *Bacillus thuringiensis* (Bt) that are produced by transgenic crops as a result of its feeding on genetically modified crops.

Conclusion

By combining clustering algorithm results with a cellular automata model, we were able to study the effect of landscape on population growth and spread of the insect pest *D. speciosa*. The results obtained by using this approach showed that the use of corn intercropped with other host plants of *D. speciosa* such as potato, soybean and bean, can affect insect dispersion in the field. Two important points related to the host crop available in an intercrop system is its position and proportion. In the case of corn, the higher its proportion in the system better is the pest control. In relation to the position, we can achieve a better control of the pest by inserting rows of corn close to the initial point of invasion. Therefore, corn can be used as a natural barrier to this pest and the availability of corn at the edged of the field is key for insect population control.

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