FORUM

Ecological Modelling of Insect Movement in Cropping Systems

Adriano Gomes Garcia[1] · José Bruno Malaquias[2] · Cláudia Pio Ferreira[2] · Maysa Pereira Tomé[1] · Igor Daniel Weber[1] · Wesley Augusto Conde Godoy[1]

Abstract

The spatio-temporal dynamics of insect pests in agricultural landscapes involves the potential of species to move, invade, colonise, and establish in different areas. This study revised the dispersal of the important crop pests *Diabrotica speciosa* Germar and *Spodoptera frugiperda* (J.E. Smith) by using computational modelling to represent the movement of these polyphagous pests in agricultural mosaics. The findings raise significant questions regarding the dispersal of pests through crops and refuge areas, indicating that understanding pest movement is essential for developing strategies to predict critical infestation levels to assist in pest-management decisions. In addition, our modelling approach can be adapted for other insect species and other cropping systems despite discussing two specific species in the current manuscript. We present an overview of studies, combining experimentation and ecological modelling, discussing the methods used and the importance of studying insect movement as well as the implications for agricultural landscapes in Brazil.

Keywords Ecological modelling · insect pests · intercropping · Bt crops · IPM

Introduction

The movement of pests within or among habitats determines their distribution and abundance in space and time (Staudacher et al. 2013). Movement can be analysed on different scales, depending on the organism size, from nanometer-sized microorganisms to large mammals. Trivial movements within a territory and migration are driven mostly by food availability, mating, climatic changes, catastrophic events, or interspecific interactions (Nathan et al. 2008; Brown 2016). The movement of polyphagous species in agricultural landscapes may expose them to different environmental conditions and quality of food sources, with significant consequences for their life history and demography (Kennedy and Storer 2000).

The Brazilian agricultural landscape consists of mosaics that differ in crop diversity and size (Pereira et al. 2012). Agricultural production is based primarily on large areas of monocultures, usually classified as "simplified landscapes" (Meehan et al. 2011), with many small polycultures among the monocultures. In the last 5 years, the agricultural area has expanded by an estimated 66%, which places Brazil among the five countries with the most area under cultivation (Calil and Ribera 2019). Brazil occupies a prominent position in global agribusiness, with grain production increasing in recent years, and has become the largest producer of soybeans and one of the largest producers of corn (maize) (USDA 2020).

The diversity of tropical crops in different regions, in response to specific climatic conditions, regional agricultural policies, and geological relief, results in different physical and temporal patterns of plant distribution. Changes in these habitats over space and time frequently cause instability in insect populations and communities (Nguyen and Nansen 2018; Paiva et al. 2020). Polyphagous insects have developed the ability to exploit different crops simultaneously and/or successively (Sarate et al. 2012; Hardy and Otto 2014). Different agricultural inputs, phenology, weather conditions, modern chemical formulations, and genetic modifications of plants influence the ability of insects to exploit food resources (Xiao and Wu 2019).

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✉ Wesley Augusto Conde Godoy
   wacgodoy@usp.br

[1] Dept of Entomology and Acarology, Luiz de Queiroz College of Agriculture, Univ of São Paulo, Piracicaba, São Paulo, Brazil

[2] Institute of Biosciences, São Paulo State Univ, Botucatu, São Paulo, Brazil

Plants are generally affected in different ways by polyphagous insects. Crops can be injured directly or indirectly (Donatelli et al. 2017). Direct injury is caused by adults and larvae eating leaves or burrowing in stems, fruits, or roots. Indirect damage results from transmission of pathogens to plants, often by sucking insects. Examples include the viral diseases of sugar beets and potatoes, carried from plant to plant by aphids (Radcliffe and Ragsdale 2002).

Whatever the negative impact of insects on plantations, i.e. damage caused by herbivory or transmission of pathogens, understanding movement patterns in insects and their association with different types of crops is of utmost importance for the spatial configuration of plantings (Ferreira and Godoy 2014). The population dynamics of highly mobile and/or polyphagous pests is ruled by a combination of demographic parameters and movement, with important implications for communities and the population genetic structure of pest insects (Mazzi and Dorn 2012).

Spatial movement of insects also influences the population genetic variability, affecting gene flow, local adaptation, and persistence (Mazzi and Dorn 2012; Arias et al. 2019). This affects the design of pest-management programmes, since knowledge of pest strains that are resistant to toxic insecticides or proteins derived from genetically modified plants can help in the spatial configuration and structure of refuges associated with crop plantings. Integrated pest-management (IPM) programmes depend on the prediction of critical densities and colonisation rates, which are associated with a pest's movement potential (Lamp and Zhao 1993; Early et al. 2018). Although planning and implementation of IPM has been viewed as the best alternative to reduce pest-induced losses to growers (Hassanali et al. 2008), pest population dynamics at larger spatial scales continues to be a major source of problems for modern agriculture (Ferreira and Godoy 2014).

The role of organism movement and spatial distribution in ecological dynamics is widely recognised (Bascompte and Solé 1998; Hanski 1999; Turner et al. 2001), and the impact of landscape patterns on populations and organism movement is a major theme of agricultural landscape ecology (Mazzi and Dorn 2012). Interpretation of movement patterns depends on the use of analytical tools to synthetically describe biological processes based on abstraction of their most important elements. This type of procedure has been performed successfully in several areas, using mathematical or computational models specifically developed to study animal movement.

The algebraic formalism to describe animal movement is usually based on the random-walk structure of statistical physics (Hastings and Gross 2012). In random walk, the movement of an animal is a stochastic process, described by a kernel function specifying the probability of an animal moving from any point within a given time (Moorcroft 2012). However, some studies have shown that insects do not always move randomly and their movements are influenced by food resources, including crops, habitats, prey, predators, or competitors (Hanan et al. 2002; Mazzi and Dorn 2012; Moorcroft 2012).

Mathematical and computational models have long been used to describe ecological processes or to predict tendencies. These models are increasingly used by entomologists, especially to model population dynamics of pests (Sisterson et al. 2005; Lima et al. 2009; Ferreira and Godoy 2014; Martinez et al. 2018). Movement modelling has historically used the Lagrangian and Eulerian approaches to analyse the movement of animals (Okubo 1980). Lagrangian movement is defined at discrete steps and time segments designed to track the movement of single individuals in landscapes, while Eulerian movement was developed to study the expected pattern of space to be used by a population or individuals (Okubo 1980; Turchin 1998; Smouse et al. 2010).

Spatial models are frequently used to investigate population dynamics from a perspective of movement. The models can be structured to incorporate both movement and population growth, by using parameters obtained from birth and death estimates (Turchin 1998). The different ways to investigate spatio-temporal dynamics depend essentially on what exactly is to be modelled. Continuum reaction–diffusion models are generally employed to investigate diffusion problems in scenarios evaluating ecological movement (Murray 2003). In this case, partial differential equations can be used to analyse the movement dynamics, simultaneously taking into account population growth and diffusion (Murray 2003).

Coupled map lattices may also be used to model the movement of populations with difference equations, regarding space as a lattice of patches connected by dispersal (Rodrigues et al. 2014). Another way to model ecological movement is the cellular automata (CA) approach, which consists of a collection of interconnected cells, usually arranged as a regular spatial grid, with each cell characterised by one of several states, interpreted as presence or absence of individuals (Kari 2012). Generally, CA are formulated from rules for how the state of a cell is changed at each time step, essentially depending on its neighbourhood (Kari 2012).

Here, we analyse and discuss the movement ecology of two polyphagous insect species, members of different orders, which attack several crop species: the cucurbit beetle *Diabrotica speciosa* Germar (Coleoptera: Chrysomelidae) and the fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). These species have attracted interest from ecological modellers in recent years, primarily because of the role of landscape in their dynamics. Knowledge of their behavioural and ecological attributes is important for understanding the spatio-temporal distribution and movement dynamics of immatures and adults in agricultural landscapes. An analysis of their movement patterns illustrates the importance of spatial approaches in the study of entomological pests

(Ferreira et al. 2014; Westbrook et al. 2016). Although in the current forum we have analysed and discussed dispersion modelling of two species of agricultural pests, this approach can be applied to other insect species and other cropping systems.

Movement ecology in *Diabrotica speciosa*

Diabrotica speciosa is a polyphagous insect that is widely distributed in South America except in Chile, and is restricted to elevations lower than 2500 m (Ávila and Parra 2002, 2003; Walsh 2003). Both adults and larvae can threaten different crops. Adults exploit leaves, shoots, pods, or fruits, reducing productivity (Ávila and Parra 2003; Walsh et al. 2020). Larvae of *D. speciosa* have an underground habit and attack roots, causing significant losses of corn, potato, bean, and soybean crops (Ávila and Parra 2002, 2003). In Brazil, in recent decades this species has caused large economic losses of off-season corn crops. The attacked roots absorb less water, reducing the productivity of the plant and increasing its susceptibility to tipping and root diseases (Marques et al. 1999). Oviposition of *D. speciosa* can be influenced by the nutritional quality of each plant, and therefore, the diversity of host plants in agricultural landscapes is generally associated with the distribution of eggs on the plants (Baldin and Lara 2001).

Larvae of *D. speciosa* develop and survive best when infesting corn roots, which are C4 plants, whereas adults perform best when feeding on C3 plants, e.g. beans and soybeans (Ávila and Parra 2003; Walsh 2003). Therefore, the successful development of larvae and adults depends on the availability of different resources in plants and/or plant parts, which are directly associated with the efficiency of nitrogen (N) use by plants; C4 plants use N more efficiently than C3 plants (Sage and Monson 1998). Host plants may also influence the fitness of insect populations in different ways for immatures and adults, which can produce variations in survival and larval weight for larvae and in fecundity for adults (Scheirs and De Bruyn 2002; Janz 2005; Gripenberg et al. 2007).

The life-history parameters and movement of *D. speciosa* as related to the agricultural calendar have been investigated in studies of spatial structure applied to heterogeneous landscapes (Ferreira et al. 2014; Garcia et al. 2014, 2020). Feeding preferences of *D. speciosa* have been investigated in detail (Walsh et al. 2020). The effects of host-plant diversity and spatial structure of heterogeneous landscapes on the movement and survival of *D. speciosa* were studied by Ferreira et al. (2014) and Garcia et al. (2014). Ferreira et al. (2014) proposed a bi-dimensional stochastic cellular automata to take into account the spatio-temporal dynamics of immature and adult stages, together with adult oviposition and emergence. The automata were designed to include specific crops that affect the fitness of *D. speciosa* immatures and adults in

different ways. The different spatial distributions of food resources, i.e. random distribution or distributions in rows and blocks (Fig. 1), illustrate different scenarios. A mean-field approximation was derived for the automata model in order to determine the conditions for insect persistence. The movement of the insect was simulated for landscapes (Fig. 1) with two types of habitats (Ferreira et al. 2014), with one resource ($p = 1$) and two resources ($p = 2$). At each time step, the density of sites occupied by immatures and adults was denoted $p1$ (t) and $p2$ (t) time, satisfying the mean-field equations, written as

$$p1_{t+1} = \theta_1(1-p1_t) + (1-\mu_1-\sigma_1)p1_t$$

and

$$p2_{t+1} = \frac{\sigma_1}{2}p1_t\left(1-p2_t\right) + \left(1-\gamma_1\right)p2_t$$

where

$$\theta_1 = 1-(1-\phi_1p2)^{25}, \mu_1 + \sigma_1 < 1, \text{and } \gamma_1 < 1.$$

The term θ_1 indicates that each *D. speciosa* female lays eggs with probability ϕ_1 for each of its 25 adjacent neighbours, defined as the Moore neighbourhood of radius two plus the central site (Garcia et al. 2014). Fecundity follows a binomial distribution (Garcia et al. 2014). If one or more eggs land on an empty site, that site becomes occupied with probability θ_1. Therefore, there is a non-linear density dependence through competition for space, decreasing immature viability and adult weight and reproductive fitness. From the equilibrium analyses, two solutions were obtained, either persistence or non-persistence of the population, depending on insect fitness (Ferreira et al. 2014). Numerical simulations using parameters estimated in the laboratory resulted in estimates of the movement of *D. speciosa* in bean, soybean, potato, and corn plantings.

Following the modelling approach used by Ferreira et al. (2014), a spatially explicit model with clustering analysis was developed to study the spatial configuration of crops, aiming to control the population of *D. speciosa* in bean, soybean, potato, and corn, used as host plants to compose intercropping systems (Garcia et al. 2014). The biological parameters for *D. speciosa* obtained from experimental studies were used to group the landscapes, and a clustering analysis was applied. Clusters were used to estimate the proximity among host plants, according to the biological parameters: oviposition rate, larval mortality rate, larva–adult development rate, and adult mortality rate (Fig. 2). The results of this analysis indicated that corn affected *D. speciosa* differently from potato, soybean, or bean. The higher the proportion of corn in the system, the better the pest control. Therefore, corn can be used as a natural barrier for this pest.
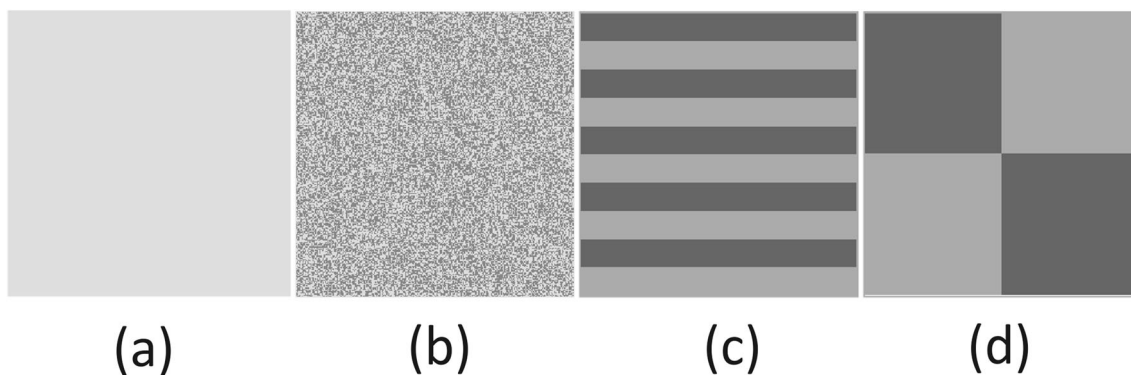
Fig. 1 Spatial configurations used in the simulations. (**a**) One habitat (τ_1), (**b**) two habitats with random distribution, (**c**) two habitats in rows, and (**d**) two habitats in blocks; in (**b**)–(**d**) we have $\tau_1 = \tau_2 = 0.5$.

Figure extracted from Ferreira et al. 2014 (doi: 10.1007/s11538-014-9975-1), with permission from Springer Nature (Bulletin of Mathematical Biology), licence no. 4946600813683

This suggests that simulations combining corn and other host plants are more useful to investigate the consequences of landscape heterogeneity for the density of *D. speciosa*.

Comparison of the simulations by observing the population densities in the plant rows (Fig. 3) showed that using an intercropping system with corn (bars in Fig. 3c) was the best strategy to reduce the population of *D. speciosa*, because this system negatively affected the spatio-temporal dynamics of the beetle in all intercropping arrangements simulated (Fig. 3). Beetles exploiting corn showed the lowest oviposition rate (corn = 0.011, soybean = 0.056, potato = 0.379, and bean = 0.394), which has the strongest effect on a population (Garcia et al. 2014). The reduced number of eggs produced by adults feeding on corn and soybean can be explained by the low availability of nitrogen in the leaves of these plants (Garcia et al. 2014).

However, one aspect of the beetle's biology was missing in the investigation of *D. speciosa* movement in heterogeneous landscapes. Female behaviour can be driven by the need to provide the best host for its offspring. Therefore, there is a parent-offspring conflict, because female adults need to choose between maximising their reproductive output, for instance on soybean, or maximising the development and growth of their larval offspring on another host, e.g. corn (Scheirs et al. 2000). If mothers choose a host that benefits the offspring, the species is considered to assume a "mother-knows-best" behaviour. To provide well-founded answers about this behaviour, Garcia et al. (2020) proposed a spatio-temporal model, using an intercrop pattern combining corn and soybean configured in rows, which provides different nutrients for different life stages. Adults were considered the

Fig. 2 Distance matrix calculated at each time step of the clustering algorithm, represented by i–iii, and the resulting dendrogram. The letters P, B, C, and S represent potato, bean, corn, and soybean crops, respectively. Figure extracted from Garcia et al. 2014 (doi: 10.1007/s10980-014-0073-4), with permission from Springer Nature (Landscape Ecology), licence no. 4946610330935
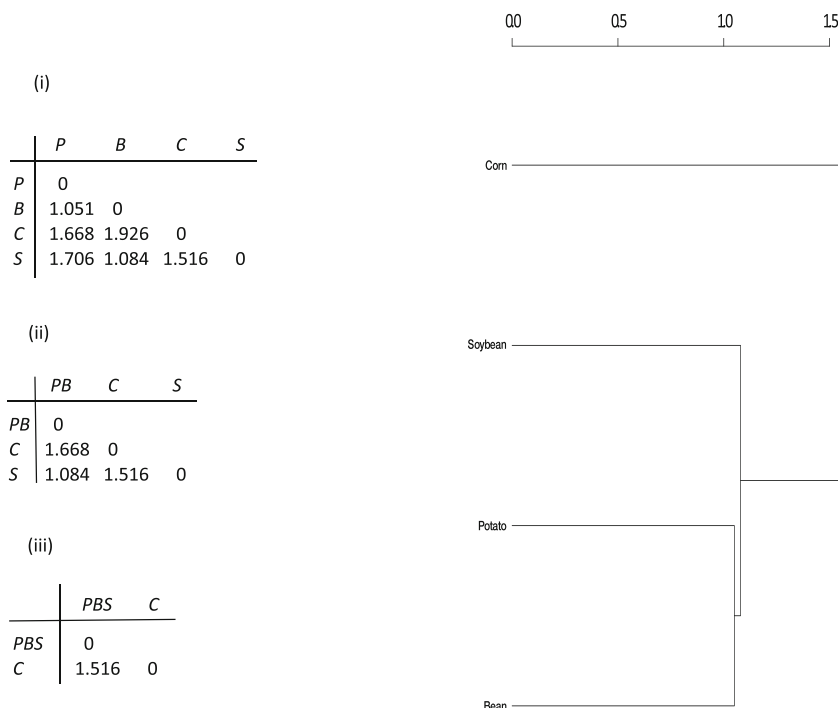

(i)

	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. 3 Population density in response to spatial patterns for bean and potato (**a**), soybean and bean (**b**), and corn and bean intercropping (**c**). Odd numbers correspond to bean rows (planting in rows) and even numbers to potato, soybean, and corn, respectively. Grey indicates adults and black indicates larvae. Figure extracted from Garcia et al. 2014 (doi: 10.1007/s10980-014-0073-4), with permission from Springer Nature (Landscape Ecology), licence no. 4946610330935
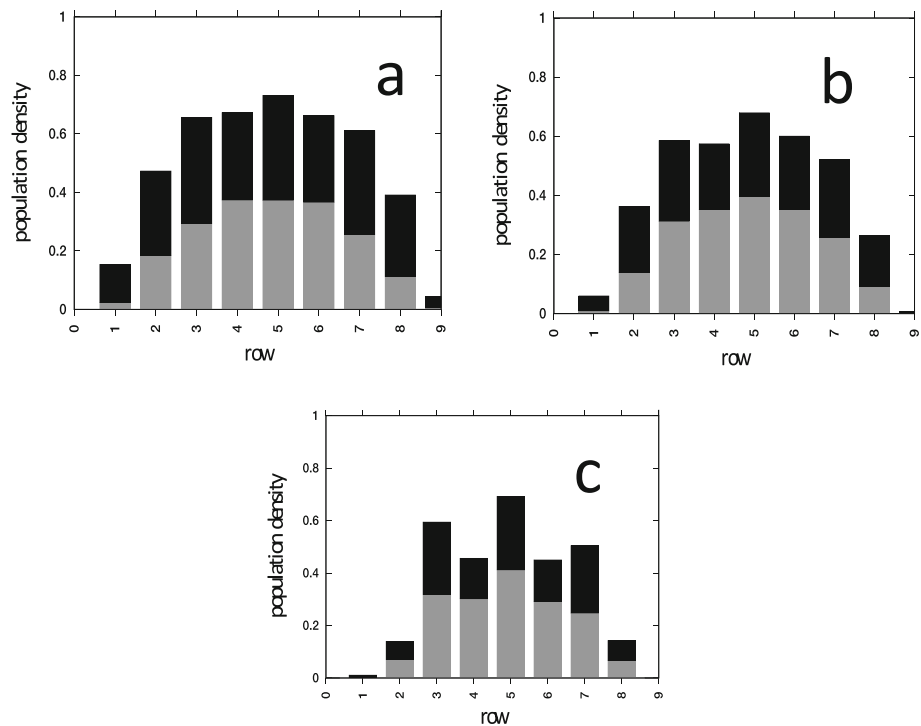
only life stage able to disperse by random or directional movement.

The model also analysed a complex landscape, designing the crops in blocks to simulate the agricultural calendar in south-eastern Brazil. Differently from the previous models, the landscape configuration changed over time and space, with the crop calendar following the cropping system usually employed in the state of São Paulo, Brazil. This crop pattern considers that crops can be attacked by insects for seven continuous months, a period characterised by post-harvest, germination, and small plants. The landscape included the presence of corn, soybean, and fallow areas.

The movement between crops was simulated by taking into account the demographic parameters studied by Garcia et al. (2014), combined with the proportion of time spent on each crop (Garcia et al. 2020). The simulations also included the foraging behaviour of *D. speciosa* females, to maximise either their own fitness or that of their offspring. The results obtained for the intercropping scenario suggested that females that foraged for corn intercropped with soybean maximised the survival of their offspring during the oviposition period, a better strategy than remaining on soybean, i.e. adopting a selfish behaviour (Fig. 4).

Intercropping offers other benefits besides those already mentioned. Intercropping helps to manage plant diseases transmitted by insect vectors by increasing the population of beneficial insects, which minimises outbreaks and helps in weed control (Maitra et al. 2019). Plants with a repellent effect can also be used for pest control. However, implementation requires a detailed design for spatial configuration, including a

study of the intercrop row pattern in a trap-crop system (Banks and Ekbom 1999). Therefore, intercropping modelling can be useful to determine the optimum spatial configuration of intercropped plants, informing management plans.

Although the intercropping strategy can potentially optimise resource utilisation and also improve pest management (Diekotter and Crist 2003; Song et al. 2010), intercropping modelling is seldom used to study the productivity of combined crops or to model the movement of pests. Crop simulation models are useful to investigate cause-and-effect relationships in crop production (Chimonyo et al. 2015), but few models have been appropriately adapted to simulate intercrop systems, particularly because they do not take into account spatial heterogeneity and ignore the multi-dimensionality often required for intercropping configuration (Nair et al. 2012).

With respect to pests, most existing studies investigate the spatial movement of herbivores in conventional crops interspersed with trap crops (Banks and Ekbom 1999). The most recent example of this approach is the study by Allen-Perkins and Estrada (2019), who investigated the movement of aphids associated with transmission of a virus to crops, in a context of intercropping including trap crops, and developing an epidemiological susceptible–infected–removed model. The study showed that the intercropping arrangements can reduce by up to 80% the number of plants affected by aphid-borne viruses and significantly slow virus propagation (Allen-Perkins and Estrada 2019).

The study by Allen-Perkins and Estrada (2019) emphasised an important aspect of plant systems with pathogen transmission. The context of this study introduced the epidemiological dimension into the discussion of insect movement, which has

a predominant role in transmission of pathogens, with important implications for monocultures. Intercropping is important for plant health; 73% of more than 200 studies comparing the frequency of pathogens, particularly foliar fungi, between monocrops and intercrops found a reduction in disease (Boudreau 2013).

Movement ecology of *Spodoptera frugiperda*

For decades, pest management has emphasised chemical control as the main control strategy for insects, primarily in extensive monocultures (Thacker 2002). However, insecticides are highly harmful to the environment and human health, and have rapidly produced resistance in pest populations (Tabashnik et al. 2013). The use of transgenic plants has become common for several agricultural crops as an alternative way to reduce pests, but resistant insects have also become established in the main agricultural crops (Tabashnik and Carrière 2017). Furthermore, intensive management practices have led to a reduction in the complexity of the landscape, which may be reflected in the decline in ecosystem services (Tscharntke et al. 2005).

A possible strategy to minimise this problem, the configuration of plantings, can ameliorate this problem, since interspersing different crop species (intercropping) or combining them with natural refuges can diversify the entomological fauna, reducing the abundance of pests (Altieri 1999; Huang et al. 2017; Peñalver-Cruz et al. 2019). However, polyphagous pests are able to move between crops and damage different plants (Garcia et al. 2020). In view of this, strategic spatial configurations of different crops should be considered, to mitigate the damage from polyphagous species.

Implementation of refuge areas (non-Bt plants) in transgenic crops has been stimulated, as an attempt to retard the development of insect resistance to Bt crops, i.e. to plants expressing toxic proteins produced by *Bacillus thuringiensis* (Berliner) (Carroll et al. 2012). The configuration of plantings, transgenic or not, can influence the movement of insects in agricultural landscapes, with important implications for pest management, especially if the pest species are polyphagous (Sisterson et al. 2005). The degree of heterogeneity of crops and the size or proportion of refuge areas in the landscapes can influence the intensity of insect movement in agricultural areas (Andow 1991). Besides, landscape features may or may not facilitate the movement of insects through the vegetation and provide information about immigration of pests to agricultural fields (Macfadyen et al. 2015). Therefore, understanding pest dynamics involves knowledge of the species demographics at different spatial levels, such as long-range migration, inter-habitat dispersal, and within-habitat movement (Hawkes 2009).

Spodoptera frugiperda is a polyphagous insect capable of feeding on approximately 100 different host plants, moving between different crops and causing serious damage. It is a major pest of Brazilian corn, cotton, and soybean, feeding during the larval phase on both vegetative and reproductive organs (Silva et al. 2017). The species is genetically differentiated into two strains, which differ in terms of food preference, biology, and behaviour, referred to as the rice strain (R-strain) and corn strain (C-strain) (Quisenberry 1991; Nagoshi and Meagher 2004). These strains are native to tropical and subtropical regions of the Americas, occur in about 100 countries worldwide, and show high potential for new invasions (Prowell et al. 2004; Clark et al. 2007; Baloch et al. 2020). Agricultural losses have also been severe in Honduras and Argentina, with damage to corn reaching up to 40% of production (Baloch et al. 2020). In January 2016, the species was recorded in West Africa, whence it spread to many countries within 2 years (Early et al. 2018; Goergen et al. 2016).
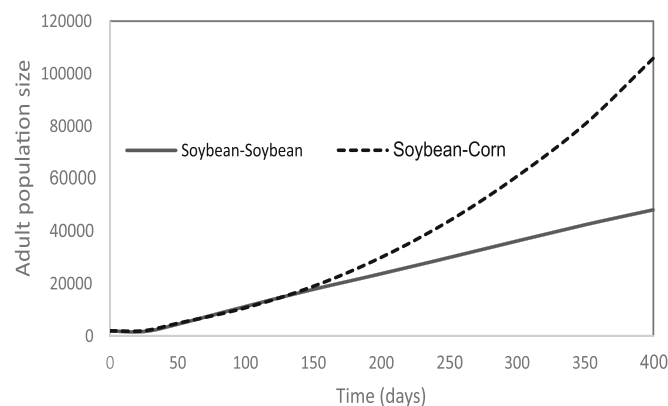

Fig. 4 Evolution of the adult population over time, with adults remaining in the same crop over the entire stage (solid line) and adults searching for a crop to maximise survival and offspring growth (dashed line). Figure extracted from Garcia et al. 2020 (doi: 10.1186/s40462-020- 00198-7) with unrestricted use (https://movementecologyjournal. biomedcentral.com/articles/10.1186/s40462-020-00198-7#rightslink) granted by Springer Nature (Movement Ecology)

Spodoptera frugiperda has also been recorded in Central Asia, India, Myanmar, Thailand (FAO 2018; Nakweya 2020), and China (Baloch et al. 2020).

Through the use of a cellular automata, different patterns of population distribution of *S. frugiperda* were investigated in order to analyse possible associations with levels of larval viability and adult longevity in corn, cotton, millet, and soybean (Garcia and Godoy 2017). The degree of spatial dispersal of *S. frugiperda* was investigated in each simulation, by calculating the Morisita index for each combination of larval viability and adult longevity. The results suggested two different spatial patterns in response to this estimation, random and aggregated (Fig. 5). Lower larval viabilities combined with higher adult longevities are related to a random distribution (Garcia and Godoy 2017). Higher larval viability and adult longevity result in an aggregated pattern. Patterns of this nature are associated with high densities, and in real scenarios, when IPM strategies are required.

Some insect populations also show resistance to insecticides and to transgenic Bt plants. Although ecological and genetic aspects of *S. frugiperda* have been thoroughly studied (Silva et al. 2017, Early et al. 2018, Xiao et al. 2020, Baloch et al. 2020, Haenniger et al. 2020, Machado et al. 2020, Richardson et al. 2020), local-scale dispersal, which is essential to establish pest-management programmes, is incompletely understood. Currently, a delay in resistance evolution is highly desired in view of the serious damage caused by *S. frugiperda* (Horikoshi et al. 2016). The most commonly recommended resistance-management strategy is maintenance of non-Bt refuge areas for susceptible insects, to provide a pool of insects that lack the resistance alleles. Mating between susceptible and resistant individuals may delay the evolution of resistance in *S. frugiperda* populations because it helps to dilute the resistance alleles.

Refuge areas can be used in a variety of efficient ways. Different spatial configurations such as seed mixture, blocks, or strips are example of ways to create refuges to slow the development of Bt-resistant pests. All these configurations have some connection to ecological traits, generally listed as factors affecting the success of refuge management in slowing the evolution of resistance in insects. Larval movement is highly important for this aspect. A computational model was developed to simulate how the movement of larvae can influence the dynamics of the evolution of resistance of *S. frugiperda* to Bt crops, using different refuge designs such as seed mixtures, blocks, and strips (Fig. 6). The sizes of refuges ranged from 20 to 50%, and the resistance of insects was classified as incomplete and complete (Garcia et al. 2016). Three rates of larval movement were investigated per time step, 0, 0.1, and 0.5.

The results of the simulations indicated that for the seed mixture, the higher the rate of larval movement, the higher the proportion of resistant insects; the strip configuration gave the opposite result. The study also showed that inclusion of larval movement is essential to analyse the evolution of resistance to Bt crops, although its influence depends on the type of resistance and particularly the design and size of refuges (Fig. 7) (Garcia et al. 2016).

A similar algorithm was combined with experimental data to investigate the movement of *S. frugiperda* larvae in Bt and non-Bt cotton (Fig. 8). The results showed that the larvae moved significantly more in Bt than in non-Bt cotton (Malaquias et al. 2017). The lower movement rate of *S. frugiperda* in non-Bt cotton may be related to the fitness cost that is usually observed in populations that maintain resistance in the absence of selection pressure (Malaquias et al. 2017).

The movement of polyphagous insects can also be stimulated by environmental influences. In particular, climatic conditions including temperature, humidity, and rain may influence the geographic distribution of *S. frugiperda*. Relationships between the distribution of *S. frugiperda* and climatic conditions were investigated by Garcia et al. (2018), validating a model and emphasising the effects of temperature variation on the development and distribution of the fall armyworm in the USA. Their study estimated the thermal

Fig. 5 Spatial patterns of insect distribution (adults) observed in simulations when the values of the proposed parameter set were varied. Random (**a**) and aggregated pattern (**b**). Figure extracted from Garcia and Godoy (2017) with internal reuse within the imprints of Springer Nature, without formal permission granted by Springer Nature (Neotropical Entomology)
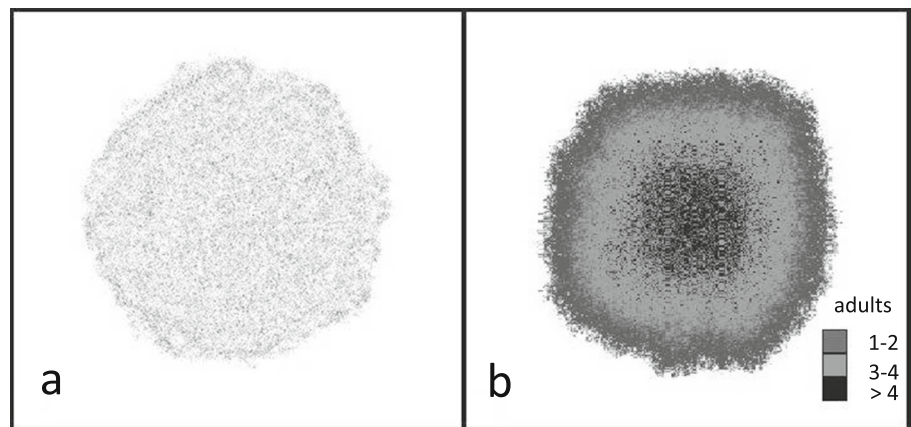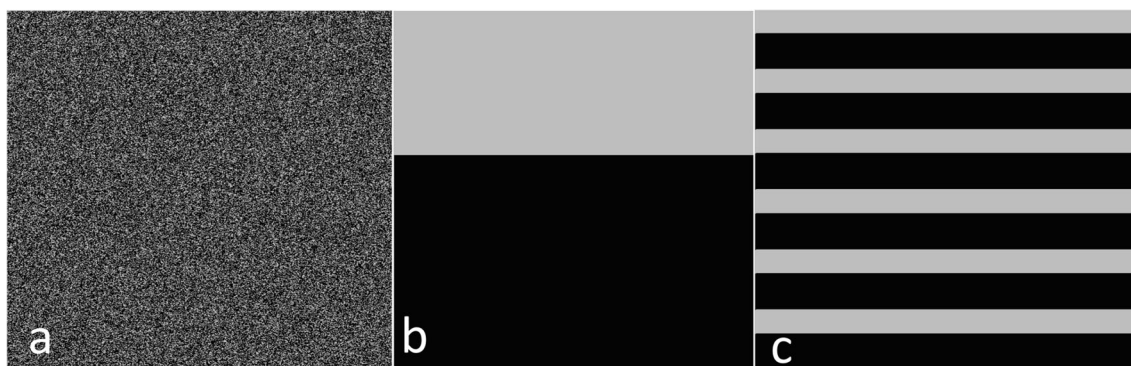
Fig. 6 Spatial configurations with refuge strategies designed for simulations of resistance evolution: (**a**) seed mixture, (**b**) blocks, and (**c**) strips. Non-Bt corn is shown in grey and Bt in black. Spatial arrangements with 40% refuge area. Figure extracted from Garcia et al. 2016 (doi:10.1016/j.ecocom.2016.07.006) under licence from Elsevier (Ecological Complexity), no. 4946620186202

constant and lower threshold temperature, in order to analyse successive generations of *S. frugiperda* at 42 locations in Florida for 11 years, using geographic information system (GIS). The highest number of generations was found in the counties farther south, which have warmer temperatures, which is important in overwintering periods to provide suitable conditions for moths (Garcia et al. 2018).

Using a complete design combining the effects of genetically modified plants and climate variables on the fall armyworm, a model was developed by Garcia et al. (2019) to describe the spatio-temporal dynamics of *S. frugiperda* in Bt and non-Bt areas, to investigate insect resistance to transgenic crops. They used a 4-year (2012–2015) FAW monitoring dataset for an area in northern Florida, USA, to fit the model to a real-time series (Garcia et al. 2019). The number of adults was predicted by constructing simulations associated with possible scenarios involving climatic changes (Fig. 9).

Outbreaks were described by the model with estimated values for parameters associated with resistance-allele frequency (0.15), migration rate (0.48), and rate of larval movement (0.04). A sensitivity analysis showed that the frequency of the resistance-allele migration rate was the main parameter

influencing the system. The simulations also suggested that an increase of 1°C would allow the insect population to double (Garcia et al. 2019). The model provided useful results, i.e. strong evidence of the effects of a gradual increase in mean temperatures on the density of *S. frugiperda*. The results of this study opened new prospects for applications of this theory in similar scenarios, such as recent infestations of the fall armyworm in Africa (Garcia et al. 2019).

Malaquias et al. (2020) investigated the influence of Bt and non-Bt cotton crops on larval dispersal and survival of susceptible and resistant *S. frugiperda* genotypes in pure and contaminated micro-landscapes. They used a model configured to evaluate the association between larval movement and resistance evolution of *S. frugiperda* in refuge areas that differed in the degrees of contamination and migration in genotype combinations (Fig. 10). Micro-landscape experiments produced data that were used to simulate a macro-landscape scenario, with the Cry1F-resistant fall armyworm genotype avoiding non-Bt cotton and the heterozygotes showing a larval-dispersal pattern similar to the susceptible genotype when the non-Bt plant was the central plant (Malaquias et al. 2020). The results suggest that *S. frugiperda* in cotton refuge
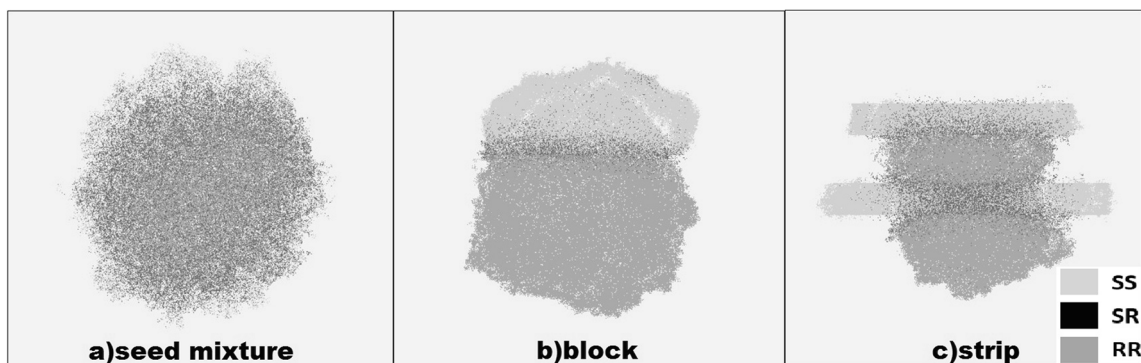

Fig. 7 Pattern of larval distribution observed in each refuge configuration after 300 time steps. Insect genotypes are indicated in the legend. Spatial arrangements were defined with 40% refuge areas, complete resistance, and rate of larval movement equal to 0.5. Figure extracted from Garcia et al. 2016 (doi:10.1016/j.ecocom.2016.07.006) under licence no. 4946620186202 from Elsevier (Ecological Complexity)
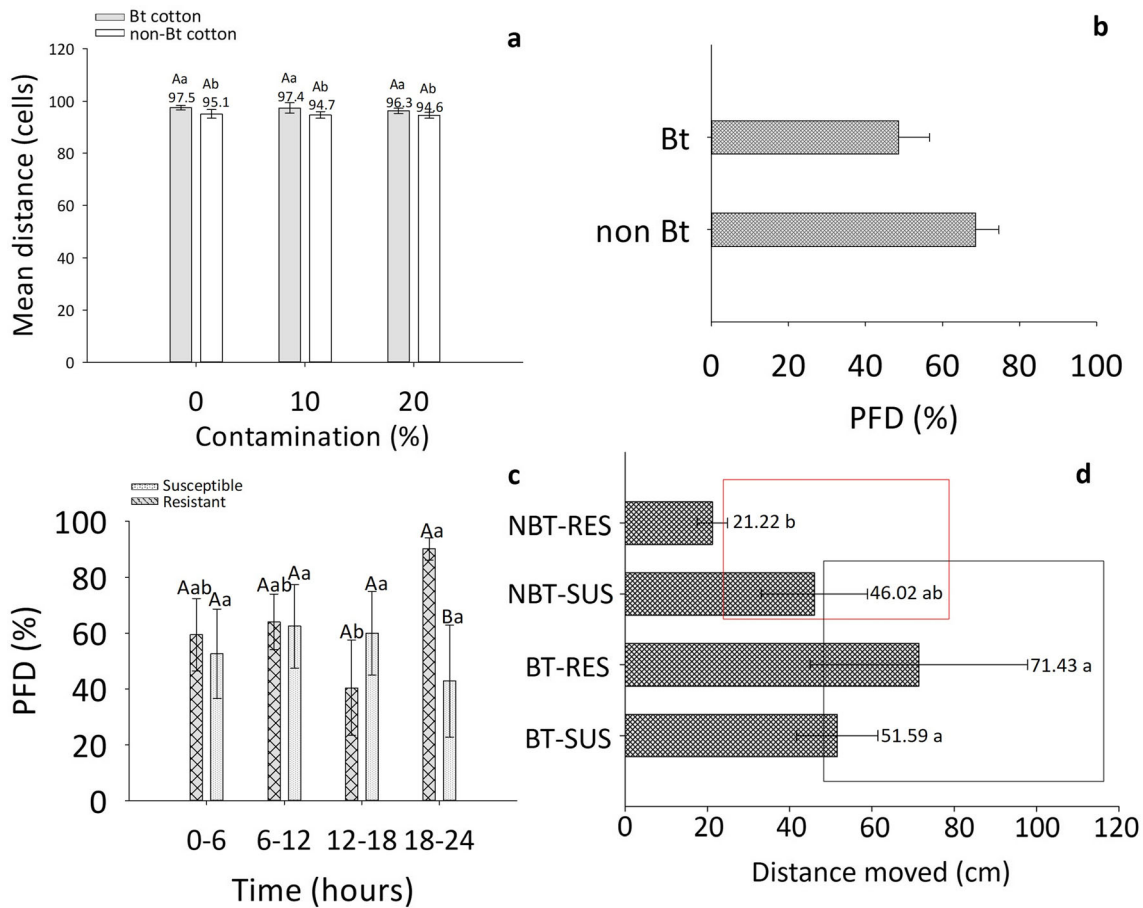
Fig. 8 Distance (mean ± SE) of *Spodoptera frugiperda* larvae from the centre of the population distribution (**a**). Percentage (mean ± SE) of post-feeding dispersal (PFD) of *Spodoptera frugiperda* strains fed on Bt and non-Bt cotton (**b**) at different time intervals (**c**). Distance moved (mean ± SE) by susceptible and Cry 1F-resistant *Spodoptera frugiperda* strains on Bt and non-Bt cotton (bottom) (**d**). Means followed by the same letters or by rectangles of the same colour were not significantly different, as determined by Tukey's test ($p = 0.05$). Capital letters comparing bars at the same time interval, and lower-case letters comparing bars of the same strain, in the top-left graph. ***Asterisks in the top-right graph indicate significant differences between means. Figure extracted and modified from Malaquias et al. 2017 (doi: 10.1038/s41598-017-16094-x) with unrestricted use (https://www.nature.com/articles/s41598-017-16094-x#rightslink) granted by Springer Nature (Scientific Reports)

areas contaminated with Bt plants may evolve resistance at least 75 times more rapidly than in areas with no contamination (Malaquias et al. 2020).

Ballooning, a passive dispersal process in which the lepidopteran neonate lowers itself on a strand of silk and is carried by the wind (Common 1990), was also investigated recently (Malaquias et al. 2021). The neighbourhood with Bt and non-Bt cotton plants was investigated on a small scale to evaluate the influence of neighbourhood on the ballooning dispersal of *Spodoptera frugiperda*. The impacts of active (walking) and passive (ballooning) larval movement were also studied experimentally, to evaluate the resistance evolution of *S. frugiperda* to Bt cotton, with different scenarios of contamination in Bt and in non-Bt fields.

The ballooning rate of Cry1F-resistant larvae when non-Bt cotton was the natal plant and Bt cotton was in the neighbourhood was half the rate as that when Bt cotton was the natal plant and non-Bt cotton was in the adjacent sites. In a non-high-dose event, the time to develop resistance was negatively associated with the rate of walking movement together with ballooning. Information about larval movement by ballooning in a mixture of Bt and non-Bt cotton plants can provide important insights for understanding the adaptation process in *S. frugiperda* and may be helpful in designing resistance-management programmes in the future (Malaquias et al. 2021).

The computational approaches currently available to apply the theoretical formalism of landscape ecology to agricultural requirements have emphasised different aspects relevant to agro-ecological scenarios. Studies by Baloch et al. (2020), Haenniger et al. (2020), Machado et al. (2020), and Richardson et al. (2020) focused on the interface between pest
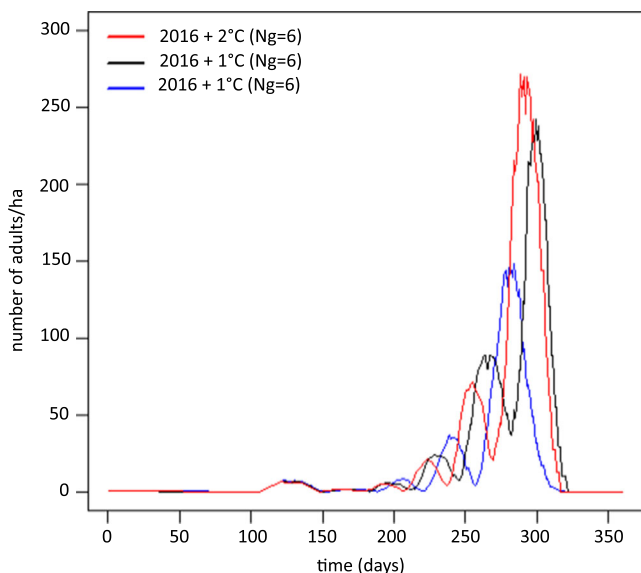
Fig. 9 Population levels estimated for 2016 and for two hypothetical simulations (increasing the temperatures by 1 and 2°C). Figure extracted from Garcia et al. 2019 (doi: 10.1007/s10340-018-1051-4) under licence no. 4946621384588 from Springer Nature (Journal of Pest Science)

management and agricultural landscapes. Studies in the framework for risk assessment and risk management, meta-population, diffusion theory, GIS, and spatial statistics have emphasised problems inherent in habitat use, such as refuges for insect resistance management in a context of Bt-transgenic crops (Caprio et al. 2004; Gilligan et al. 2005; Caprio et al. 2009; Andow et al. 2010; Carrière et al. 2004). Interest in modelling to investigate movement, dispersal, distribution, and population dynamics of insects, and the use of other approaches, such as CA coupled with fuzzy logic, fractals, percolation and synchronisation and individual/agent-based approaches have increased, in attempts to better understand the spatial structure of pest populations associated with different spatial configurations of plantings (Tonnang et al. 2017).

Species spatial distribution has been studied theoretically, using different mathematical approaches. Many studies of metapopulation dynamics have used a more general approach, with spatially implicit models that average the effects of all landscape components (Hanski 1999). Modelling approaches to link theoretical analyses of the landscape ecology to agricultural requirements should also emphasise aspects relevant to agro-ecological scenarios, including the particularities of each crop (Holzkämper and Seppelt 2007). When the spatial heterogeneity of landscapes influences the species dynamics and ecological processes, site-intrinsic aspects integrating the landscape become important. Several factors such as habitat quality, resource availability, and dispersal barriers should be taken into account in order to improve comprehension of the spatial patterns of species distribution and abundance.

The analysis of the movement of insects between Bt and non-Bt plants by Garcia et al. (2016), followed by Garcia et al.
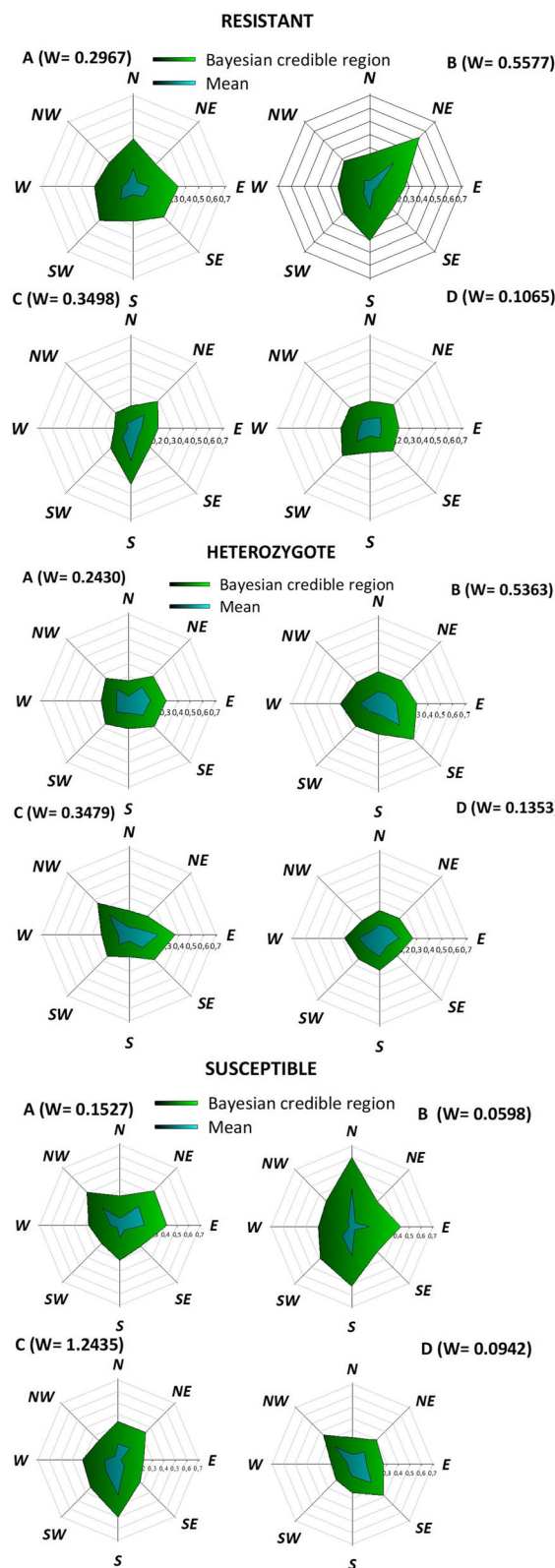
◀ **Fig. 10** Frequency distribution of Cry 1F-resistant (top-left graph), heterozygous (top-right graph), and susceptible *Spodoptera frugiperda* paths (bottom graph). The blue area refers to the mean frequency of insects, and the green area refers to the Bayesian credible region. T1, central non-Bt plant and adjacent non-Bt plants; T2, central non-Bt plant and adjacent Bt plants; T3, central Bt plant and adjacent non-Bt plants; and T4, central Bt plant and adjacent Bt plants. Figure extracted from Malaquias et al. 2020 (doi: 10.1007/s10340-019-01145-1) with permission from Springer Nature (Journal of Pest Science), licence no. 4946630529663

(2018, 2019) and Malaquias et al. (2017, 2020, 2021), was motivated by the previous studies investigating the movement of pests in intercropping scenarios (Ferreira et al. 2014; Garcia et al. 2014) and by the lack of resistance-modelling studies that included larval movement. This movement is a key element in the evolution of resistance of insect pests with high rates of dispersal of immatures, given the interest of agribusiness in applying a seed-mixture refuge (random arrangement) (Cerda and Wright 2004; Carroll et al. 2012). Our results have provided important lessons, especially focused on the movement of pests associated with Bt crops. Important aspects of the results from studies by Garcia et al. (2016, 2019) and Malaquias et al. (2017, 2020) agree with a previous study that also used modelling to evaluate the movement of insects. The results suggested that under certain conditions, such as seed mixtures of Bt and non-Bt plants combined with high pest dispersal rates between crops, can significantly increase the evolution of insect resistance to Bt plants (Caprio et al. 2016).

Final remarks

Spatially explicit models, particularly cellular automata, have potential for use in investigating the movement of polyphagous insects, since the models are structured to evaluate the movement of insects in different spatial configurations of crops, especially intercropping.

Two scenarios, intercropping and transgenic crops, inspired the development of computational algorithms to model the movement of polyphagous pests in agricultural systems. The results indicated critical spatial configurations to control insect proliferation.

The computer simulations performed indicated the best spatial configurations for delaying insect resistance to transgenic crops, taking into account their movement between Bt and non-Bt crops.

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Declarations

Conflict of interest The authors declare no competing interests.

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