From IBM to IPM: Using individual-based models to design the spatial arrangement of traps and crops in integrated pest management strategies

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ABSTRACT

The development of alternative pest-control strategies based on the spatial design of cropping systems requires a thorough understanding of the spatial links between the pest and its environment. Mechanistic models, especially individual-based models (IBMs), are powerful tools for integrating key behaviours, such as habitat selection and dispersal, with spatial heterogeneity. In this paper, we used an IBM calibrated and evaluated from real data to represent the spatial dynamics of the banana weevil in relation to the cropping system. We considered crop fragmentation and mass trapping as tools for suppressing pest numbers. Our simulation results showed that manipulating crop residues in the area surrounding each pheromone trap greatly improved trap efficiency. For an intensive banana plantation in fallow, traps were most effective when situated at the transition zone between banana area and fallow so as to maximize the trapping of weevils escaping the fallow. The model also showed that weevil numbers decreased when fragmentation of banana plantations was reduced.

1. Introduction

Integrated pest management (IPM) strategies must consider key processes of insect behaviour, such as habitat selection, mating behaviour, dispersal, and predator–prey interactions (Petit et al., 2003; Roitberg, 2007). Habitat selection by insects is widely used in the "push–pull" control strategy in which pests are repelled (or "pushed") from the crop and are simultaneously attracted (or "pulled") by traps or a trap crop (Cook et al., 2007). Insect communication by sexual or aggregative pheromone is a widely used behaviour for mass trapping or mating disruption (Khan et al., 2008). The limited dispersal capacities of some insects are considered in a crop destruction strategy in which pests are unable to cross large areas of fallow to reach new habitats (Rhino et al., 2010). Perceptual ranges of insects are principal factors affecting predator–prey interactions (Bianchi et al., 2009). In banana agroecosystems, innovative IPM strategies are increasingly used to reduce the use of insecticides and herbicides. They may employ addition of cover crop (Duyck et al., 2011), inclusion of fallow in rotation sequences (Rhino et al., 2010), mass trapping (Rhino et al., 2010), and use of biological control agents (Akello et al., 2009; Padilla-Cubas et al., 2010). Understanding spatial ecology of pests

becomes necessary to develop and implement those innovative IPMs strategies.

Space has traditionally been ignored or treated as an implicit variable in pest-suppressive strategies (Kropff et al., 1995). With the recent emphasis on alternative methods of pest control, however, researchers have explicitly considered space as a means to link a pest to its environment (Potting et al., 2005). In the case of insect pests, alternative control strategies include those based on the spatial arrangement of traps (Yamanaka, 2007), of semi-natural habitats (Tscharntke et al., 2007), or of alternative crops (Barari et al., 2005) in the landscape. Pheromone traps are used in mass trapping to maintain pest numbers within acceptable bounds (Witzgall et al., 2010). Beyond services provided by agro-ecosystems (Moonen and Barberi, 2008), semi-natural habitats (forests, hedgerows, field margins, fallows, and meadows) provide overwintering sites or alternative sources of pollen and nectar for insects and especially for parasitoids of pests (Musters et al., 2009), and these habitats therefore contribute to "top-down" pest control. Pheromone traps, semi-natural habitats, and alternative crops will greatly influence movements, egg-laying tactics, and mortality risks of insects and consequently their spatial distribution and related damages (Huffaker and Gutierrez, 1999). Because of its intrinsic complexity, the study of insect behaviour in spatially complex environments (i.e., in the real world) can benefit from spatially explicit, mechanistic models.

There is a growing interest in the use of such models as exploratory tools for the design of innovative cropping systems

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via spatial arrangement of resources (Kropff et al., 2001; Lo-Pelzer et al., 2010). These models, which consider landscape organization as a primary tool to suppress pest numbers, combine spatial processes in an integrated approach (Potting et al., 2005). They focus either on the population in "aggregated models" or on individuals in "individual-based models" (IBMs).

Aggregated models have been used to study the effect of landscape heterogeneity on insect spatial patterns (Vinatier et al., 2011b). Habitat fragmentation has been studied via metapopulation models (Banks and Ekbom, 1999), and the effect of orchard boundaries has been studied via reaction-diffusion models (Tyson et al., 2007). Parasitoid–pest interactions have been investigated using a lattice model (Lopes et al., 2010). Despite a synthetic formalism that makes them analytically tractable, aggregated models do not explicitly consider individual behaviour in response to environment, which is considered an important component of pest management (Choi et al., 2004; Roitberg, 2007).

IBMs are well suited for representing individual behaviours, such as mate-finding (Byers, 1991), attraction to pheromone traps (Byers, 1999; Yamanaka et al., 2003), or predator–prey interactions (Bianchi et al., 2009). They follow the principle that population properties will emerge from the representation of individual behaviours (Grimm and Railsback, 2005). In IBMs, each individual is explicitly modelled and acts according to a set of rules. IBMs are spatially explicit because exact locations of each habitat element and each individual are known. Recently, IBMs have been used to study the efficacy of agro-ecosystem diversification for pest control by enabling virtual modification of a landscape matrix (Potting et al., 2005).

Mechanistic, spatially explicit IBM models intended for the design of innovative IPM strategies that take into account habitat spatial organization have yet to be validated with real data. The IBM developed by Potting et al. (2005) is theoretical and based on arbitrarily chosen parameters. We think that a mechanistic approach with a strong reliance on data collected in the field will greatly improve the realism of the emerging properties of IBMs.

In this paper, we use a modelling approach to represent the spatial dynamics of an insect pest in relation to its environment. We took as a case study the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae), which lives in spatially heterogeneous banana agroecosystems. We chose an IBM that has already been validated by real data on this pest (Vinatier et al., 2009). Parameters of habitat preference based on a radiotelemetry data set measured on this pest (Vinatier et al., 2010) and estimated by Vinatier et al. (2011a) were added to this IBM. We considered crop fragmentation by fallow (Rhino et al., 2010) and mass trapping (Tinzaara et al., 2005b) as principal tools for suppressing pest numbers. We used the model to explore the effects on trap efficiency of (i) modifying the environment surrounding one trap, (ii) arranging multiple traps in a fallow surrounded by a banana plantation, and (iii) fragmenting a banana crop area with multiple fallows. The modelling study was performed to test how IBMs can contribute to development of innovative IPM strategies.

2. Materials and methods

2.1. The COSMOS model

The simulations described here are based on a modified form of the IBM developed earlier for this pest, called COSMOS. Weevil's and banana's individual traits values used in COSMOS can be found in Vinatier et al. (2009). COSMOS runs on a daily time step. The processes underlying the spatial pattern of the insect are explicitly modelled at the individual level. The environment is spatially explicit and represented by a grid of cells containing habitat elements that are mutually exclusive (banana plant, crop residues, trap, ditch, or bare soil) and/or agents (insects, banana plants). A cell size of 1 m² was chosen to characterize the habitat variability, following Marzluff et al. (2004). The grid is considered as toroïdal to avoid edge effects in the simulations, i.e. weevils that would disappear outside the map area reappear onto the opposite side of the map. Each agent passes through different stages: egg, larva, pupa, and adult for insects and maiden sucker, preflowering, post-flowering, and harvesting stages for banana plants. Insects act according to a set of rules that depend on the properties of their current location. Egg-laying, which occurs only on cells with banana plants, depends on the number of adults in the cell and on the stage of the banana plant. The development of plants, eggs, larvae, and pupae are temperature-dependent. The mortality of each insect stage is considered as a constant in the model.

In the previous model, movement was considered as deterministic and to occur only from plant to plant. In the model developed in this paper, the movement depends on the habitat features of each cell. At each time step, the probability that an individual will move from the current cell to a surrounding cell in the individual's perceptual range is assessed according to a potential given by a dispersal kernel and habitat quality of the cells (Vinatier et al., 2011a). An individual's decision to move to a new cell is based on a multinomial probit of all the potentials of the cells within the perceptual range (see Appendix A for more details on the calibration of the movement probabilities and Table A1 for values of dispersal kernel and habitat qualities).

2.2. Crop system

Banana plants are considered to be semi-perennial, and plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner, 1994). Only one sucker per mat is selected by farmers. Banana leaves, trunks of harvested plants, and rejected suckers are regularly cut by farmers throughout the year and form a layer of crop residues. The duration of a banana plantation depends on the production areas. In the French West Indies, Costa Rica, and Brazil, plantations last about 5 years (i.e., for six successive cropping cycles) before replanting is required as a result of damage caused by insect pests and pathogens. In Africa and other areas, plantations last much longer than 5 years. In all cases, when the grower determines that a plantation (or part of a plantation) should be replanted, plants are killed by the injection of herbicides. After destruction, the treated area is left fallow for approximately 1 year before it is replanted.

2.3. Study species

The banana weevil *C. sordidus* is a walking insect whose activity is nocturnal and cryptic. *C. sordidus* occurs in all countries where its unique host plant, the banana, is present (Gold et al., 2001). Adults prefer moist environments and feed on banana plants or on their residues. Females lay eggs at the base of the host plant, and the larvae grow inside the corm. A plantation infested with banana weevils can be considered as a mosaic of different elements, each element having a potential effect on dispersal of adults. The elements of this mosaic include mats of banana plants, crop residues, bare soil, and ditches.

The control of *C. sordidus* populations is based on pheromone mass trapping (Rhino et al., 2010). Yellow pitfall traps containing an aggregation pheromone are buried in the soil. The chemical used in the traps is based on the aggregation pheromone sordidine, which is emitted by *C. sordidus* males and which attracts both males and females (Beauhaire et al., 1995). Despite the recent advances in the control of *C. sordidus* by the combination of fallow and mass
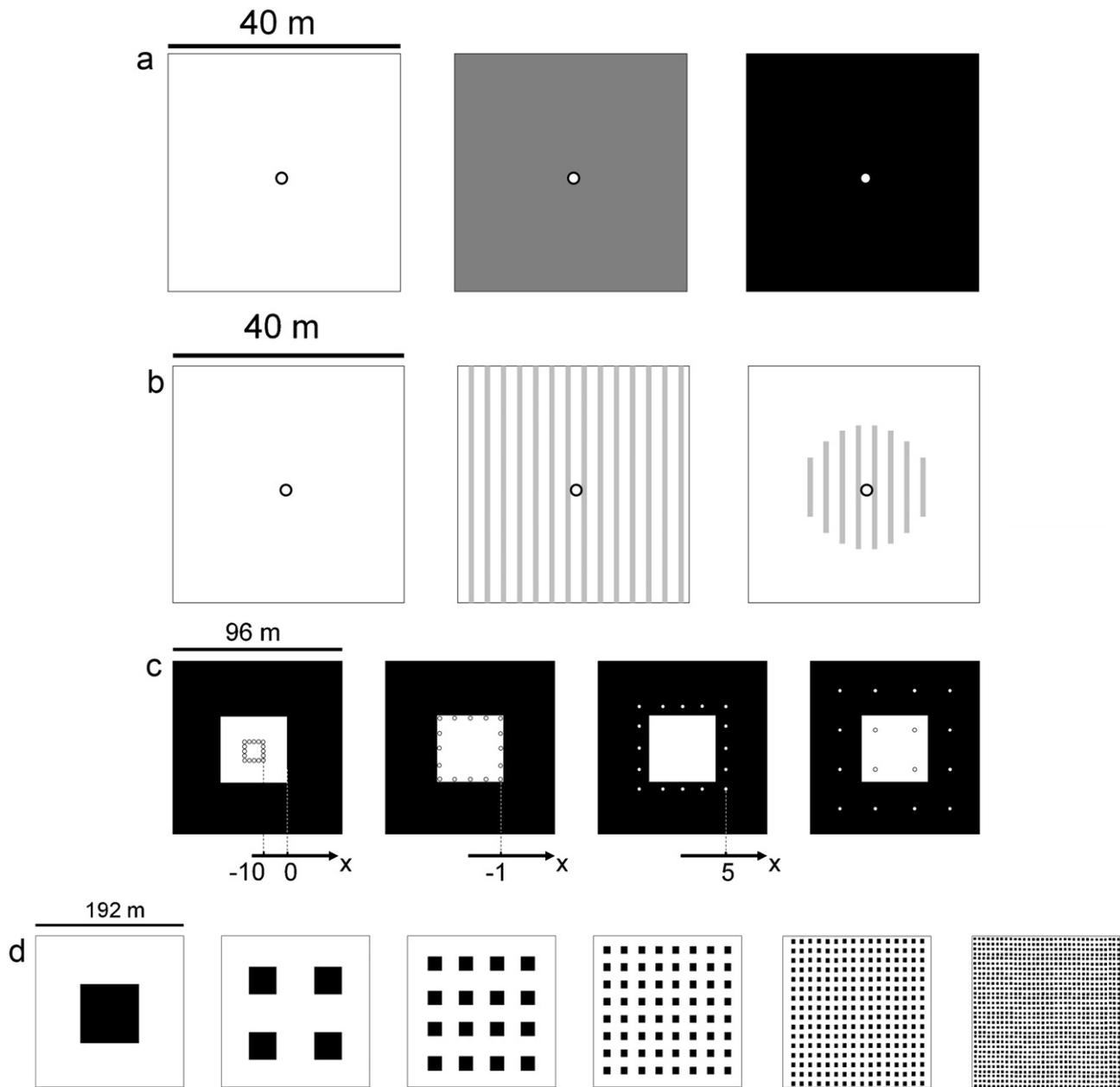
Fig. 1. Overview of the patterns used to test (a and b) environments surrounding the trap, (c) optimal spacing of traps in a fallow area surrounded by a banana plantation, and (d) fragmentation of a banana plantation. High density (2500/ha) of banana plants, low density (1100/ha) of banana plants, and fallow (bare soil) areas are in black, dark grey, and white, respectively. The trap is indicated by a white point. Vertical lines in light grey correspond to the lines of crop residues. (a) from left to right, one trap surrounded by: bare soil; a low density of banana plants; and a high density of banana plants. (b) from left to right, one trap surrounded by: bare soil; crop residues in continuous lines; and crop residues in continuous lines with incremental removal of residue from the perimeter. (c) from left to right, spatial arrangement of traps in a square at −10 m, at −1 m, or at 5 m from the border of the field, (according to direction indicated on the X-axis), and regularly distributed over the grid. (d) from left to right, fragmentation of a 192 × 192 cell field of fallow in 1 patch, 4 patches, 16 patches, 64 patches, 256 patches, and 1024 patches of banana plants.

trapping (Rhino et al., 2010), additional information is needed on the best spatial arrangement of traps.

2.4. IPM strategies tested using the COSMOS model

2.4.1. The environment surrounding a trap

We hypothesized that trap efficiency should decrease when the trap is surrounded by attractive habitats, such as crop residues or banana plants.

Using the COSMOS model, we tested three environments surrounding one trap that was located at the centre of a 40 × 40 cell grid (i.e., 1600 1-m^2 cells occupying 0.16 ha): (i) bare soil exclusively, (ii) banana plants regularly planted at 2500 plants/ha (2 m × 2 m), and (iii) banana plants regularly planted at 1100 plants/ha (3 m × 3 m) (Fig. 1a). At initialization, 100 adults were released into each cell of the grid, and the number of adults caught was recorded after 60 days of simulation. The probability of being caught at a given distance from the trap was recorded and averaged over 20 repetitions.

We also tested the spatial management of crop residues surrounding a trap located at the centre of the grid; this represented the case of a recently destroyed, fallow field. We compared the temporal dynamics of population on a 40 × 40 cell grid surrounded by (i) bare soil (T0), (ii) crop residues in continuous lines, each line being separated by 3 m (T1), and (iii) the same configuration as in T1, with incremental removal of residues (we assumed that

weevils inside the crop residues fell on the ground when the residues were removed) from the border to the middle of the field such that the remaining residue occupied a circular area whose diameter was reduced by 3 m every week (T2). At initialization, 500 adults were randomly introduced all over the grid (Fig. 1b). The number of catches per trap was recorded at each time step during 130 days, averaged over 20 repetitions.

2.4.2. Optimal spacing of traps in an intensive banana plantation in fallow

In areas of intensive production, banana plantations usually last 6–9 years before being destroyed by herbicide application, and the destroyed areas are then left in fallow for one year (Lassoudière, 2007). In the current study, the fallow area corresponded to one-ninth of the total area. The virtual banana field on which heterogeneity was manipulated was a 96 × 96 cell grid (1 m² per cell, total area of the grid = 1 ha), with a fallow area in a central square of 32 × 32 cells. This corresponds to a common situation in banana cropping systems in that fallow fields are frequently surrounded by planted fields (Lassoudière, 2007). As in real situations, banana plants were spaced at 2 × 2 m, giving 2500 banana plants/ha.

Using the model field described in the previous paragraph, we tested a variety of permanent arrangements of mass trapping during 1 year. Trap density was set at 16/ha (a total of 16 traps in the grid), which is considered economically feasible for commercial plantations. The traps were arranged in a square of different sizes (the diameter ranged from 1 to 30 m) so that the distance from the perimeter of the square to fallow–banana interface ranged from 0 m (traps were at the interface) to −15 m or to 15 m; the negative distance indicates that the traps were in the area with planted bananas and the positive distances indicate that the traps were within the fallow area (Fig. 1c). In one additional arrangement, the traps were not arranged in a square but were arranged regularly over the entire grid (Fig. 1c). In all cases, adults of *C. sordidus* were randomly set all over the grid at a density of 1500 individuals/ha. The total number of adults on the grid and the number of adults captured per trap were recorded 1 month and 1 year after the beginning of the simulations and were averaged over 20 repetitions.

2.4.3. Fragmentation and size effects in extensive banana plantations

In areas of extensive production, banana plants are regularly planted (2 m × 2 m) in patches of varying sizes (Lassoudière, 2007). We considered a grid consisting of banana plants and bare soil in the proportion 1:9. At initialization, the grid was composed of 2500 bananas/ha and 1500 weevils/ha. We tested the effect of varying patch fragmentation through six spatial patterns (from $4^0 = 1$ patch to $4^5 = 1024$ patches) for three different sizes of field (0.25 ha = 48 × 48 cells, 1 ha = 92 × 92 cells, and 3.7 ha = 192 × 192 cells). Note that for each size of field, the proportion between banana area and fallow area was constant (Fig. 1d). Results were averaged over 20 repetitions.

2.5. Statistical and modelling tools

The model was developed with Netlogo software (Wilensky, 1999). Maximum likelihood estimations of dispersal parameters were obtained with R software (R Development Core Team 2010) using package "stats4" (Appendix A).

3. Results

3.1. The environment surrounding a trap

The probability that weevils were trapped increased with their proximity to traps and was higher when traps were surrounded
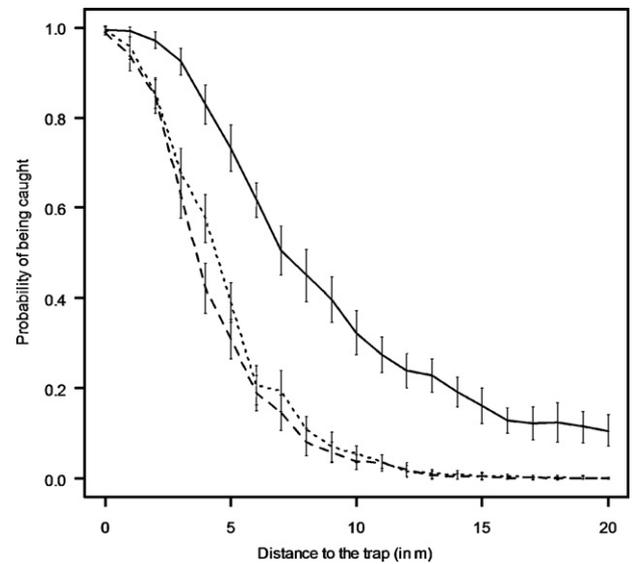

Fig. 2. Probability density curves generated by the COSMOS model of a 40 × 40 cell grid with one trap located on the centre of the grid. The area is covered by bare soil (solid line), by bananas regularly planted at 1100/ha (dotted line), or by bananas regularly planted at 2500/ha (dashed line). Curves are issued from a loess spline on 20 repetitions. Vertical lines represent standard deviations with 20 repetitions.

with bare soil than with banana plants (Fig. 2; see Fig. 1a for trap and environment). Increasing the density of banana plants did not significantly modify the probability of being caught.

Fig. 3 shows the temporal dynamics of trap capture simulated by the COSMOS model for the three treatments: T0 (trap surrounded by bare soil); T1 (trap surrounded by residue in rows); and T2 (trap surrounded by residue in rows and with residue area decreasing over time) (see Fig. 1b for trap arrangement). The cumulative number of weevils trapped was always greater with T0 than T1, and the number trapped was similar for T1 and T2 until day 70. After day 70, the number trapped with T2 increased rapidly and surpassed that with T0. After day 70, the remaining area of crop residue in T2 contained almost all the uncaught weevils. The weevils were sufficiently close to the trap to be caught, so that the level of trap captures increased rapidly.
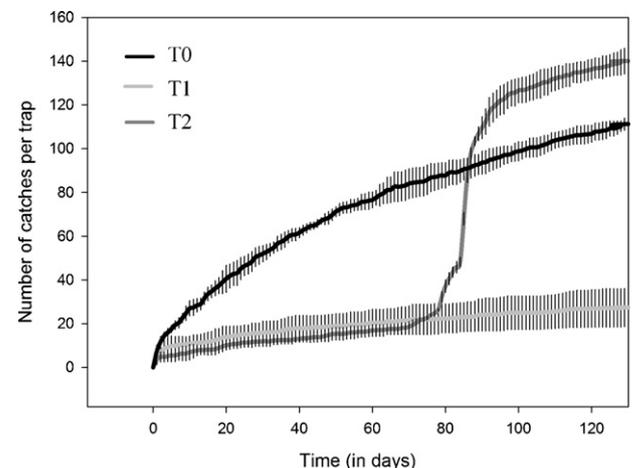

Fig. 3. Temporal dynamics of cumulative number of weevils caught per trap as simulated by the COSMOS model on a 40 × 40 cell grid (adult number at initialization = 500). The trap is surrounded by: bare soil (T0); crop residues in continuous lines with 3 m between lines (T1); crop residues in continuous lines with 3 m between lines and with incremental removal of residues from the border to the middle of the field (diameter of residue circle was decreased by 3 m per week) (T2). Vertical lines represent standard deviations with >20 repetitions.
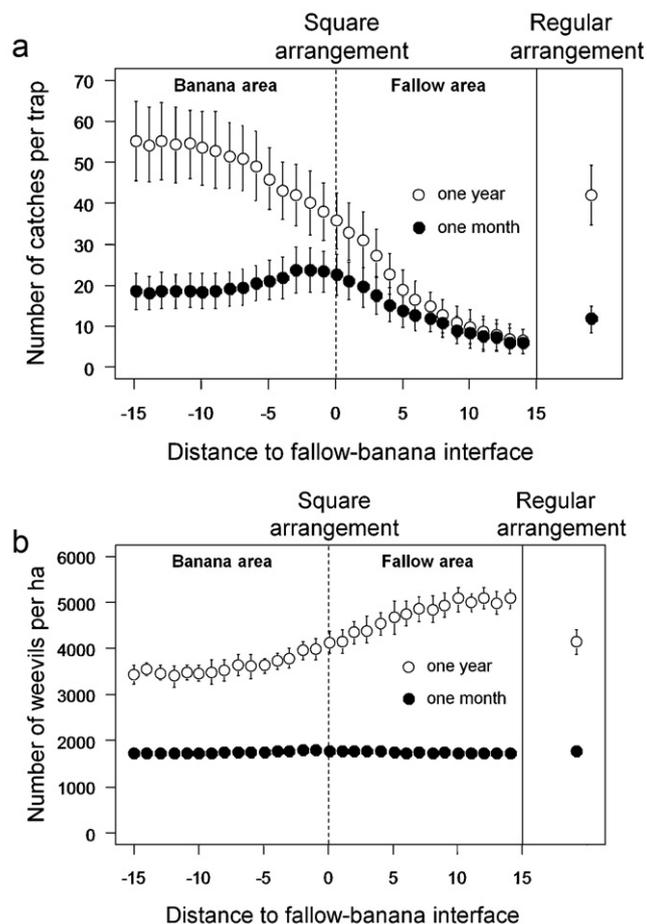
Fig. 4. Means (points) and standard deviations (bars) of (a) trap efficiency and (b) numbers of weevils per ha as a function of distance to the fallow–banana interface when traps were arranged in a square and as a function of a regular distribution of traps. Data are from 1-month (black point) and 1-year (white point) simulations using the COSMOS model. Standard deviations are based on 20 runs of the model.

3.2. Optimal spacing of traps in a fallow surrounded by a banana plantation

Fig. 4 shows the influence of the spatial arrangement of traps (see Fig. 1c for arrangement) on insect suppression and trap efficiency. For traps arranged in a square, both short- and long-term simulations (i.e. after one month and one year, respectively) indicated that the traps were more efficient and consequently the number of weevils per ha lower in the banana area than in the fallow area (Fig. 4a and b). In the fallow area, the low efficiency of traps distant from the fallow–banana interface was probably caused by the close proximity of traps resulting in competition between traps. Efficiency of regularly arranged traps (Fig. 4a) and the resulting population levels (Fig. 4b) were situated at the middle between cases of squared-arranged traps in banana and in fallow area. For traps regularly arranged and in comparison with traps in square, the lower level of trap competition in fallow area counterbalanced the lower number of traps in the banana area. After 1 month of simulation, trapping was highest when traps were located at the fallow–banana interface (Fig. 4a), because traps at this interface captured weevils that escaped the fallow area, as indicated by weevil residence time in each cell (data not shown). Effect of traps on weevil numbers was only pronounced for long-term simulations, as in short term simulations, the slight difference in number of caught weevils (almost 100 weevils) was negligible in comparison with the total number of weevils per ha (Fig. 4b).
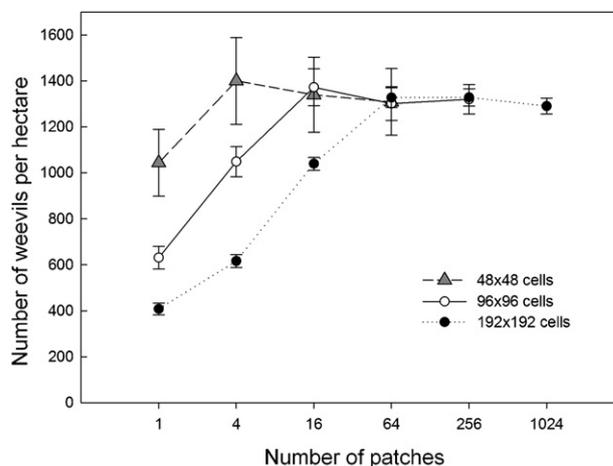
Fig. 5. Simulated numbers of weevils per ha after 1-year as a function of fragmentation level and field size. At initialization of the COSMOS model, weevils were randomly distributed in the fields. Each cell is 1 m × 1 m. Vertical lines indicate the standard deviations for >20 runs of the model.

3.3. Fragmentation and size effects in extensive banana plantations

Fig. 5 shows the effect of fragmentation on weevil numbers after 1-year simulations. Weevil numbers increased with the level of fragmentation and levelled off when the number of patches exceeded 4, 16, and 64, for a field of 48 × 48 cells, 96 × 96 cells and 192 × 192 cells, respectively. For the same level of fragmentation, weevil numbers and variation in weevil numbers decreased when the size of the field increased (Fig. 5).

4. Discussion

4.1. The environment surrounding a trap

Our first objective was to study how the efficiency of individual traps could be improved through manipulation of the surrounding environment. According to the assessment of habitat attractiveness (Appendix A), the trap is about 100 times more attractive than bare soil and is the most attractive element in a banana plantation. Crop residues and banana plants, however, compete with traps for weevils.

When decreasing banana plant density was considered as a potential tool for increasing mass trapping efficiency, a two-fold decrease in the density of plants caused only a slight increase in trap efficiency. The small effect of this tool could be explained by the inter-plant distance, which was much shorter than the perceptual range of weevils in both high and low density plantations. Trap efficiency was significantly increased when the trap was only surrounded by bare soil, as experimentally demonstrated by Rhino et al. (2010).

Crop residues can be managed by farmers and are another potential tool for increasing the efficiency of mass trapping. The results showed that incremental removal of crop residues from the periphery to the trap location significantly improved trap catches in the absence of banana plants. This could be explained by the relative attractiveness of crop residues in comparison with bare soil. At each time when an outer ring of residues was removed, weevils located in the removed ring moved to the closest area of crop residues, i.e., they moved toward the trap.

The consideration of habitat arrangement as a possible factor affecting trap efficiency is relatively novel (Spurgeon and Raulston, 2006). Research on trap efficiency has generally concerned pheromone dose (Branco et al., 2006), climatic variables

(Tinzaara et al., 2005a), or trap features (Reddy et al., 2009). However, our spatial model demonstrated that the spatial arrangement and composition of habitat should be considered in mass trapping strategies.

4.2. Optimal spacing of traps in a fallow surrounded by a banana plantation

Our second objective was to study the spatial arrangement of multiple traps in a fallow area surrounded by a banana plantation. The results of the simulation procedure indicated that traps should be located at the banana–fallow interface in the period immediately after the fallow is established. We suspect that weevils on bare soil escaped this unsuitable habitat to aggregate in the transition zone between the fallow area and the planted area. Oehlschlager et al. (1995) pointed out the importance of this zone in mass trapping strategies. Furthermore, locating traps along the perimeter of the fallow area increased the inter-trap distance and thereby reduced potential competition between traps, as emphasized by Bacca et al. (2006). Because trap relative attractiveness was calibrated in the absence of trap competition (see Appendix A), we considered no interference between traps, either positive or negative. For example, there is no additivity of trap attraction radii when trap radii are superposed. This formalism could lead to an underestimation of trap efficiency when traps are grouped but is the more tractable than the alternative in discrete-choice models. Very few spatial models simulate pheromone trap effectiveness (Byers, 1993; Yamanaka et al., 2003; Byers, 2009), and they only consider the dispersing stage of the pest population. Our model, by considering all insect stages, facilitates the understanding of the long-term effects of mass trapping strategies.

4.3. Fragmentation and size effects in extensive banana plantations

The third objective of this study concerned patch fragmentation. Our results showed that weevil numbers increased with the fragmentation of the banana area. We suspect that a highly fragmented area of bananas results in high connectivity (shorter distances) between patches of banana plants. The randomly distributed weevils had a greater probability of locating and moving to a suitable patch when patches were small and abundant rather than when patches were large but few. At the field scale, this result contrasts with Haynes et al. (2007), whose experiments indicated no effect of micro-fragmentation on the density of flying insects (*Melanoplus femurrubrum*). At the landscape scale, Pichancourt et al. (2006) found with a modelling approach that numbers of a crawling insect (*Abax parallelepipedus*) were greater with a single large patch of wood than with several small patches of wood. The authors argued that highly fragmented landscapes allow insects to die more frequently when they move between patches. In our case, mortality does not depend on the habitat that is traversed; instead, the main source of population loss is due to individuals that fail to find a suitable patch.

For a given fragmentation level, the larger the size of the field, the larger the distance to cover between each fragment. In that way, increasing the size of the field with a given pattern limits weevil numbers, because a weak perceptual range prevents weevils from assessing large field patterns. This result can have important management implications in that low fragmentation of a banana plantation will cause greater suppression of the insect pest over a large area than over a small area. Our IBM has the advantage of explicitly simulating individual perceptual ranges of insects so as to elucidate factors that determine insect numbers at the landscape scale. In doing so, the model aims at bridging the gap between individual behaviour and population processes (Grimm and Railsback, 2005).

5. Conclusion

Our study showed that, for the design of sustainable cropping systems for IPM purposes, IBMs are powerful tools because they consider three key points. First, IBMs simulate individual behaviour of insects and therefore are well suited for IPM strategies based on behaviour manipulation (Potting et al., 2005). Second, the explicit consideration of space allows IBMs to test various landscape arrangements including pheromone trap locations and crop development. Third, the IBMs can successfully use information from small-scale experiments collected at the level of the individual level to simulate pest dynamics at the field scale. We consider that models with a strong reliance on real data are better than theoretical ones for designing IPM strategies. Individual-based modelling provides a flexible way to extrapolate properties of plant–pest interactions to novel conditions and therefore helps in the design of innovative cropping systems.

Appendix A.

The probability of moving from cell *a* to cell *b* in the grid within a temporal unit was a first-order Markov chain defined as:

$$Pr(a \rightarrow b) = \frac{\alpha_{h(b)} f_{\beta_{h(a)}}(d_{ab})}{\sum_{k=1}^{m} \alpha_{h(k)} f_{\beta_{h(a)}}(d_{ak})} \tag{1}$$

where $\alpha_{h(k)}$ is the relative preference for habitat h of cell k, d_{ak} the distance between cells a and k, and $f(d_{ak})$ is the dispersal kernel depending on this distance of the form $\exp(-\beta_{h(a)} \cdot d_{ak})$.

The 10 unknown parameters (α_h and β_h with h = [trap, host plant, crop residues, bare soil, ditch]) were estimated via maximum likelihood estimation (Vinatier et al., 2011a) on the basis of a radio-tracking data set measured on this species (for more details on the tracking method, see Table A1 and Vinatier et al., 2010). Constraints were added in the model: the sum of alphas equals one, and each parameter is positive. β_T was fixed to 100 because the probability of escaping the trap is null. A complete version of this movement model and its evaluation can be found in Vinatier et al. (2011a).

The radio-tracking data set consisted of pairs of daily observations of approximately 800 males and 800 females of *C. sordidus* followed in experiments, in which the mosaic of habitats was experimentally manipulated. The data were collected on seven experiments (three are described in Vinatier et al. (2010), two in Vinatier et al. (2011a) and the two lasts come from unpublished data). Locations of insects and habitat elements were noted on a 1-m² cell grid that corresponded to the resolution of the model.

Table A1 shows that the trap was the most preferred habitat, followed by host plant and crop residue, which were equally preferred. Bare soil and ditch were the least preferred (Table A1). Regarding

Table A1
Parameter estimates of the movement of *C. sordidus* in the individual-based model, based on the radio-tracking data set.

	Mean	Standard error
Relative habitat preference		
α_T	0.86357375	0.0227554224
α_P	0.07559439	0.0129049226
α_C	0.05181051	0.0089547495
α_B	0.0064581	Fixed
α_D	0.00256325	0.0004704881
Parameter of the dispersal kernel		
β_T	100	Fixed
β_P	2.06518544	0.0368306669
β_C	2.09589287	0.0479089734
β_B	1.09817321	0.0253469307
β_D	0.72382497	0.1040634209

Note: the letters indicate the habitat type: T, trap; P, host plant; C, crop residue; B, bare soil; D, ditch.

parameter β, which defines the shape of the dispersal kernel, the higher the value of β_i for the current habitat i, the greater the probability that the individual will remain in habitat i. The value of β_i was highest for the host plant or the crop residue, intermediate for the bare soil, and lowest for the ditch (Table A1). Consequently, the movement rate was highest when the current habitat was ditch, was intermediate for bare soil, and was the lowest for crop residue and host plant.

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