

A tool for testing integrated pest management strategies on a tritrophic system involving pollen beetle, its parasitoid and oilseed rape at the landscape scale

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Abstract The intensification of agriculture has led to a loss of biodiversity and subsequently to a decrease in ecosystem services, including regulation of pests by natural enemies. Biological regulation of pests is a complex process affected by both landscape configuration and agricultural practices. Although modeling tools are needed to design innovative integrated pest management strategies that consider tritrophic interactions at the landscape scale, landscape models that consider agricultural practices as levers to enhance

biological regulation are lacking. To begin filling this gap, we developed a grid-based lattice model called Mosaic-Pest that simulates the spatio-temporal dynamics of *Meligethes aeneus*, a major pest of oilseed rape, and its parasitoid, *Tersilochus heterocerus* through a landscape that changes through time according to agricultural practices. The following agricultural practices were assumed to influence the tritrophic system and were included in the model: crop allocation in time and space, ploughing, and trap crop planting. To test the effect of agricultural practices on biological regulation across landscape configurations, we used a complete factorial design with the variables described below and ran long-term simulations using Mosaic-Pest. The model showed that crop rotation and the use of trap crop greatly affected pollen beetle densities and parasitism rates while ploughing had only a small effect. The use of Mosaic-Pest as a tool to select the combination of agricultural practices that best limit the pest population is discussed.

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Introduction

The intensification of agriculture has led to a loss of biodiversity, and subsequently to a decrease in ecosystem services provided by semi-natural habitats;

semi-natural habitats are those non-cultivated habitats that are adjacent to farmland and that are rich in plant and insect species (Tschardt et al. 2005). Among the many services that they provide, semi-natural habitats are important food sources for animals such as pollinators, granivorous and omnivorous arthropods, and farmland birds and mammals (Petit et al. 2011). These habitats also enhance biological regulation of pests by providing alternative food sources for predatory species (Hawes et al. 2003) or nectar and pollen sources for parasitoid species (Rusch et al. 2011). Parasitoids feed on flowers in grasslands and oilseed rape fields before searching for hosts. There is an urgent need to understand the role of such services to increase agro-ecosystem sustainability.

Researchers are increasingly recognizing that assessment of biological regulation of pests requires a landscape perspective (Bianchi et al. 2010). Empirical studies have shown the importance of factors that explain pest densities at the landscape scale, and these include field-margin management (Olson and Wäckers 2007), proportion of semi-natural habitats, (Rusch et al. 2011), and insecticide treatments (Ricci et al. 2009). By identifying factors affecting population dynamics at the landscape scale, these empirical studies provide hypotheses on the underlying mechanisms behind these effects and on the scale at which they act. The empirical studies, however, generally produce short-term data sets, making it difficult to understand mechanisms and long-term dynamics. It follows that inferring mechanisms and long-term dynamics from empirical studies at the landscape scale is difficult to achieve without modelling tools.

It is only recently that the spatial heterogeneity of the environment has been considered in one-species models of weeds (James et al. 2011), insects (Vinatier et al. 2009), and mammals (Hamilton et al. 2006). Modelling is now considered a powerful tool for inferring mechanisms from spatial patterns (Vinatier et al. 2011b), and especially for inferring the nature of tritrophic interactions between plants, pests, and parasitoids. Although tritrophic models have so far focused on demographics in simple, small, and time-invariant landscapes (Charnell 2008; Bianchi et al. 2009; Baeza and Estades 2010), it is now necessary to consider agricultural practices that change the landscape as levers that can enhance biological regulation of pests; crop rotation, for example, modifies the year-to-year allocation of habitat elements (Bianchi et al.

2010). There is an urgent need to develop a mechanistic framework for the study and modelling of tritrophic systems at the landscape scale.

The pollen beetle (*Meligethes aeneus* F.) (Coleoptera, Nitidulidae) is a major pest of winter oilseed rape (*Brassica napus* L.). After an overwintering period in woodlands, adults migrate in the spring to grasslands or oilseed rape fields to feed but they only oviposit in oilseed rape fields. Pollen beetles can be regulated by univoltine parasitoids (Jourdeuil 1960) and especially by *Tersilochus heterocerus* (Rusch 2010). Parasitoids overwinter as diapausing adults within host cocoons in the soil where oilseed rape was grown in the previous season; they emerge in the spring, and migrate first to grasslands to feed, and then to oilseed rape fields for oviposition. Both the parasitoid and the pollen beetle require complementary and supplementary resources for feeding, egg laying, and overwintering. Resources are present in semi-natural habitats, i.e., in woodlands and grasslands, but also in cultivated areas.

Empirical studies have pointed out the contrasting effects of some landscape elements on pest regulation. Semi-natural habitats, for example, act both as overwintering sites for pollen beetles and as nectar sources for parasitoids (Rusch et al. 2011). Pollen beetle densities have been shown to be negatively related to the proportion of oilseed rape in the landscape (Zaller et al. 2008). Agricultural practices such as ploughing seem to affect pest regulation at the landscape scale because mouldboard ploughing reduces the survival and emergence of parasitoids in the soil (Nilsson 2010; Rusch et al. 2011). A push–pull strategy takes advantage of the preference of *M. aeneus* for turnip rape (*Brassica rapa*) over oilseed rape in that turnip rape is used as a trap crop (Cook et al. 2007). However, the link between mechanisms and observed patterns at the landscape scale remains poorly understood, in particular because spatio-temporal dynamics of the landscape in previous years affect pest dynamics in subsequent years (Gladbach et al. 2011).

In this paper, we present a spatially explicit, deterministic, and cohort-based population model called Mosaic-Pest that describes the relationship between a pest, its parasitoid, and the landscape. The model takes into account agricultural practices (ploughing, crop allocation and rotation, use of trap crop) that could affect pest densities. The model differs from other models because it considers the

landscape as a mosaic of patches that change in time according to crop management practices (Baudry et al. 2003). Furthermore, the model considers that the suitability and attractiveness of patches of a given habitat for a given species change with life-cycle stage (feeding, egg laying, overwintering). Dynamic features of the landscape have been rarely considered in models of host–parasitoid interactions because models usually describe landscape with landscape metrics (e.g., fragmentation) that remain constant through time (Bianchi et al. 2009; Bianchi et al. 2010).

The model contained 32 parameters that described pollen beetle and parasitoid life cycles. After the range of uncertainties for each parameter was estimated based on the available literature, the best value of each parameter was chosen by comparing the range with a real data set; details on this procedure and on the parameter values are presented in a companion paper (Vinatier et al. submitted). The companion paper points out the influence of parameters' uncertainties and landscape configuration on model outputs, whereas the present paper focuses on the influence of combinations of agricultural practices on pest regulation, in order to test integrated pest management strategies.

We hypothesise that landscape features (including those related to the distribution of crops and cultural practices) are the most influential factors affecting pest densities.

In the first part of the paper, we present the mechanisms underlying spatial patterns of population densities according to the literature available on the tritrophic system (oilseed rape, pollen beetle, and parasitoid), and we also indicate how we represent these mechanisms in a model.

In the second part of the paper, we use the model to explore the effects of alternative agricultural practices that limit populations of beetles via top-down or bottom-up effects. We focus our simulation study on practices likely to affect pollen beetle densities at the landscape scale, i.e., crop allocation in space and time, the presence or absence of ploughing, and the use of a trap crop in the oilseed rape fields. We tested combinations of these practices according to a complete factorial design to detect positive or negative interactions among practices. Because landscape complexity, i.e., the proportion of semi-natural habitats, could modify the effect of the tested practices, we also ran our simulations on several real maps representing various levels of landscape complexity.

Although this research was motivated by a specific case study involving oilseed rape, it is meant to demonstrate the general approach of using mechanistic models to develop innovative integrated pest management strategies.

Methods

Overview of the model

Spatial representation of landscape

We chose a spatially explicit framework that includes four habitat types (oilseed rape fields, previous oilseed rape fields, woodlands, and grasslands) because of their different influences on insect overwintering, feeding, and egg laying. The rest of the grid consists of unsuitable habitats for the pollen beetle and the parasitoid. Landscape maps were projected onto a grid of 100×100 cells with a cell length of 50 m. The grid resolution was large enough to discriminate habitat elements but small enough to limit computing time. Border effects with respect to dispersal were avoided by using a toroidal landscape structure. The model focuses on landscape factors and neglects possible effects of wind, hygrometry, or temperature.

Landscapes

We considered realistic landscapes by using 35 non-overlapping maps (35 map patterns) of 2,500 m radius from an agricultural territory in northwestern France ($49^{\circ}25'N$, $1^{\circ}12'E$). This territory consists of farmland, small woodland fragments, hedgerows, and grasslands (Fig. 1). The delimitation of each field was determined based on aerial photographs (BD ORTHO[®], IGN, 2004) and on the official SIG-based system used by farmers to declare crops and apply for subsidies (Registre Parcellaire Graphique, Règlement communautaire no. 1593/2000). A mean temperature data set for each map was obtained from a previous study in this region (Rusch et al. 2011).

Modelling of population dynamics

Population dynamics of the insects (pest and parasitoid) are modelled by following, in each cell, the number of parasitoids and pollen beetles. Populations

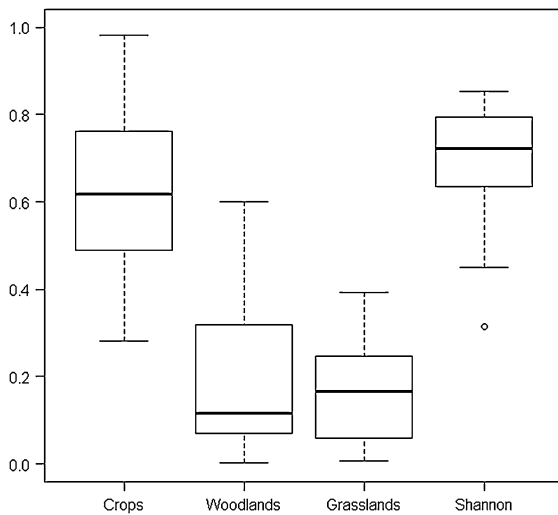


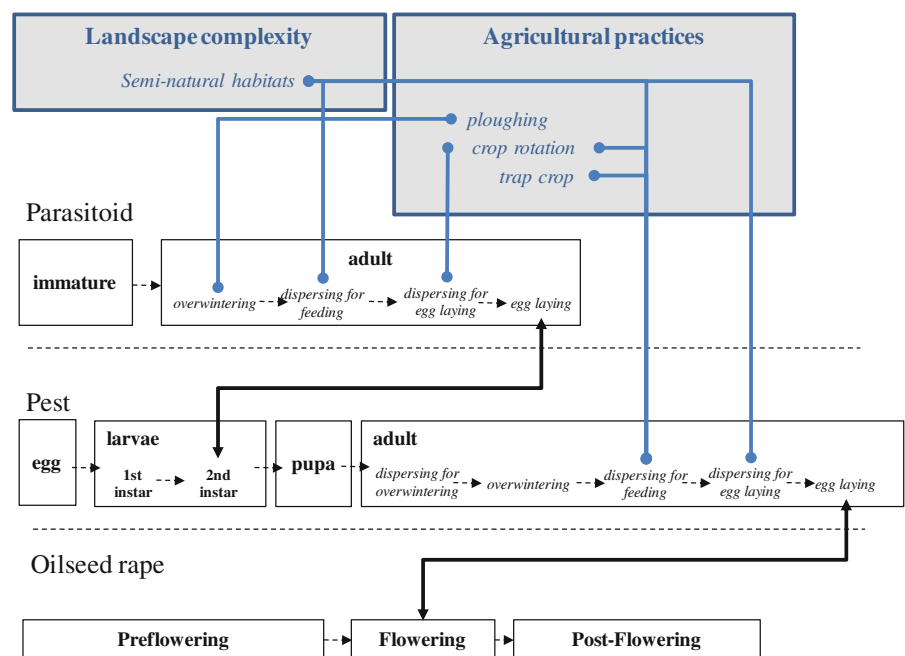
Fig. 1 Box plot of the distribution of habitat proportions over the whole map area among the 35 studied maps. The Shannon Index measures the diversity of habitats among maps. For each group, *vertical lines* represent the extreme of the lower whisker, the lower quartile, the median, the upper quartile and the extreme of the upper whisker, respectively

are further characterized by stage for immature insects or by status for adults. The parasitoid changes stage from immature to adult, and the pollen beetle changes from egg, first instar larvae, second instar larvae, pupa, to adult. Adults of both insects change status from

dispersing towards overwintering sites (pollen beetle only), overwintering, emerging, dispersing for feeding, dispersing for egg laying, to egg laying. Oilseed rape plants pass through three stages until harvest: pre-flowering, flowering, and post-flowering (Fig. 2). Mosaic-Pest progresses with daily time steps. Every simulation begins on January 1. On this date, parasitoids are overwintering in the soil where oilseed rape was planted in the previous year, and pollen beetles are overwintering in woodland soil: the new generation (produced before January) of the parasitoid has remained as diapausing adults within host cocoons in the soil, whereas new adults of the pollen beetle have dispersed to the overwintering sites, which are woodlands. The effect of cultural practices (e.g., soil tillage or use of trap crops) is taken into account through the parameters describing population dynamics. We considered the initial number of insects per cell to be the same for all cells of a particular habitat type in all maps, i.e., the number of *M. aeneus* and *T. heteroceris* in each map is proportional to the area of woodlands and oilseed rape fields of the previous year, respectively.

The development of the oilseed rape crop is based on cumulative degree-days after planting (Boyardieu 1991). We distinguished three stages in crop development with respect to flowering (pre-flowering, flowering, and post-flowering) because the flowering

Fig. 2 Overview of stage (*in bold*) and status (*in italic*) in a tritrophic system as modelled by Mosaic-Pest. *Bold arrows* correspond to interactions between levels. *Dotted arrows* correspond to transition rates between each status



stage is the most attractive for pollen beetles and parasitoids (Cook et al. 2002).

The model was developed with Netlogo software (Wilensky 1999). Statistical analyses and multiple simulation procedures were conducted with R software (R Development Core Team 2010).

Procedures

Transition between stages and mortality

The model considers one cohort for each species, i.e., all individuals of the population of a given species have the same developmental stage at a given time. For each cohort of a given species, the developmental stage is initialized at emergence (i.e., at the end of the overwintering period) by a thermal threshold T_{th} for *M. aeneus* (Nilsson 1988a) and by a sum of thermal thresholds (base 0 °C) since egg laying ST_{th} for *T. heterocerus* (Jourdeuil 1960).

For each species s at the end of a given stage/status i (as determined by the duration δ^i , that corresponds to the time between beginning and end of stage/status i), the population number of the cohort N_t is multiplied by a transition probability $\pi_{i \rightarrow i+1}^{s,til}$ which changes the stage/status from i to $i + 1$:

$$N_{t+1}^{s,i+1} = \pi_{i \rightarrow i+1}^{s,til} \times N_t^{s,i} \quad (1)$$

The survival rate for immature stages of the insects is defined by a constant. The survival rate of *T. heterocerus* pupae depends on soil tillage (Nilsson 2010) denoted as *til*. For adult beetles, the survival rate depends on the power of the distance covered by the population during dispersal, following the formalism developed by Zollner and Lima (2005), because mortality factors are most important during this period for *M. aeneus* (Nilsson 1988b). We assumed that the same mechanism could be applied to *T. heterocerus*, based on Arrignon et al. (2007). The total collapse of a cohort is determined by the maximal longevity of the species, which is less than 1 year.

Dispersal

Dispersal of both species occurs just after emergence. Two dispersal events occur successively for both species. Emerging adults first move from last year-oilseed rape fields (parasitoids) or woodland (pollen

beetle) to grasslands (feeding sites) and then move to oilseed rape fields (egg-laying sites). We considered a third event only for *M. aeneus*: the next generation disperses to overwintering sites, i.e., woodlands.

For each dispersal event, redistribution of individuals in space occurs instantly at the end of the dispersal flight period. In accordance with Taimr et al. (1967), dispersal of *M. aeneus* is not affected by the configuration of the terrain, wind, or gender. We assumed that *T. heterocerus* dispersal was also unaffected by these factors.

We consider a cell-to-cell redistribution mechanism based on a negative exponential dispersal kernel (Vinatier et al. 2011a). For each cell a of the grid, the population $N_a^{s,i}$ (species s and status i) is redistributed according to the potentials P of the m cells of its perception window $\omega^{s,i}$.

Each potential of a given cell b is calculated according to:

$$P(b) = \frac{a_{h(b)} \exp(-\beta^{s,i} \times d_{ab})}{\sum_{c \in \omega^{s,i}} a_{h(c)} \exp(-\beta^{s,i} \times d_{ac})} \quad (2)$$

where $\alpha_{h(c)}$ is the relative preference for habitat h of cell c , d_{ac} is the distance between cells a and c , and $\exp(-\beta^{s,i} \times d)$ is the dispersal kernel depending on the species, its stage, and this distance. Potentials are normalized to 1, i.e., $\sum_{b \in \omega^{s,i}} P(b) = 1$. For computational reasons, we chose to calculate the value of the dispersal kernel at the centre of each cell of the grid (centre method) instead of integrating the dispersal kernel within each cell (integrated method) (Slone 2011).

The relative preference α_h of a given habitat h depends on the species and the status of the population. For both *M. aeneus* and *T. heterocerus* at the end of the overwintering period, we considered that grasslands and oilseed rape fields are equally attractive for feeding (i.e., $\alpha_{grasslands} = \alpha_{oilseed\ rape\ fields} = 1$), and that all other habitats are non-attractive (i.e., $\alpha_{woodlands} = \alpha_{other\ crops} = 0$) (Williams and Cook 2010). After feeding, we considered that both *M. aeneus* and *T. heterocerus* fly exclusively to oilseed rape fields, and we set the relative preference of other habitats to 0. The effect of a trap crop (turnip rape) was added in the model by setting $\alpha_{turnip\ rape} = 17 \times \alpha_{oilseed\ rape\ fields}$ (Cook et al. 2006). We assume that *T. heterocerus* is primarily attracted by the host plant of *M. aeneus*, following Williams and Cook (2010).

After arriving in the cell containing oilseed rape, *T. heterocerus* begins to search for susceptible hosts inside the cell. We also considered the dispersal flight of newly emerged *M. aeneus* searching for overwintering sites by setting the preference to 1 for woodlands and to 0 for the other habitats.

The perception window $\omega^{s,i}$ corresponds to the maximal distance covered by species *s* at a given status *i* during the dispersal flight (Arthur et al. 1996). We considered that $\omega^{s,i}$ depends on the nutritional status of the species because, for example, floral resources increase longevity of insect parasitoids (Araj et al. 2008). We assumed that insects with greater longevity are able to cover larger distance than those with lesser longevity. For this reason, $\omega^{s,i}$ is different for the first and the second dispersal events for both species and for the third dispersal event for *M. aeneus*.

Fecundity and parasitism

Adult *M. aeneus* lay eggs from the beginning to the end of oilseed rape flowering period, with a maximal duration of 60 days (Ekbom and Popov 2004). The mean number of eggs per adult per day is considered constant and is denoted as φ . Number of hosts at day *t* Λ_t , i.e., number of new second stage larvae of *M. aeneus*, is given by:

$$\Lambda_t = \varphi \times \left(N_{t-(\delta^{egg}+\delta^l)}^{Ma,adult} \times \pi^{Ma,egg} \times \pi^{Ma,l1} \right) \quad (3)$$

During the parasitism phase, the number of parasitized hosts per cell is given by the Thompson model with a type II functional response (Mills and Getz 1996), according to the observations of Jourdeuil (1960) on *T. heterocerus*. As the Thompson model for parasitism applies for discrete generations models, it was adapted to this discrete time model by considering that the fecundity was constant over time for *T. heterocerus* (i.e. daily fecundity = total fecundity/egg-laying duration) and that the populations of hosts and parasitoids were stable during egg-laying, which allowed us to partition the newly produced stage 2 larvae into the ones that would remain healthy and the ones that would become parasitized:

$$H_{t+1} = H_t + \Lambda_t \times \left(1 - \exp\left(-\rho \frac{N_t^{Th,adult}}{\Lambda_t}\right) \right) \quad (4)$$

and:

$$P_{t+1} = P_t + \Lambda_t \times \exp\left(-\rho \frac{N_t^{Th,adult}}{\Lambda_t}\right) \quad (5)$$

where ρ is the per capita parasitoid attack rate, $N_t^{Th,adult}$ is the number of adult parasitoids at time *t*, and H_t and P_t are the number of nonparasitized and parasitized hosts at time *t*, respectively.

Factorial design of the virtual experiment

Cultural practices and biological regulation

Each field in the landscape was identified, and crop allocation in the model was done on a field basis. Crop allocation in space and time was determined by (i) the duration (in years) of the crop rotation sequence (oilseed rape appearing only once in each rotation), and (ii) the proportion of oilseed rape in the first year of the rotation in comparison with the whole farmland area. Thus, the long-term mean of the proportion of oilseed rape in the landscape was controlled by rotation length.

Four cultural practices were considered with two modalities for each: *trap crop* (present or absent); *ploughing* (performed or not performed); *crop rotation* (3 or 6 years), and *crop allocation* (a variable or constant proportion of oilseed rape from year to year). The effect of *biological regulation* (i.e., regulation by the parasitoid) was tested to disentangle the effect of cultural practices on the pollen beetle alone and on both beetles and parasitoids.

Presence or absence of ploughing was applied simultaneously on all the fields of the map. When we considered the effect of trap crop, we assigned turnip rape crops to each cell of the internal border of contiguous fields containing oilseed rape, i.e., on a 50-m-wide border. This trap crop width is greater than in the field (Cook et al. 2002), but we could not reduce this width for computing reasons.

As noted above, we considered rotation lengths of 3 or 6 years, and we considered two types of crop allocations. When crop allocation (oilseed rape proportion) remained constant during the crop rotation, the proportion of oilseed rape was simply the inverse of rotation length in years (Fig. 3a). When crop allocation was variable, the proportion of oilseed rape in the first year was set to 0.7, and the proportion in the

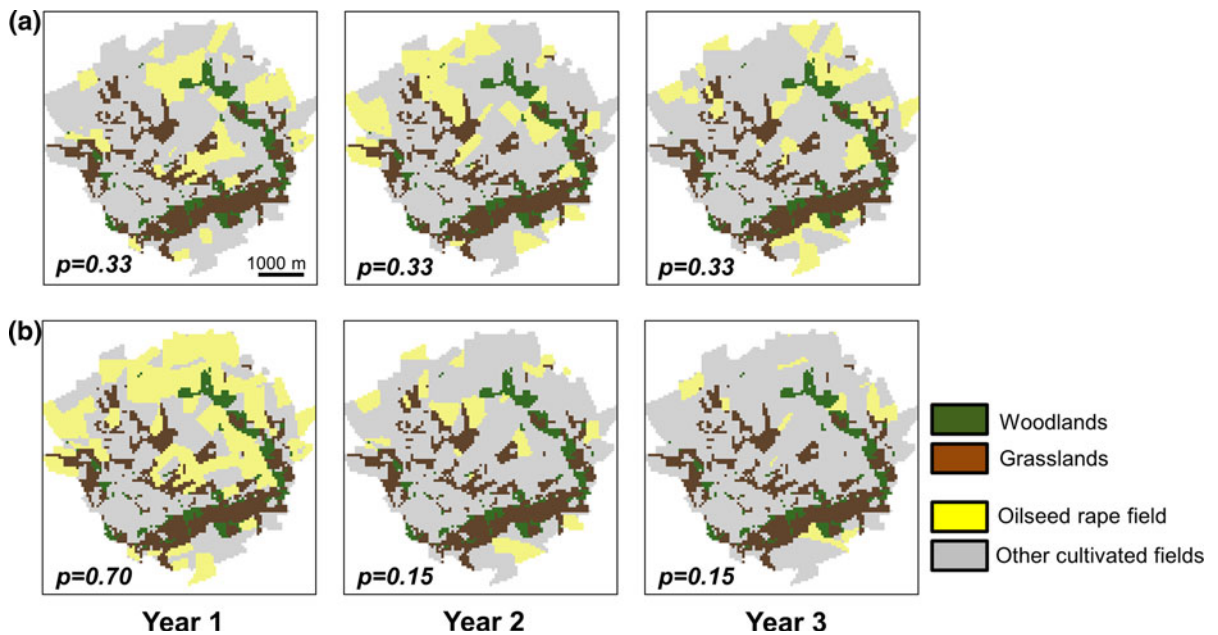


Fig. 3 Example of a map where crop allocation was assigned on a 3-years sequence with **a** a constant proportion of oilseed rape fields, and **b** a high proportion of oilseed rape fields in the following years was 0.3 divided by rotation length minus one year (Fig. 3b).

Each combination of studied factors was simulated 10 times because crop allocations were randomly generated for each map under the constraints induced by the crop rotation and crop allocation factors.

Statistical analysis of the simulations

Following the work of Viaud et al. (2008), a complete factorial design was constructed with the input factors presented above, i.e., with map pattern, biological regulation, trap crop, ploughing, crop rotation, and crop allocation. There were 35 modalities for map pattern and two modalities for each of the other five factors. As a consequence, 11,200 simulations ($2^5 \times 35 \times 10$) were required. Initialization procedures were described in the first part of the “Methods” (see “Overview of the model”). The duration of each simulation was 12 years (4,380 time steps) because we were concerned with long-term effects on the populations. At the end of each year, we determined the mean number of pollen beetles adults per m^2 and the parasitism rates over the whole map, and we averaged the values over the 10 repetitions. There was only one value collected per map and per simulation to avoid

first year (proportion of oilseed rapes the following year is: 0.3 divided by two years). The proportion of oilseed rape fields (p) relative to the total farmland area is indicated in each panel

autocorrelation effects. Assuming that the system was not chaotic, we averaged the values over the last 6 years (after at least one full crop rotation) to avoid the effects of different crop allocations in time.

The complete factorial design was analysed using an ANOVA on generalized linear models. Pair-wise interactions were considered in the model. Pollen beetle densities and parasitism rates were analysed using a Poisson log-linear model and a Binomial model, respectively (Warton and Hui 2010). Overdispersion was accounted for using quasi-Poisson and quasi-Binomial models. A sensitivity index of each parameter was calculated from the ANOVA table by dividing the parameter’s sum of squares by the total sum of squares (Monod et al. 2006). A high sensitivity index indicated a large influence of an input factor on a response variable (the levels of pollen beetles and parasitism).

Results

The model simulated the movement of the beetle and parasitoid populations between habitats as they sought the habitats suitable for the successive phases of their life cycles. The limited dispersal ability of the insects

was correctly simulated, as illustrated by the fact that population densities were on average ten times higher in the borders of patches than in the centre and twenty times higher in the direction where the populations came from (Fig. 4). The comparison of the simulated data versus data from an independent study by Thies and Tschamtké (1999) revealed that the model reproduced with accuracy the increase of parasitism rates when the proportion of non-crop areas in the landscapes increases: the slopes of the relationship between percentage of non-crop area and parasitism rate were the same, although the intercepts were different (Fig. 5).

Table 1 shows the results of the ANOVA model for pollen beetle densities; the generalized linear model was no over-dispersed (dispersion parameter = 0.8). Sensitivity indices and signs of the estimated effects indicated that *biological regulation* and *trap crop* had a strong negative and positive influence on pollen beetle densities, respectively. *Crop rotation* and *ploughing* had a very small but significant influence on pollen beetle densities. On the other hand, the impact of *crop allocation* was negligible.

The same ANOVA model also explained most of the variability in parasitism rate (Table 2; dispersion parameter = 0.02). The ranking of the effects of cultural practices on parasitism rates was different from the ranking of the effects on pollen beetle

densities. Parasitism rates were strongly and negatively influenced by *crop rotation* (i.e., parasitism rate was higher for 3-year rotations than for 6-year rotations), and less strongly but positively influenced by *trap crop*. Impact of *crop allocation* was significant but less important than *crop rotation*, and the effect of ploughing was not significant. The most important interaction effect for parasitism was for *Trap crop* × *Map pattern*.

Figure 6 illustrates the interactions between the significant cultural practices and biological regulation for pollen beetle density. Because ANOVA analyses (Tables 1, 2) showed negligible influence of crop allocation and ploughing, we only considered the cases with a constant proportion of oilseed rape and no ploughing. The most important and positive interaction effect was for *crop rotation* × *biological regulation* (Table 1). The effect of *trap crop* was significant and positive in both the presence and absence of biological regulation (Mann–Whitney *U* test, $P < 0.001$). The positive effect of trap crop on pollen beetle densities (Fig. 6a) was due to the trap crop flowering before the oilseed rape, which lengthened the favourable period for egg laying by pollen beetles. This trap crop effect was not counterbalanced by pollen beetle regulation by parasitoids, despite the positive influence of trap crop on parasitism rates (Table 2). Although Fig. 6b indicates a significant

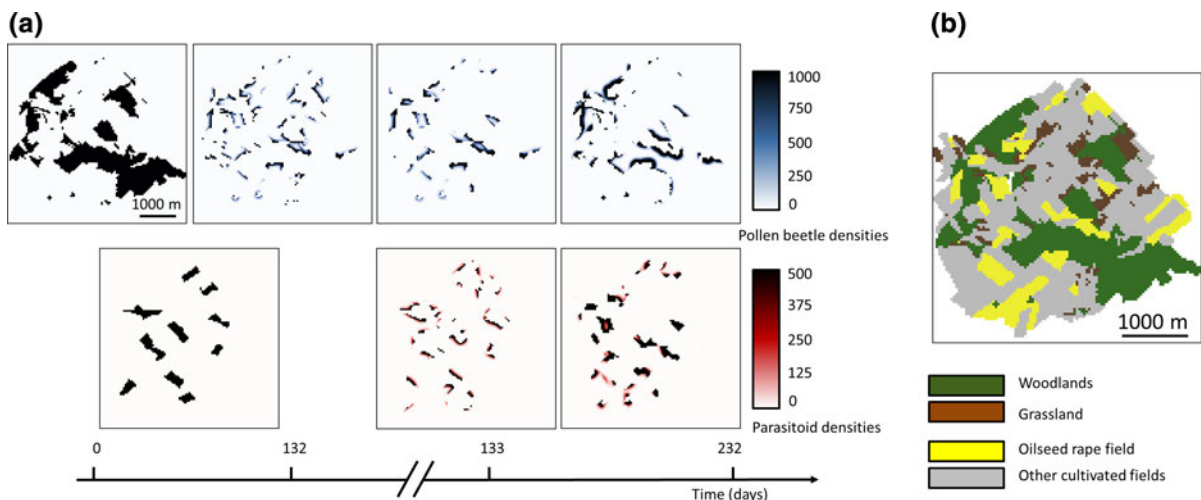


Fig. 4 Visualisation of the spatial dynamics of the host–parasitoid system issued from a 1-year simulation with the Mosaic-Pest model. **a** Map sequence of population levels of pollen beetles (*up*) during overwintering, after dispersing for feeding, egg laying, and overwintering. Map sequence of

population levels of parasitoids (*bottom*) during overwintering, after dispersing for feeding than egg-laying. **b** Map of the corresponding habitat in the landscape. The simulation corresponds to the scenario without trap crop and tillage and with biological regulation

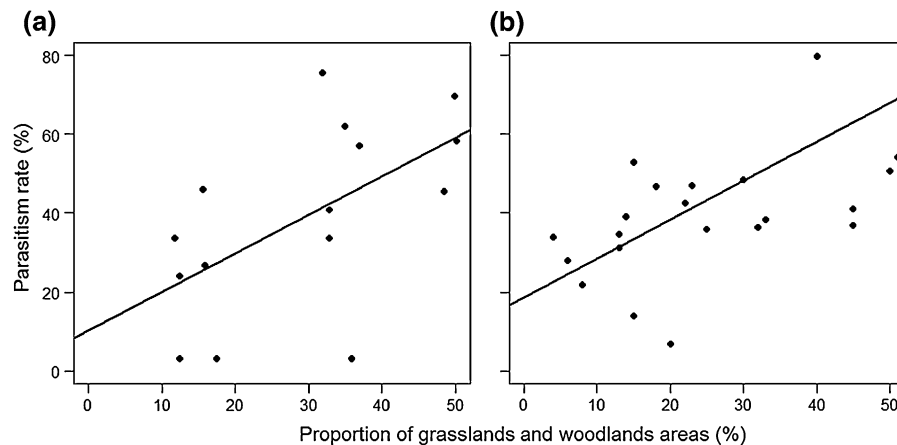


Fig. 5 Comparison of the parasitism rates versus the percentage of non-crop areas (grasslands and woodlands) for **a** an experimental study conducted on agricultural landscapes around the city of Göttingen (Germany) without using tillage, trap crop, insecticides [adapted from a figure by Thies and Tschardtke (1999)] and **b** simulations of the model on agricultural

landscapes of northwestern France for the same agricultural practices and a three-year rotation. Each line corresponds to a linear model fitted to the data **a** $Y = 7.8 + 0.9 X$; $F = 6.5$, $P = 0.02$, $R^2 = 0.33$, $N = 15$, and **b** $Y = 18.6 + 1.0 X$; $F = 45$, $P < 0.001$, $R^2 = 0.50$, $N = 35$

effect of crop rotation (Mann–Whitney U test, $P < 0.001$) in both the presence and absence of biological regulation, the effect of rotation length differed depending on the presence or absence of biological regulation: pest densities were greater with 6-year rotations than with 3-year rotations in the presence of biological regulation but the opposite was true in the absence of regulation. Because the proportion of oilseed rape in the landscape was set to the inverse of the rotation length, lengthening the crop rotation decreased the connectivity of areas of varying habitats in a given year. In the absence of biological regulation, this caused an increase in pollen beetle mortality during dispersal events and therefore a decrease in their densities. In the presence of biological regulation, this mortality effect was counterbalanced by a limitation of biological regulation by parasitoids, the latter being also influenced by the connectivity between semi-natural habitats and previous as well as current oilseed rape fields. Thus, the simulations showed that the parasitoid was more affected than the pollen beetle by the reduced proportion of land cropped to oilseed rape.

Discussion

As pointed out by Hughes et al. (1997), validation of spatio-temporal models is often difficult to assess

rigorously, especially on landscape scale because sampling investment is too important. We attempted to check whether the model was structurally realistic, i.e., to enable the model to represent the real tendencies of the studied system and we based our validation procedure on the comparison of observed patterns issued from independent studies realised at landscape scale, as demonstrated below. Mosaic-Pest revealed global trends of the system that are consistent with the known behaviour of the system. For example, the model simulated higher parasitism rates at the border of the field than in its centre. Büchi (2002) empirically detected higher predation rates in oilseed rape fields bordered by flower strips, the latter being considered as habitat for predators. The higher level of pollen beetle densities in crop edges than in the centre revealed by Mosaic-Pest was also observed experimentally by Ferguson et al. (2000) on another host–parasitoid system in oilseed rape fields. Another pattern that the model successfully represents is the increase of parasitism rates with the increase in the proportion of non-crop areas simulated by the model, which has been observed experimentally by Thies and Tschardtke (1999). The propensity of the model to simulate the system with realism was also confirmed by field advisors and experts in an international congress (Vinatier and Valantin-Morison 2011). The model illustrated the negative effect of a longer crop sequence (i.e., a lower proportion of oilseed rape) on

Table 1 Results of ANOVA analyses testing for the effects of cultural practices, landscape configuration (map pattern), and biological regulation by a parasitoid on the density of pollen beetles per m² averaged over the last 6 years of 12 years of simulations with the Mosaic-Pest model

	Densities of pollen beetles (Poisson model)		
	df	<i>P</i> value	SI (%)
Main effects			
Crop allocation	1	<0.001	0.0
Crop rotation	1	<0.001	0.9
Biological regulation	1	<0.001	15.0
Trap crop	1	<0.001	30.6
Ploughing	1	<0.001	0.01
Map pattern	34	<0.001	47.5
Interaction effects			
Crop allocation × Crop rotation	1	<0.001	0.05
Crop allocation × Biological regulation	1	<0.001	0.06
Crop allocation × Trap crop	1	0.002	0.01
Crop allocation × Ploughing	1	0.006	0.0
Crop allocation × Map pattern	34	<0.001	0.15
Crop rotation × Biological regulation	1	<0.001	3.0
Crop rotation × Trap crop	1	0.001	0.01
Crop rotation × Ploughing	1	0.44	0.0
Crop rotation × Map pattern	34	<0.001	1.6
Biological regulation × Trap crop	1	0.001	0.5
Biological regulation × Ploughing	1	<0.001	0.0
Biological regulation × Map pattern	34	<0.001	2.0
Trap crop × Ploughing	1	0.1	0.01
Trap crop × Map pattern	34	<0.001	0.55
Ploughing × Map pattern	34	0.99	0.01

SI (sensitivity index) equals the deviance divided by the total deviance

Bold values indicate the effects that are significant (*P* value < 0.05)

biological regulation, which occurs because decreased connectivity between the previous and current oilseed rape affects the parasitoid more than the pollen beetle. This finding is consistent with Baudry et al. (2003), who assumed that temporal variability of connectivity between fields could affect insect densities and consequently biological regulation.

Crop allocation variance between years, despite its effects on year-to-year connectivity of oilseed rape fields, did not influence the long-term demography of pollen beetles. This is probably because the high level of biological regulation in the second year of crop allocation (resulting from the high number of previous oilseed rape fields in the landscape) is counterbalanced by the low parasitism level in the subsequent years in the crop sequence (resulting from the lower proportion of oilseed rape).

Mosaic-Pest highlighted the contrasting effects of trap crops, which increase pollen beetle densities via demographic effects and decrease pollen beetle

densities via an increase of biological regulation. This result indicates that, when a trap crop is used as part of a push–pull strategy (Cook et al. 2003), an insecticide should be applied to destroy the beetle population that develops on the trap crop. However, this result depends on the carrying capacity of both oilseed rape and turnip rape plants, which could be overestimated in the model and should be better estimated with further experiments.

The negligible effect of ploughing on both pollen beetles densities and parasitism rates was surprising because ploughing has been identified as significant by Rusch et al. (2012). We hypothesize that, in our simulations, the per capita parasitism rate was sufficiently high to counterbalance the decrease in parasitoid numbers due to ploughing.

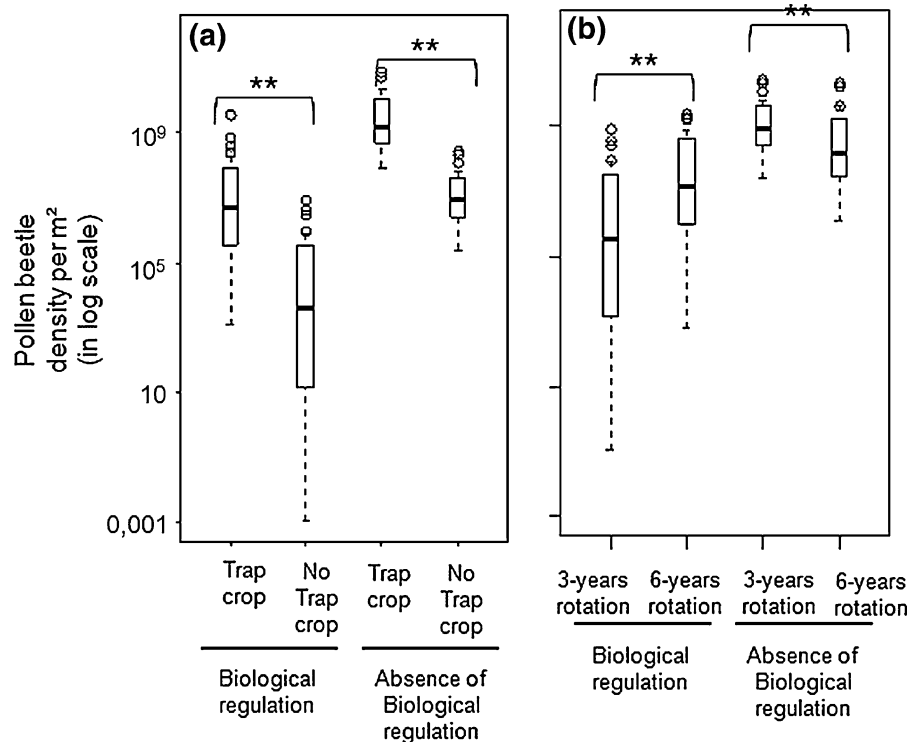
The model includes several simplifying assumptions regarding its objective or the lack of empirical information on some processes. We followed the general tendency to neglect wind effects in long-term

Table 2 Results of ANOVA analyses testing for effects of cultural practices, landscape configuration, and biological regulation on the parasitism rates averaged over the last 6 years of 12 years of simulations with the Mosaic-Pest model

	Parasitism rates (Binomial model)		
	df	P value	SI (%)
Main effects			
Crop allocation	1	<0.001	4.0
Crop rotation	1	<0.001	58.2
Trap crop	1	<0.001	13.1
Ploughing	1	0.64	0.0
Map pattern	34	<0.001	9.5
Interaction effects			
Crop allocation × Long crop rotation	1	0.03	0.07
Crop allocation × Trap crop	1	0.23	0.07
Crop allocation × Ploughing	1	0.04	0.02
Crop allocation × Map pattern	34	0.007	0.8
Crop rotation × Trap crop	1	<0.001	1.7
Crop rotation × Ploughing	1	0.21	0.02
Crop rotation × Map pattern	34	<0.001	3.7
Trap crop × Ploughing	1	0.01	0.1
Trap crop × Map pattern	34	<0.001	8.3
Ploughing × Map pattern	34	0.98	0.3

SI (sensitivity index) equals the deviance divided by the total deviance
 Bold values indicate the effects that are significant (P value < 0.05)

Fig. 6 Box plots ($n = 35$) illustrating the simulated ranges and medians (horizontal black lines) for pollen beetle density as affected by biological regulation, a trap crop, and rotation length. The data were obtained from a 12-year simulation using Mosaic-Pest and were averaged over 10 repetitions for each map and for the last 6 years of simulation. All simulations were obtained with time-invariant crop allocation and no ploughing. **a** Effect of trap crops with and without biological regulation (crop rotation was fixed to 3 years), and **b** effect of rotation length with and without biological regulation (no trap crops were used). Stars indicate a significant difference ($P < 0.001$, Mann–Whitney U test)



simulations of insect spatio-temporal dynamics (Barclay and Vreysen 2011). We also did not consider density-dependent effects in cells such as Allee effects

or density-dependent dispersal or fecundity because there is no literature, to our knowledge, to calibrate these for our studied species. The effect of varying

climate conditions was not included in the model because Mosaic-Pest is not meant to predict pest populations under a specific set of climatic conditions but is rather meant to evaluate the efficacy of management strategies such as soil tillage, use of trap crops, or crop rotation.

The number of simulations tested with the Mosaic-Pest model was highly depending on computational capacities of the computers. In fact, spatially explicit model used at landscape scale required large amounts of computer processor power, the latter being also depending on the type of programming language (for example C++, Java, Python, etc.) used to program the model. The choice of the Netlogo platform to implement our model was motivated by the simplicity of its language, and its quantity of pre-written simulation tools. However, some issues regarding the spatial resolution of the raster could be solved by using lower-level languages.

As a tool for testing integrated pest management strategies, Mosaic-Pest could be improved in several ways. For example, it would be useful to link pollen beetle densities to crop damage. Although equations describing the relationship between beetle density and crop damage have been published (Hansen 2004), they do not take into account compensatory plant responses (Williams and Free 1979), and for this reason they were not included in Mosaic-Pest. The effect of pesticide applications could easily be integrated in the model. Individual farmer practices should also be included in Mosaic-Pest by adding a sub-model that considers agents (farmers) with their own decision rules. The model can thus be seen as a virtual laboratory to drive farmer practices for a better comprehension of a host–parasitoid complex at landscape scale.

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