Supplement of

Keep your enemies closer: enhancing biological control through individual movement rules to retain natural enemies inside the field

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S1 Presentation of the models following the ODD protocol

S1.1 Foraging model

S1.1.1 Model description

The description of our individual-based Foraging model follows the ODD protocol (Grimm et al., 2006, 2010). The model was implemented in NetLogo (Tisue and Wilensky, 2004).

S1.1.2 Purpose

The purpose of this model is to understand how the qualities of three categories of habitats in agricultural landscapes affect the residence time of natural enemies in the agricultural plot, and thereby affect the potential biological control. The Foraging model also serves as a “null hypothesis” by providing a most simplistic approach to movement rules that can be compared to more complex models.

S1.1.3 Entities, state variables, and scales

We are not representing pests in the model but only a generic natural enemy species. The Foraging Model has only one entity, namely individual natural enemies. They are described by a set of simple state variables characterising the location of the natural enemy and its movement ability.

- Localisation (x, y)
- Habitat sensitivity (%)
- Movement ability (energy e)

Time steps (ts) are abstract, as well as space units (pixels). Space is described in two dimensions. The typical simulated plot is a 500 pixels wide square, but its size can be varied by the experimenter.

The three habitat types are the agricultural crops, the grassy field margins (GFMs) and the hedgerows. The quality of each habitat type can be varied so that each can be considered hostile, favourable or of intermediate quality, from the point of view of the natural enemy.

S1.1.4 Process overview and scheduling

The processes of the simulation model are described in the flowchart (Fig. S1). At each time step, the submodel Forage is executed for all natural enemies in a random order, and defines their next location. The residence time calculations are then executed for each pixel, and summarised at the end of the simulation.
**S1.1.5 Design Concepts**

*Basic principles:* The movements of natural enemies are mainly foraging movements based on “movement ecology” and “habitat selection” literature and based on a simple non-specific behavioural assumption: movement is a biased random walk affected by local habitat quality (Bartumeus et al., 2005; Bell, 1991). As a result, movements in the model are in part imposed by the random walk, but some adaptation has been taken into account.

*Emergence:* The dynamic of natural enemies’ movements and the resulting residence time in the habitat categories emerge from the foraging behaviour of the individuals. The interplay between movement, habitat qualities and their spatial organisation is not straightforward.

*Adaptation:* Natural enemies adapt their movement to the habitat cell they are to move on: better cells have a higher probability to be chosen for the next movement. A habitat sensitivity parameter is provided in the inputs, that increase the probability that the best cell is ignored, and a random cell is chosen instead. Due to these parameters, individual optimise the time spent foraging in favourable habitats, and minimise the time spent in unfavourable habitats.

*Objectives:* Not relevant.

*Learning:* Not relevant.

*Interaction:* Not relevant.

*Prediction:* Not relevant.

*Sensing:* Natural enemies perceive the habitat quality of the cell they are on at the beginning of the time step, and that of the eight neighbouring cells.

*Stochasticity:* In the model, the construction of plots (Initialisation section f.) and the individual movements are stochastic. Movements are classically modelled by random processes (Codling et al., 2008) because unpredictability of food distribution for a predator implies stochasticity in the search.
Observation: At each time step, each pixel occupation status is stored, and its residence time is incremented if at least one individual is located on it. When the simulation is over (when all individuals have depleted their energy pool), the mean residence time and its variance, and the proportion of unvisited pixels are calculated for each habitat type, and stored for statistical calculations in R (R Core Team, 2011). Mean field residence time and its variance are calculated over the residence times of all pixels belonging to a given habitat type, summed over all simulation time steps.

S1.1.6 Forage Submodel

At each time step, individuals compare the habitat quality of eight neighbouring cells, and identify the best one. This core process may be affected, according to the habitat sensitivity parameter that has been introduced to compare different species responses to sets of habitat qualities. This parameter illustrates interspecific variability in sensitivity to habitat quality (i.e. generalist vs specialist species). The probability that a random cell is chosen instead of the better one is inversely proportional to the habitat sensitivity of the species (i.e. a species with a low habitat sensitivity would have a higher probability to ignore the better cells and engage in a pure random walk).

At each time step, the remaining energy pool was decremented by 1-q/100, where q represents habitat quality of the current cell. This mechanism allows us to mimic the direct and indirect costs of movement (Bonte et al., 2012) that are high in hostile habitats and low in favourable habitats. The habitat sensitivity parameter (Table 1) is used to alter the effect of habitat quality on movement cost, as a proxy of interspecific differences in habitat sensitivity.

A random value [-1 <RV> 1] is added to the pixel cost with a probability equal to the habitat sensitivity of the species/100 (i.e. adding noise around the cost value). The costs of diagonal and orthogonal moves are identical.

S1.1.7 Initialisation

The model is initialised by assigning habitat types to cells (either “hedgerow”, “grassy field margin” or “agricultural plot”). A habitat quality parameter is then attributed to each pixel according to its habitat type, and the quality that has been attributed to it in the inputs. 2000 individuals are then distributed on random hedgerow cells, with a random initial orientation, and an energy pool of 500e representing their intrinsic initial movement ability.

S1.1.7.1 Plot Generation

Fields shapes and patterns are obtained using a method similar to a T-tessellation (Papaïx et al., 2014) that consists of seeding the landscape with a defined number of randomly distributed seeds, each of which is a departure point for three edges that eventually form a rectangle (Figure 1). This method allowed probabilistic control on the number of polygons, their size and shape, while exploring a diversity of spatial distributions of field shapes and sizes (Figure 1). In order to focus on habitat quality, the patch density is kept constant to maintain a stable landscape structure throughout the simulations (see Supplement S2 for the effect of patch density) and we alter only habitat quality for each landscape element (between extreme values 1 and 99, respectively hostile and favourable, other values ranging from 5 to 95 with a 5 interval). The landscape is a 500 pixels wide square treated as a torus, and is composed of 10 to 12 fields surrounded by 4 pixels-wide hedgerows and 5 pixels-wide GFMs (similar to a typical bocage landscape, Burel et al., 1998; Thenail and Baudry, 2004). Although the field-GFM-hedgerow trio is used as an example for clarity, the structure could apply to fields surrounded by other types of borders.

S1.1.7.2 Foraging Parameters
The values used in our case study for foraging parameters are provided in Table 1. They are designed to represent two hypothetical species, to illustrate the sensitivity of the model to differences in habitat sensitivity. An "insensitive species" with a movement behaviour that allows individuals to free themselves from local habitat conditions to reach more easily another region of the landscape: in the Foraging model that species is characterised by a lower value of the sensitivity to habitat quality parameter (Table 1). On the contrary, the "sensitive species" is characterised by a movement behaviour that depended more strongly on local conditions (Table 1) with a higher sensitivity to habitat and lower directional persistence.

S1.2 The Routine & Direct Movements model

S1.2.1 Model description

The description of our individual-based Routine & Direct Movements (RDM) model follows the ODD protocol (Grimm et al., 2006, 2010). The model was implemented in NetLogo (Tisu and Wilensky, 2004).

S1.2.2 Purpose

The purpose of this model is to understand how the qualities of three categories of habitats in agricultural landscapes affect the residence time of natural enemies in the agricultural plot, and thereby affect the potential biological control. The RDM model is designed to illustrate a different approach to movement, compared to the Foraging model and the SMS. In the RDM model, individuals react to changes in habitat quality by changing the shape of their path and the probabilities to pass habitat boundaries (instead of choosing a destination cell at each step).

S1.2.3 Entities, state variables, and scales

We are not representing pests in the model but only a generic natural enemy species. The RDM model has only one entity, namely individual natural enemies. They are described by a set of simple state variables characterising the location of the natural enemy and its movement ability.

- Localisation (x, y)
- Habitat sensitivity (%)
- Movement ability (energy e)

Time steps (ts) are abstract, as well as space units (pixels). Space is described in two dimensions. The typical simulated plot is a 500 pixels wide square, but its size can be varied by the experimenter.

The three habitat types are the agricultural crops, the grassy field margins (GFMs) and the hedgerows. The quality of each habitat type can be varied so that each can be considered hostile, favourable or of intermediate quality, from the point of view of the natural enemy.

S1.2.4 Process overview and scheduling

The processes of the simulation model are described in the flowchart (Fig. S1). At each time step, the submodel RDM is executed for all natural enemies in a random order, and defines their next location. The residence time calculations are then executed for each pixel, and summarised at the end of the simulation.
S1.2.5 Design Concepts

**Basic principles:** The movements of natural enemies are mainly foraging movements based on “movement ecology” and “habitat selection” literature and based on simple non-specific behavioural assumptions: movement is a correlated random walk whose shape is affected by local habitat quality and contrast at habitat boundaries (Bartumeus et al., 2005; Bell, 1991; Van Dyck and Baguette, 2005). As a result, movements in the model are in part imposed by the random walk, but some adaptation has been taken into account.

**Emergence:** The dynamic of natural enemies’ movement and the resulting residence time in the habitat categories emerge from the movement behaviour of individuals. The interplay between movement, habitat qualities and their spatial organisation is not straightforward.

**Adaptation:** Natural enemies adapt their movement to the habitat cell they are located on. On favourable habitat, they move slowly and sinuously, and tend to avoid crossing towards unfavourable habitats. On the contrary, on unfavourable habitats, they move fast and almost straight, and direct to each favourable habitat encountered. Due to these changes, they optimise the time they spend foraging in favourable habitats and minimise the time they spend in unfavourable habitats. The habitat sensitivity parameter is added to compare different scenarios with different species response to landscape. The effect of habitat quality on the sinuosity of the path and on the probability to cross a boundary are proportional to the habitat sensitivity of the species: an insensitive species will be more likely to ignore the current habitat quality when defining its path sinuosity, and to ignore the contrast of a boundary when deciding if it is to cross it.

**Objectives:** Not relevant.

**Learning:** Not relevant.

**Interaction:** Not relevant.

**Prediction:** Not relevant.

**Sensing:** Natural enemies perceive the habitat quality of the cell they are on at the beginning of the time step, and that of the eight neighbouring cells.
**Stochasticity**: In the model, the construction of plots (Initialisation section f.) and the individual movements are stochastic. Movements are classically modelled by random processes (Codling et al., 2008) because unpredictability of food distribution for a predator implies stochasticity in the search.

**Observation**: At each time step, each pixel occupation status is stored, and its residence time is incremented if at least one individual is located on it. When the simulation is over (when all individuals have depleted their energy pool), the mean field residence time and its variance, and the proportion of unvisited pixels are calculated for each habitat type, and stored for statistical calculations in R (R Core Team, 2011). Mean field residence time and its variance are calculated over the residence times of all pixels belonging to a given habitat type, summed over all simulation time steps.

**S1.2.6 RDM Submodel**

At each time step, individuals read the habitat quality of their current cell. According to their quality, they define the sinuosity of their path (a higher quality habitat causes higher sinuosity). The sinuosity of the path is then used to select stochastically a tentative cell for the next movement among the eight neighbour cells. If that tentative cell has a different habitat quality than the cell of origin, a boundary-crossing routine is executed. The individual chooses stochastically whether to cross that boundary, with a probability that is proportional to the contrast between both origin and destination pixel. The habitat sensitivity parameter was added in order to compare different scenarios with different species response to landscape. The effect of habitat quality on the sinuosity of the path and on the probability to cross a boundary are proportional to the habitat sensitivity of the species: an insensitive species will be more likely to ignore the current habitat quality when defining its path sinuosity, and to ignore the contrast of a boundary when deciding if it is to cross it.

At each time step, the remaining energy pool was decremented by \(1-q/100\), where \(q\) represents habitat quality of the current cell. This mechanism allows us to mimic the direct and indirect costs of movement (Bonte et al., 2012) that are high in hostile habitats and low in favourable habitats. The habitat sensitivity parameter (Table 1) is used to alter the effect of habitat quality on movement cost, as a proxy of interspecific differences in habitat sensitivity. A random value \([-1 <RV> 1]\) is added to the pixel cost with a probability equal to the habitat sensitivity of the species/100 (i.e. adding noise around the cost value). The costs of diagonal and orthogonal moves are identical.

**S1.2.7 Initialisation**

The model is initialised by assigning habitat types to cells (either “hedgerow”, “grassy field margin” or “agricultural plot”). A habitat quality parameter is then attributed to each pixel according to its habitat type, and the quality that has been attributed to it in the inputs. 2000 individuals are then distributed on a random hedgerow cell, with a random initial orientation, and an energy pool of 500e representing their intrinsic initial movement ability.

**S1.2.7.1 Plot Generation**

Fields shapes and patterns are obtained using a method similar to a T-tessellation (Papaïx et al., 2014) that consists of seeding the landscape with a defined number of randomly distributed seeds, each of which is a departure point for three edges that eventually form a rectangle (Figure 1). This method allowed probabilistic control on the number of polygons, their size and shape, while exploring a diversity of spatial distributions of field shapes and sizes (Figure 1). In order to focus on habitat quality, the patch density is kept constant to maintain a stable landscape structure throughout the simulations (see Supplement S2 for the effect of patch density) and we alter only habitat quality for each landscape element (with a 5 interval, from 1 to 99, respectively hostile to
favourable). The landscape is a 500 pixels wide square treated as a torus, and is composed of 10 to 12 fields surrounded by 4 pixels-wide hedgerows and 5 pixels-wide GFMs (similar to a typical bocage landscape, Burel et al., 1998; Thenail and Baudry, 2004). Although the field-GFM-hedgerow trio is used as an example for clarity, the structure could apply to fields surrounded by other types of borders.

S1.2.7.2 RDM Parameters

The values used in our case study for foraging parameters are provided in Table 1. They are designed to represent two hypothetical species, to illustrate the sensitivity of the model to differences in habitat sensitivity. An “insensitive species” with a movement behaviour that allows individuals to free themselves from local habitat conditions to reach more easily another region of the landscape: in the RDM model that species is characterised by a lower value of the sensitivity to habitat quality parameter (Table 1). On the contrary, the “sensitive species” is characterised by a movement behaviour that depended more strongly on local conditions (Table 1) with a higher sensitivity to habitat and lower directional persistence.
S2 Effects of movement ability, population size and patch density

Figure S2.1. Mean field residence time (in ts, A — C) and proportion of unvisited field pixels (0 ≥ p ≤ 1, D-F) as a function of interactions between movement ability (pixels, A, C, D, F), population size (number of individuals at initiation, A, B, D, E), and patch density (number of fields in the landscape, B, C, E, F). C: the three lines are shown but overlap.
Figure S3.1. Examples of individual movement paths (yellow lines) generated by the RDM model (Routine & Direct Moves: A, C) and the SMS (Stochastic Movement Simulator: B, D). Agricultural fields (dark green) are separated by grassy field margins (light green) surrounding hedgerows (black). The habitat qualities of agricultural fields, grassy field margins and hedgerows vary (respectively of quality 55, 30, 15 in figures 5A, B and 15, 30, 55 in figures 5C, D). N = 50 individual paths, paths length = 200 p.

References


Baguette, M. and Van Dyck, H.: Landscape connectivity and animal behaviour: functional grain as a key


