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Supplement of

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

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1 Additional information

3 S1 Presentation of the models following the ODD protocol

5 S1.1 Foraging model

6 S1.1.1 Model description

7 The description of our individual-based Foraging model follows the ODD protocol (Grimm et al.,
8 2006, 2010). The model was implemented in NetLogo (Tisue and Wilensky, 2004).

9 S1.1.2 Purpose

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

15 S1.1.3 Entities, state variables, and scales

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

- 20 • Localisation (x, y)
- 21 • Habitat sensitivity (%)
- 22 • Movement ability (energy e)

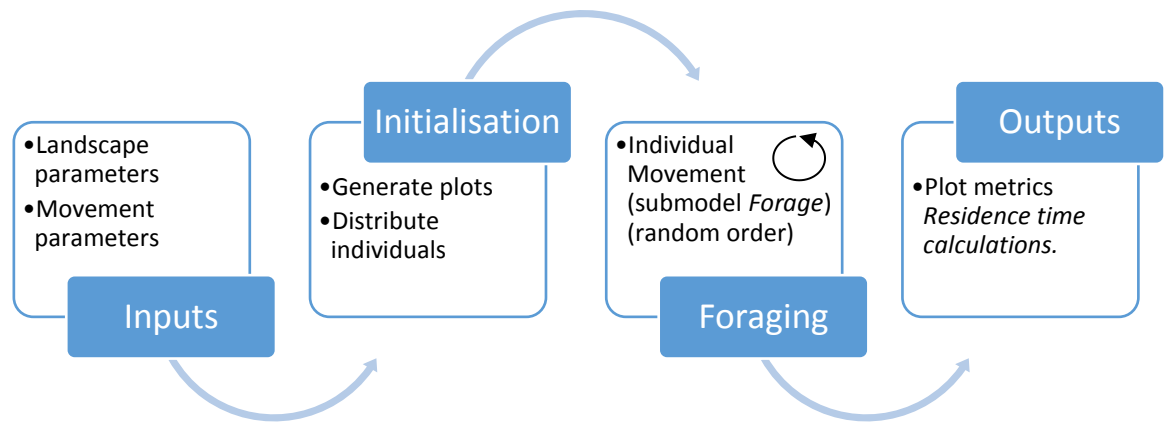
23 Time steps (ts) are abstract, as well as space units (pixels). Space is described in two
24 dimensions. The typical simulated plot is a 500 pixels wide square, but its size can be varied by
25 the experimenter.

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

29 S1.1.4 Process overview and scheduling

30 The processes of the simulation model are described in the flowchart (Fig. S1).

31 At each time step, the submodel *Forage* is executed for all natural enemies in a random order,
32 and defines their next location. The residence time calculations are then executed for each
33 pixel, and summarised at the end of the simulation.



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Figure S1.1. Flowchart of the Foraging model.

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S1.1.5 Design Concepts

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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.

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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.

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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.

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Objectives: Not relevant.

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Learning: Not relevant.

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Interaction: Not relevant.

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Prediction: Not relevant.

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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.

58

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.

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

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68 **S1.1.6 Forage Submodel**

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

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

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82 **S1.1.7 Initialisation**

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

87 *S1.1.7.1 Plot Generation*

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

100 *S1.1.7.2 Foraging Parameters*

101 The values used in our case study for foraging parameters are provided in Table 1. They are designed to
102 represent two hypothetical species, to illustrate the sensitivity of the model to differences in habitat sensitivity. An
103 “insensitive species” with a movement behaviour that allows individuals to free themselves from local habitat
104 conditions to reach more easily another region of the landscape: in the Foraging model that species is
105 characterised by a lower value of the sensitivity to habitat quality parameter (Table1). On the contrary, the
106 “sensitive species” is characterised by a movement behaviour that depended more strongly on local conditions
107 (Table 1) with a higher sensitivity to habitat and lower directional persistence.

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109 **S1.2 The Routine & Direct Movements model**

110 **S1.2.1 Model description**

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

114 **S1.2.2 Purpose**

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

121 **S1.2.3 Entities, state variables, and scales**

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

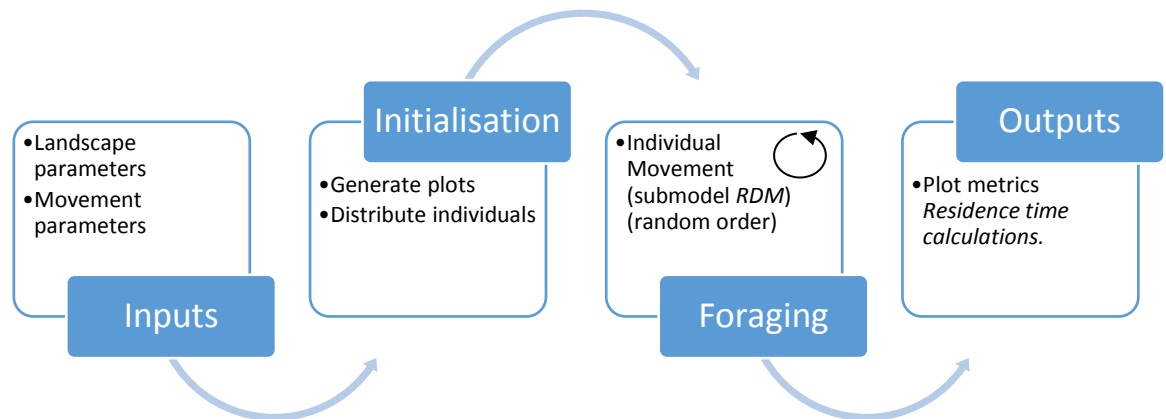
- 126 • Localisation (x, y)
- 127 • Habitat sensitivity (%)
- 128 • Movement ability (energy e)

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

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

135 **S1.2.4 Process overview and scheduling**

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



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Figure S1.2. Flowchart of the RDM model.

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S1.2.5 Design Concepts

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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.

167 *Stochasticity*: In the model, the construction of plots (Initialisation section f.) and the individual
168 movements are stochastic. Movements are classically modelled by random processes (Codling et al., 2008)
169 because unpredictability of food distribution for a predator implies stochasticity in the search.

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

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177 **S1.2.6 RDM Submodel**

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

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

194

195 **S1.2.7 Initialisation**

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

200 *S1.2.7.1 Plot Generation*

201 Fields shapes and patterns are obtained using a method similar to a T-tessellation (Papaix et al., 2014) that
202 consists of seeding the landscape with a defined number of randomly distributed seeds, each of which is a
203 departure point for three edges that eventually form a rectangle (Figure 1). This method allowed probabilistic
204 control on the number of polygons, their size and shape, while exploring a diversity of spatial distributions of field
205 shapes and sizes (Figure 1). In order to focus on habitat quality, the patch density is kept constant to maintain a
206 stable landscape structure throughout the simulations (see Supplement S2 for the effect of patch density) and we
207 alter only habitat quality for each landscape element (with a 5 interval, from 1 to 99, respectively hostile to

208 favourable). The landscape is a 500 pixels wide square treated as a torus, and is composed of 10 to 12 fields
209 surrounded by 4 pixels-wide hedgerows and 5 pixels-wide GFMs (similar to a typical bocage landscape, Burel et
210 al., 1998; Thenail and Baudry, 2004). Although the field-GFM-hedgerow trio is used as an example for clarity, the
211 structure could apply to fields surrounded by other types of borders.

212 *S1.2.7.2 RDM Parameters*

213 The values used in our case study for foraging parameters are provided in Table 1. They are designed to
214 represent two hypothetical species, to illustrate the sensitivity of the model to differences in habitat sensitivity. An
215 “insensitive species” with a movement behaviour that allows individuals to free themselves from local habitat
216 conditions to reach more easily another region of the landscape: in the RDM model that species is characterised
217 by a lower value of the sensitivity to habitat quality parameter (Table1). On the contrary, the “sensitive species” is
218 characterised by a movement behaviour that depended more strongly on local conditions (Table 1) with a higher
219 sensitivity to habitat and lower directional persistence.

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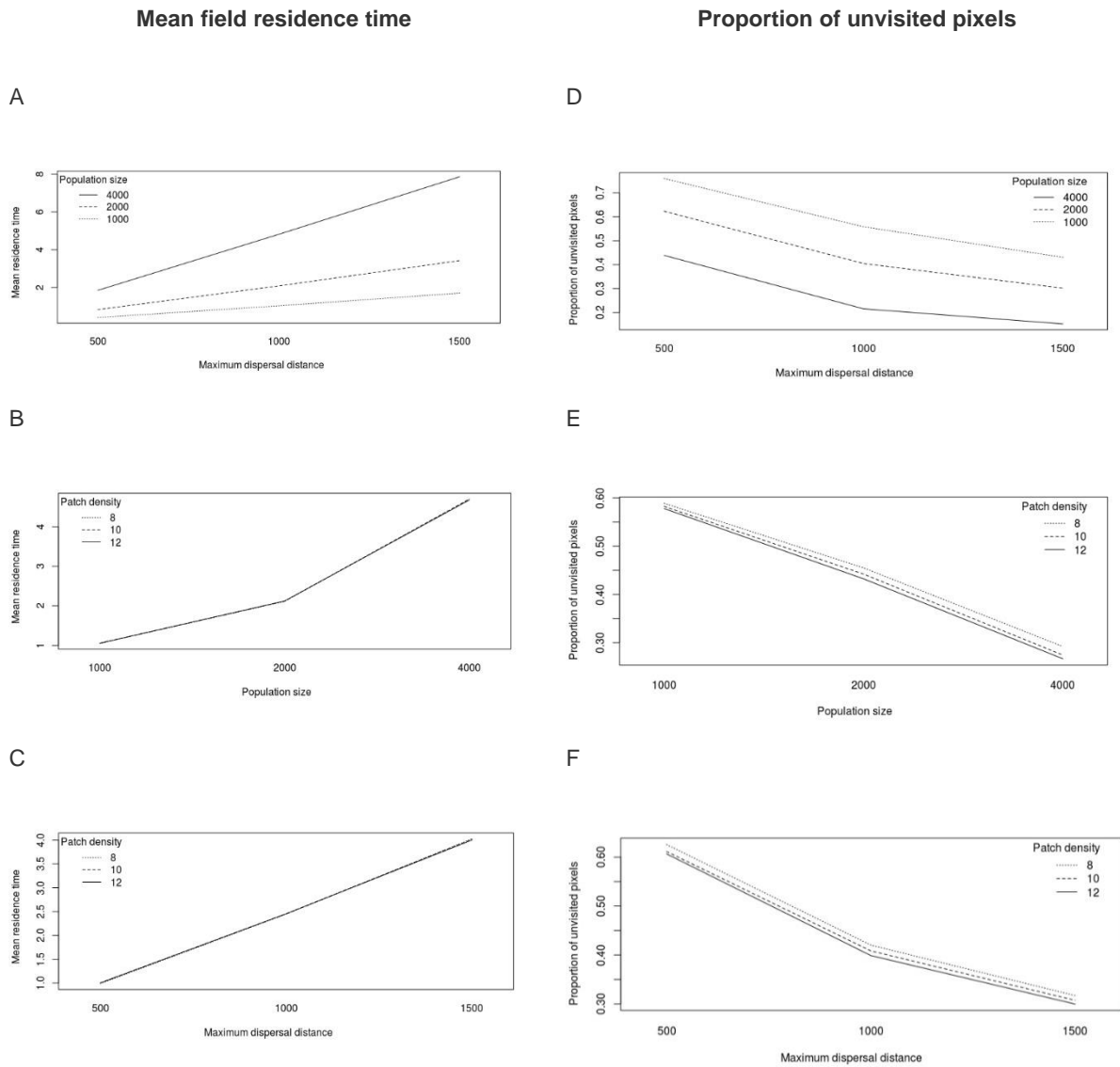
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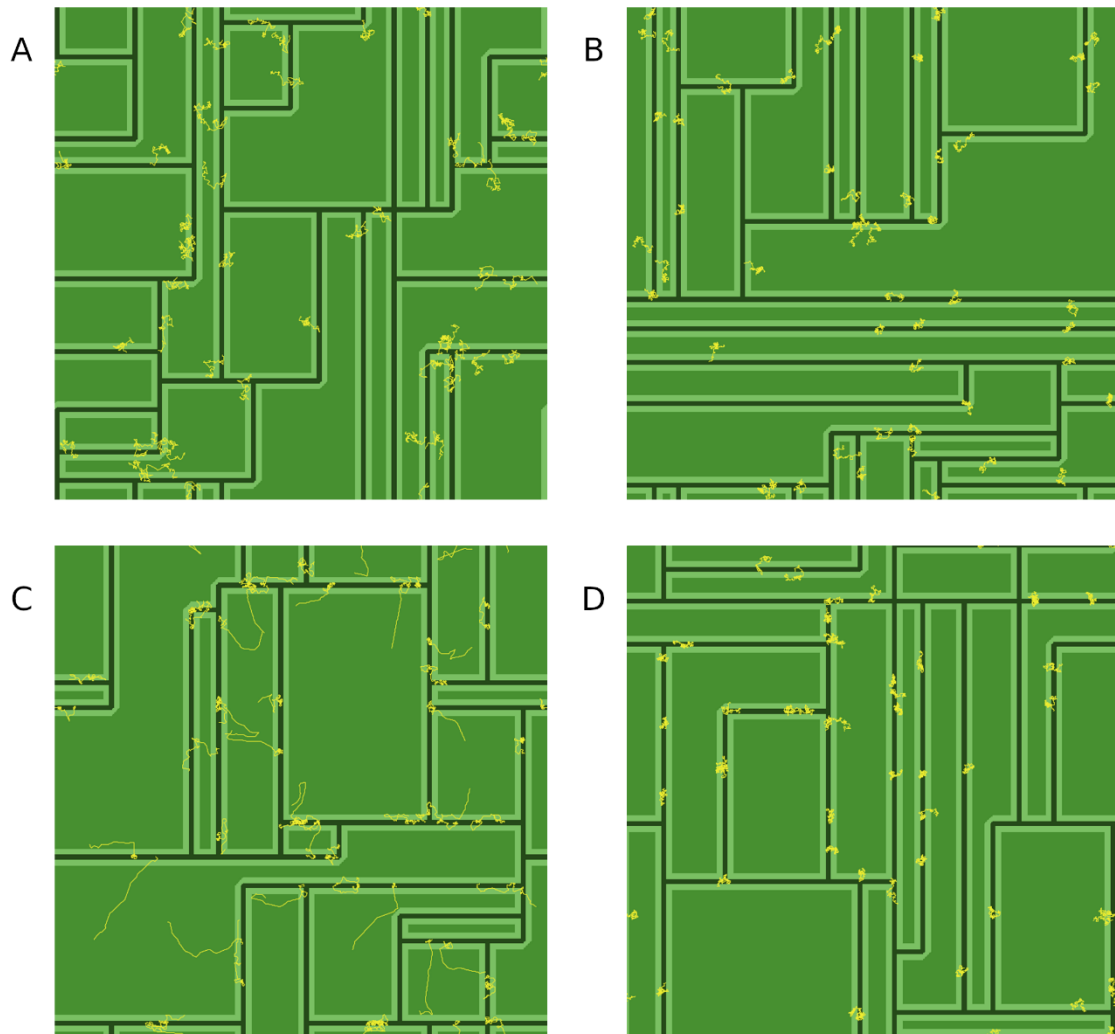
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S2 Effects of movement ability, population size and patch density



225 Figure S2.1. Mean field residence time (in ts, A — C) and proportion of unvisited field pixels ($0 \geq p \leq 1$, D-F) as a
226 function of interactions between movement ability (pixels, A, C, D, F), population size (number of individuals at
227 initiation, A, B, D, E), and patch density (number of fields in the landscape, B, C, E, F). C: the three lines are
228 shown but overlap.



229 *Figure S3.1. Examples of individual movement paths (yellow lines) generated by the RDM model (Routine & Direct Moves: A, C)*
 230 *and the SMS (Stochastic Movement Simulator: B, D). Agricultural fields (dark green) are separated by grassy field margins (light*
 231 *green) surrounding hedgerows (black). The habitat qualities of agricultural fields, grassy field margins and hedgerows vary*
 232 *(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.*

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