

Spatial effects in an individual-based model of the interaction of species at different trophic levels

¹Chivers, W. J., ²W. Gladstone and ³R. D. Herbert

¹School of Design, Communication and Information Technology, Faculty of Science and Information Technology
University of Newcastle, GPO Box 127, Ourimbah NSW 2259, Australia. E-Mail: william.chivers@newcastle.edu.au

²School of Applied Sciences, Faculty of Science and Information Technology
University of Newcastle, GPO Box 127, Ourimbah NSW 2259, Australia. E-Mail: william.gladstone@newcastle.edu.au

³Affiliation as ¹, E-Mail: ric.herbert@newcastle.edu.au

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ABSTRACT

A spatial individual-based model of producer-consumer interaction is described. The model includes a two-dimensional grid of cells in which a producer organism grows according to a logistic equation, and individual herbivores which move towards cells high in producer biomass to consume the producer. Herbivores die of starvation if their energy reserve is too low or they may reproduce asexually if they have eaten sufficiently. The individuals in the model are the herbivores and the matrix cells—the producers are represented only as an attribute of the individual cells. The model was built as simply as possible with parsimonious producer-consumer interaction and consumer behavior.

In this paper we consider spatial effects in the model. We test the effect of three independent variables: a) the distance over which the herbivores may move per time step, b) a torus matrix compared with an edged matrix and c) the size of the space matrix. We also comment on the inclusion of space itself into the model algorithm. The effect of the three independent variables on population size is tested by using a 3-factor ANOVA for herbivore and producer populations. The model is executed ten times for each of 18 combinations of levels of the three factors. We find a significant Distance \times Edge \times Matrix interaction for the herbivores. The variation in population among the three matrix sizes at each move distance differed depending on whether an edge was present or not. For the producers the ANOVA showed a significant Distance \times Matrix interaction which arose because the variation in population among the three matrix sizes was not consistent across the three move distances.

The effects of two factors were clearly evident in the graphical display of the model, but not highly significant in the statistical procedure. The effect of an edge is evident when the populations are graphed over time or when the graphical display of the software is observed during a simulation. The herbivore

population changes over time with an edge present are not as smooth as without an edge. Watching the graphical display reveals a cycle of near population extinctions as a majority of herbivores move towards high populations of producers only to be trapped by the edge and die of starvation. Observation of the graphical output reveals that such large falls in population in a small number of time steps do not occur to the same extent when an edge is not present.

The herbivore maximum move distance also has an effect on the model dynamics which is not evident in the statistical analysis. An increasing move distance results in greater fluctuations in the herbivore population and an increased likelihood of extinction. Observing the model graphical output as the move distance increases, the herbivores move to areas of greater producer biomass more quickly, resulting in greater fluctuations in both populations. If the move distance is too great, the herbivore population is able to consume too much of the producer population in too few time steps and becomes extinct. This danger of extinction during steady state dynamics increases as the matrix size decreases.

We also find metapopulation behavior emerging from the interactions between the individual herbivores and cells, where patches and transient barriers emerge and disappear, with local extinctions and recruitment occurring. This behavior was not explicitly coded into the model.

The contribution of this paper to the modeling of ecological systems is threefold. First, we demonstrate that the details of distance moved, the existence of an edge and the size of the space involved do affect model dynamics and we argue that these details should be included in model descriptions in the literature. Second, we demonstrate that a simple algorithm of producer-consumer interaction can exhibit behavior characteristic of metapopulation theory. Third, we argue that graphical output of a spatial model can reveal details of behavior which are not evident in the population means.

1 INTRODUCTION

The use of individual-based modeling (IBM) can facilitate understanding of a system and even decision-making in resource management (Grimm 1999, Judson 1994 and Łomnicki 1999). The use of individual-based modeling has grown in ecology in the last 2-3 decades (DeAngelis *et al* 2001, Grimm 1999 and Łomnicki 1999). Individual-based models may also explicitly include space, as may mathematical or other models. Arguments for the inclusion of space are similar to those for the use of IBMs themselves: such models more closely simulate some aspects of the natural system being modeled, aspects which are important for the question being researched. In the case of IBMs, discrete individuals with potentially unique state and behavior may be included, as may their individual interactions on local levels. The inclusion of space in a model allows the modeler to expose individuals to only other individuals in the local vicinity, rather than to the whole population. Models which do not explicitly involve space rely on the principle of mass action, whereby individuals mix instantly and randomly, and hence all individuals in the system have an equal chance of interaction with all other individuals. This is clearly not the case in real ecological systems, and researchers who find that the inclusion of space in their models affects model dynamics include DeAngelis and Petersen (2001), Donaldson and Nisbet (1999), Keitt and Johnson (1995), McCauley *et al* (1993) and Schneider (2001)

The use of IBM has not grown as the early pioneers may have hoped, and the reasons for this include the difficulty of describing an IBM and the lack of standard practices (Grimm 1999). The lack of standard practice in describing IBMs in the literature makes replication of these models impossible. For example, consequences of the size of the space used in a model are reported by authors including Donaldson and Nisbet (1999) and Schneider (2001), who find that the size of the space matrix affects the stability of the model. Acosta (2002) finds a similar effect interacting with dispersal dynamics. Few authors, however, report the exact size of the space used. In a brief survey no authors were found to mention whether their space was a torus or an edged space.

Similarly, the distance over which individuals may move in one time step is found to affect the stability of the populations of DeAngelis and Petersen (2001), McCauley *et al* (1993) and Wilson *et al* (1993). These authors report that the higher the mobility of prey organisms, the more stable the prey populations. DeRoos *et al* (1991) finds that limited mobility in a predator-prey model reduces population fluctuations, although average densities remain unaffected. Many other authors, however, do not report this detail in

their descriptions of their models.

In this paper we consider the effects of space on a simple producer-consumer system. We find that the inclusion of space itself into the model algorithm, the distance over which the consumers may move per time step, the existence of an edge on the matrix and the size of the space matrix affect model dynamics and we argue that these details should therefore be reported by the builders of spatial models. We find that the inclusion of space introduces behavior similar to that described by metapopulation theory, and we find that the graphical output from the model is useful in understanding the dynamics of the model.

2 METHOD

2.1 Design

The effect of three independent variables (matrix size, edge use and move distance) on population size was tested by using a 3-factor ANOVA for herbivore and producer populations in a spatial, individual-based producer-consumer model. The model was executed ten times for each of eighteen combinations of factor levels listed below. The data collected were the mean population levels for each execution of the model reaching 1000 time steps. In cases where the herbivore population became extinct, either in transient dynamics at the start of the simulation or during steady-state dynamics, the means were not used because the transient dynamics would then represent a larger portion of the total time steps in these cases than for cases running 1000 steps. Table 1 lists these extinctions. For the purposes of the ANOVA the factors matrix size and move distance were treated as random factors (three levels) and edge use was treated as a fixed factor (two levels). To test the assumption of homogeneity of variance, Cochran's C test was used.

The independent variables and their levels are:

- The size of the matrix: $g_w = g_h = 100, 141$ or 200 giving 10000, 20000 or 40000 cells.
- The use of an edge: $g_e = 0$ or 1 .
- The herbivore maximum move distance per time step: $h_{md} = 1, 2$ or 4 .

2.2 Description of the spatial model

The spatial IBM described here simulates a producer and consumer species in a two-dimensional space, and the energy flow between the two species. The individuals in the model are the cells of the grid

and the members of the consumer species—the members of the producer species are not represented as individuals. Members of the consumer species are born, reproduce and possibly die of starvation. The producer species grows in each cell and is eaten by individual consumer, which move between cells.

Cells and consumers are created as discrete objects in the computer memory, each with a potentially unique state and resulting behavior. The attributes of each cell are the current biomass of producer—the units of biomass are undefined—and an integer number of consumers. The attributes of the consumers are a current position and resource level, the latter representing the energy reserves carried by living organisms and also not formally defined.

The producer species in each cell grows according to the logistic growth model of classical ecology (see, for example, Adler (1998) pp224-226). Each cell has an individual biomass of a producer organism, a growth rate for the producer and a maximum carrying capacity for the producer. The biomass of the producer organism in each cell is assigned randomly when the simulation is started for the simulations reported here. It then grows towards the maximum capacity of the cell as the simulation progresses. Producer biomass is lost from a cell when a consumer eats the producer in the cell.

The resource level of each consumer increases as the consumer eats the producer in its current cell, and decreases with time, as the consumer moves from cell to cell and as the consumer reproduces. If a consumer does not eat enough resources it will die and be removed from the simulation.

When the model is started a given number of consumers are created and assigned to cells in the grid randomly. In each time step of the simulation, each consumer eats a given percentage of the producer species in the cell then compares the current cell with neighboring cells. If a neighboring cell has a higher biomass of producer the consumer will move to that cell.

The model inputs are as follows—the input values used to produce Figure 1 and Figure 2 are also listed here:

- The width and height of the grid in cells ($g_w = 100$ and $g_h = 100$)
- The existence or otherwise of an edge to the matrix ($g_e = 0$).
- The producer growth rate of each cell ($p_r = 0.02$)
- The maximum producer population of each cell ($p_K = 200$)

- Initial number of herbivores ($h_{p0} = 100$)
- Initial resource level of the herbivores ($h_{r0} = 1000$)
- Percentage of producer eaten per cell per time step ($h_{pe} = 80$)
- Trophic efficiency of the herbivores ($h_{te} = 100$)
- Herbivore maximum move distance ($h_{md} = 1$)
- Herbivore move cost ($h_{mc} = 10$)
- Herbivore move level of stochasticity ($h_{ms} = 2.0$)
- Metabolic tax per cycle for the herbivores ($h_{mt} = 100$)
- Reproductive cost for the herbivores ($h_{rc} = 1000$)

The generalized nature of this model means that many predator-prey systems could be represented in the terms of this model. Our decision to refer to producer and consumer organisms was arbitrary.

2.2.1 Model output

The model output includes

1. The population of consumers per time step and the mean producer biomass per cell per time step. Figure 1 shows cycling population levels similar to those of the Lotka-Volterra equations of classical ecology. The appearance of this graph is highly dependent on the model parameter values, as the other figures in this paper illustrate.

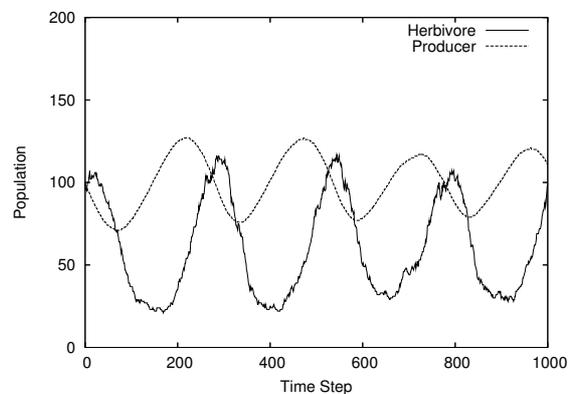


Figure 1. Population levels for 1000 cycles

2. A graphical display of each cell (Figure 2). The brightness of each cell indicates the cell producer biomass—the brighter the cell, the closer the biomass is to the maximum p_K value in the matrix. The white cells indicate the presence of a consumer. Figure 2 shows the matrix after 1000 time steps and is the final state of the simulation graphed in Figure 1. The dark areas have low producer biomass and are areas from which the consumers have recently moved. The brighter areas have had longer to recover from consumer grazing, and are the areas towards which the consumers are moving.

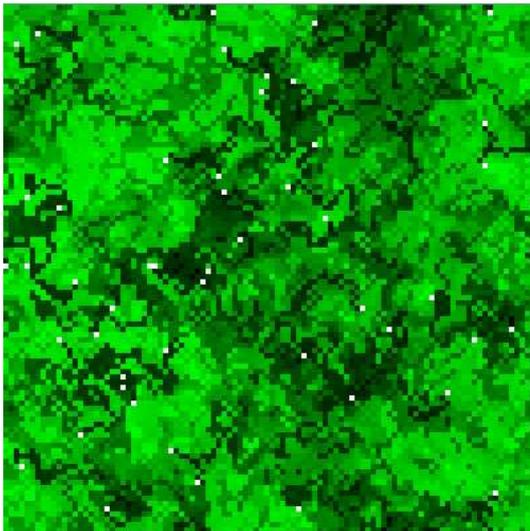


Figure 2. Graphical output after 1000 cycles

2.2.2 Initialization

At the start of the simulation the cells are created in the computer memory in a matrix or grid of g_w width and g_h height in cells. The matrix may or may not have an edge (g_e)—an edge cannot be crossed by the herbivores. The lack of an edge results in a torus (wrap-around) effect. Each cell is assigned a random producer biomass chosen from between zero and the maximum p_K value for the cell). The herbivores are then created and assigned to random cell addresses. The number of herbivores created is h_{p0} , and each is given an initial resource level of h_{r0} .

2.2.3 Processing per cycle

The processing which then occurs during each time step is as follows:

1. Each cell producer biomass advances one step towards the maximum carrying capacity of the

cell, p_K , according to the growth rate of the cell, p_r . The logistic growth model is expressed here as the stepping function used in the computer code: $N_{t+1} = N_t + N_t p_r (1 - \frac{N_t}{p_K})$. Each cell has an individual p_r and p_K value, however these values are uniform across the matrix in the simulations reported here.

2. Each herbivore compares the current cell producer biomass with the neighboring cells, and moves to the cell with the highest effective producer biomass. The number of neighboring cells considered depends on how far the herbivores may move, h_{md} . The effective producer biomass of a cell is calculated using the actual producer biomass, the presence of other herbivores and the cost of moving to the cell, $h_{mc} \times movedistance$. A level of stochasticity is involved—the final h_{ms} (herbivore move level of stochasticity) percentage of the effective producer biomass is randomly chosen before a decision to move is made.
3. Each herbivore eats the given percentage of producer on the new cell, h_{pe} . The cell producer biomass is reduced and the herbivore resource level is increased, taking into account the trophic efficiency of the herbivore h_{te} .
4. The cost for each herbivore of living one time step is h_{mt} , and this is subtracted from the resource level carried by the herbivore. Herbivores which do not have sufficient resources to live one more time step die of starvation and are removed from the simulation—this is the only way a herbivore dies.
5. Any herbivores with sufficient resources to live one more time step *and* reproduce then produce an offspring asexually at a resource cost of h_{rc} . The new individual is placed on the same cell as the parent, but with the parameter set used in the simulations reported here, the new individual usually moves away in the next time step as two herbivores on one cell halves the effective producer biomass of the cell when a decision to move is made.

3 RESULTS

3.1 Matrix size, edge and move distance

The variances of the herbivore data were heterogeneous (Cochran's $C = 0.34$, $P < 0.01$). This is not a problem for the interpretation of the ANOVA results because this analysis is robust to departures from the assumption of homogeneity of variances for the sample sizes ($n = 10$) used in these tests. The

3-factor ANOVA found a significant Distance \times Edge \times Matrix interaction ($F_{4,162} = 2.98, P < 0.05$). The variation in population among the 3 matrix sizes at each move distance differed depending on whether an edge was present or not (Figure 3).

The different matrix sizes of 10000, 20000 and 40000 cells introduce a possible confounding effect: the different numbers of cells may be expected to result in differing numbers of herbivores as with more cells there are greater energy reserves available in the larger biomass of producers. We adjusted for this by dividing the herbivore numbers by two for matrix size 20000, and by four for matrix size 40000. The resulting ANOVA produced identical significant effects and interactions. This is an important result: the number of herbivores per cell rises as the matrix size increases.

The variances of the producer data were homogeneous (Cochran's $C = 0.15, P > 0.05$). The 3-factor ANOVA showed a significant Distance \times Matrix interaction ($F_{4,162} = 42.63, P < 0.001$) which arose because the variation in population among the 3 matrix sizes was not consistent across the 3 move distances (Figure 4). The populations for each of the matrix sizes were significantly different from one another at distances moved 1 and 2, but the populations of matrix sizes 1 and 2 were not significantly different at distance moved 3.

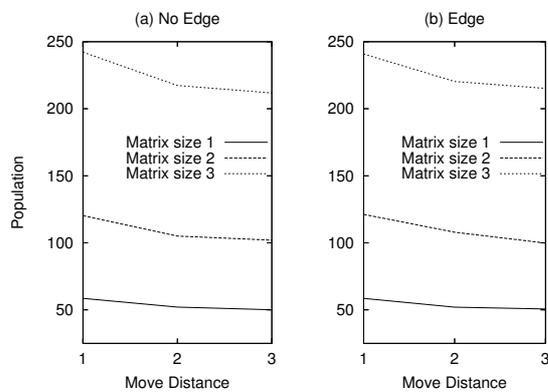


Figure 3. The herbivore three-way interaction

The statistical procedure found no main effect of edge, but found this factor to be significant in the three-way interaction for the herbivores. The effect of an edge, however, is evident when the populations are graphed over time or when the graphical display of the software is observed during a simulation. Figure 5 graphs the population levels with move distance $h_{md} = 3$ and the edge $g_e = 0$ and 1. The herbivore population changes with an edge present are not as smooth as without an edge. Watching the graphical display reveals a cycle of near population extinctions as a majority of herbivores move towards high populations of producers only to be trapped

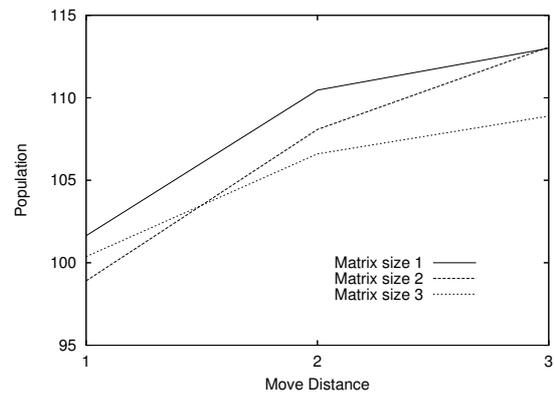


Figure 4. The producer two-way interaction

by the edge and die of starvation, as illustrated in Figure 6. Such large scale falls in population in a small number of time steps do not occur to the same extent when an edge is not present.

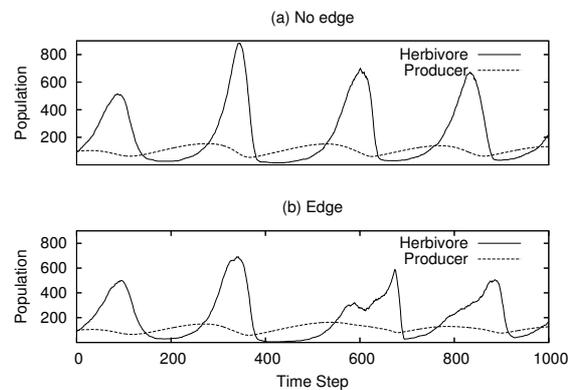


Figure 5. Edge effects with a move distance of 3

3.2 The effect of move distance

The herbivore maximum move distance ($h_{md} = 1$) has an effect on the model dynamics and the viability of the herbivore population which is not evident in the statistical analysis. If all other parameters are kept constant, an increasing h_{md} results in greater fluctuations in the herbivore population and an increased likelihood of extinction. Figure 7 illustrates herbivore maximum move distances $h_{md} = 2$ and 3, the only change in parameters from Figure 1. In figure 7b the herbivore population becomes extinct, which occurs in approximately 50% of cases with this set of parameters.

3.3 Simulations not reaching 1000 time steps

The means analyzed by the statistical procedure were only gathered from simulations which reached 1000 time steps. Table 1 lists unsuccessful simulations.

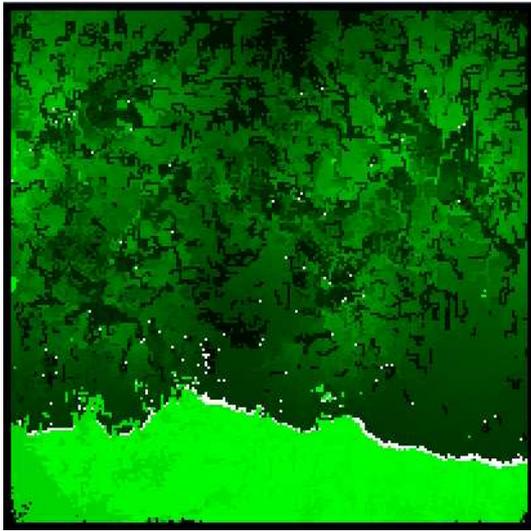


Figure 6. Edge effects with a move distance of 3, Matrix size 200×200 . The herbivores move towards high concentrations of producers, to be trapped against the edge at the bottom of the image.

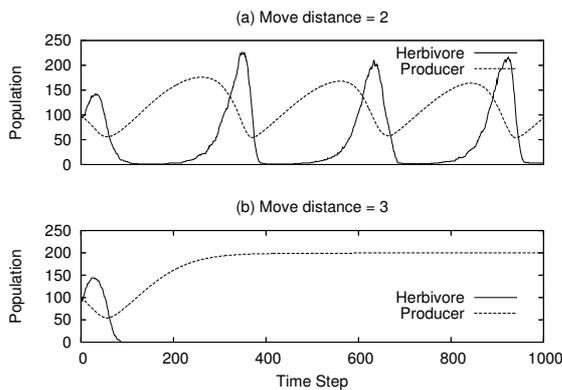


Figure 7. Move distances of 2 and 3 cells

Transient dynamics are observed at the start of a simulation, where population levels settle from the arbitrary starting levels. Steady-state dynamics are observed when the simulation is displaying relatively stable cycling populations.

Table 1. Herbivore extinctions before 10 successful simulations. TD: Transient dynamics; SSD: Steady-State Dynamics. Only those parameter sets resulting in extinctions are tabled.

Mv dist	Edge	Matrix size	Extinctions
3	0	1	TD:19, SSD:3
2	1	1	SSD:2
3	1	1	TD:7, SSD:3
3	0	2	SSD:3

4 DISCUSSION

The statistical procedure finds a significant interaction of matrix size (g_w and g_h), edge (g_e) and herbivore maximum move distance per time step (h_{md}) for the herbivore population, supporting the finding of Acosta (2002), and a significant interaction of matrix size and herbivore maximum move distance per time step for the producer population. The effects of an edge and of herbivore maximum move distance are also observed in the shape of the population graphs and in the behavior of the individuals in the model graphical output.

As the herbivore maximum move distance increases, the herbivore population tends to decrease, although the magnitude of this effect changes with the edge and matrix size for the herbivores—as the matrix size increases, the effect of move distance on the herbivore population decreases. Observing the model graphical output as the move distance increases, the herbivores move to areas of greater producer biomass more quickly, resulting in greater fluctuations in both populations. If the move distance is too great, the herbivore population is able to consume too much of the producer population in too few time steps and becomes extinct. This danger of extinction during steady state dynamics increases as the matrix size decreases. DeRoos *et al* (1991) also finds that limited mobility in a predator-prey model reduces population fluctuations, although average densities remain unaffected. These findings complement those of DeAngelis and Petersen (2001), McCauley *et al* (1993) and Wilson *et al* (1993), who find the opposite result for the producers: the higher the mobility of prey organisms, the more *stable* the prey populations.

The existence of an edge around the matrix affects the dynamics of the herbivore population. This effect is observed in the shape of the graph and the model graphical output, rather than in overall population means. When the matrix has an edge, the herbivores tend to become trapped against it and die out. The producers near the edge then start to recover biomass, and the remaining herbivores towards the centre of the matrix then start to move to the edges, repeating the cycle. This results in sharp drops in the herbivore population and almost instant changes of graph slope, as illustrated in Figure 5b.

The herbivore population per cell rises as the matrix size increases, although this effect varies with the edge and maximum herbivore move distance. The cycle of herbivores moving to areas rich in producer, consuming too much of the producer biomass and dying out, recovery of the consumer biomass and finally new herbivores moving in is observed in the model graphical output. This dynamic is amplified by a greater matrix area resulting in overall larger

mean herbivores per cell. These metapopulation dynamics are the most significant difference between this model and a non-spatial model of producer-consumer dynamics. They occur in this model despite the lack of explicitly defined patches. The metapopulation effect is reduced with increasing herbivore move distance, and with decreasing matrix size. If the matrix size is too small, persistence of the herbivores is impossible even if the producer p_r and p_K are increased (these results are not detailed in this paper but are observed consistently). Our finding that persistence is impossible in small homogeneous habitats but prolonged in larger more complex habitats with slow dispersal in which patches and barriers emerge is similar to the finding of Acosta (2002), who finds a similar effect interacting with dispersal dynamics. Donaldson and Nisbet (1999), Schneider (2001) and Wilson *et al* (1993) also report that the size of the space affects the stability of the model. This fundamental aspect of metapopulation theory emerges in these models from the individual interactions at a local level—these outcomes are not explicitly coded. They are a result of the transient patches and barriers which are evident in the graphical output of the model.

In this paper we have described a parsimonious model of producer-consumer interaction which involves space and the consequent local interactions between individuals. We investigate the effects of move distance, an edge and the size of the matrix and we find that these factors do affect the model dynamics, and should therefore be part of the description of similar models. A significant finding is the metapopulation-like behavior of local extinctions and recruitment of the consumer species due to the local interactions in space. The simple algorithm of the model does not specifically code this behavior. The importance of the graphical output of the model in addition to the population levels in observing and understanding the model dynamics is highlighted.

This research leads us in two directions: to test the significance of some or all of the model parameters not yet tested, and to compare more formally the behavior of this model with metapopulation theory. A combination of these directions poses the question: which of the parameters and which aspects of the model algorithm result in the behavior which resembles that of a metapopulation?

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