Spatial effects in an individual-based model of producer-herbivore interaction

W. J. Chivers, W. Gladstone and R. D. Herbert
Faculty of Science and Information Technology
University of Newcastle, Australia.
william.chivers@newcastle.edu.au

Abstract

In this paper we describe an individual-based model of the interaction between a producer and herbivore species. The interaction occurs in a two-dimensional matrix of individual cells. The producer organism grows in the cells and the herbivores move between the cells, towards areas of high concentration of producer. Herbivores may die of starvation or they may reproduce asexually. The model is not built to represent a specific existing system, but is a parsimonious generalized model of producer-herbivore interaction designed to test spatial effects.

While the model algorithm is kept simple—the herbivores have no learning or social behavior and have a minimal foraging strategy—the model displays some characteristics of real systems such as metapopulation behavior. We find significant effects on the herbivore and producer populations of the maximum move distance per step of the herbivores, the shape of the two-dimensional matrix, the quality of a corridor between patches habitable by the herbivores and edge effects with fuzzy edges. The behavior of the model is comparable with empirical observations found in the literature and we suggest that this simple model may be used to investigate the mechanism of these real effects.

1 Introduction

The use of individual-based modeling can facilitate understanding of a system and even decision-making in resource management (Grimm 1999, Judson 1994, Lomnicki 1999), and the use of individual-based modeling has grown in ecology in the last 2-3 decades (DeAngelis et al. 2001, Grimm 1999, Lomnicki 1999). Individual-based models may 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 may 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 whole populations. 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).

We have built a model to investigate the effects of space on a producer-herbivore system. The behaviour of the model is similar to that of real systems and of other models reported in the literature, for example the herbivore move distance effects are similar to those reported by DeAngelis and Petersen (2001), McCauley et al. (1993) and Wilson et al. (1993); the effects of matrix width and corridor quality are similar to the findings of Haddad (1999), Laurance and Laurance (1999) and
Bennett (1999) and edge effects in this model reflect those of Bennett (1999) and Zheng and Chen (2000). Our findings and those in the literature are more fully explored in Section 5.

2 Description of the spatial model

The spatial IBM described here simulates a producer and herbivore species in a two-dimensional space, and the energy flow between the two species. The individuals in the model are the cells of the matrix and the members of the herbivore species. The members of the producer species are not represented as individuals, but rather producer population is an attribute of individual cells. Members of the herbivore species are born, reproduce and possibly die of starvation. The producer species grows in each cell and is eaten by individual herbivores, which move between cells.

Cells and herbivores are created as discrete objects in the computer memory, each with a potentially unique state and resulting behavior. The attributes of each cell include the current population of producer, growth rate and maximum population of producer, and an integer number of herbivores. The attributes of the herbivores include a current position and resource level, the latter attribute representing the energy reserves carried by living organisms. The resource level units are not formally defined.

The producer species in each cell grows according to the logistic growth model of classical ecology. Each cell has an individual population of a producer organism, a growth rate for the producer and a maximum carrying capacity for the producer. The population of the producer organism in each cell is assigned randomly when the simulation is started and then grows towards the maximum capacity of the cell as the simulation progresses. The producer population of a cell is reduced when a herbivore eats the producer in the cell.

The resource level of each herbivore increases as the herbivore eats the producer in its current cell, and decreases with time, the cost of move distance between cells and as the herbivore reproduces. If a herbivore does not eat enough resources it will die and be removed from the simulation.

When the model is started a given number of herbivores are created and assigned to cells in the matrix randomly. In each time step of the simulation, each herbivore 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 producer population the herbivore will move to that cell. If two or more herbivores are present in a cell the resources are divided evenly, and this is taken into account when herbivores compare their neighboring cells when making a decision to move.

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 matrix in cells ($m_w = 100$ and $m_h = 100$)
- The existence or otherwise of an edge to the matrix ($g_e = 0$). No edge results in a torus or wrap-around effect.
- 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 ($h_p_0 = 100$)
- Initial resource level of the herbivores ($h_r_0 = 1000$)
- 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 herbivore organisms was arbitrary.
2.1 Model output

The model output includes:

1. The population of herbivore per time step and the mean producer population 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 dependent on the model parameter values, as the other figures in this paper illustrate.

2. A graphical display of each cell (Figure 2). The brightness of each cell indicates the cell producer population—the brighter the cell, the closer the population is to the maximum $p_K$ value in the matrix. The white cells indicate the presence of a herbivore. Figure 2 shows the matrix after 1000 time steps and is an intermediate state of the simulation graphed in Figure 1a. The dark areas have low producer population and are areas from which the herbivores have recently moved, and the brighter areas have had longer to recover from herbivore grazing and are the areas towards which the herbivores are moving. Note that after 1000 time steps the initial random distribution of producer population is no longer evident with the parameters sets used here.

2.2 Initialization

At the start of the simulation the cells are created in the computer memory in a matrix of $m_w$ width and $m_h$ height in cells. The matrix may or may not have an edge (ge) — 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 population 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 a constant initial resource level of $h_{r0}$.

2.3 Processing per cycle

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

1. Each cell producer population advances 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. These values are uniform across the matrix in the simulations reported here unless otherwise described.
2. Each herbivore compares the current cell producer population with the neighboring cells, and moves to the cell with the highest effective producer population. The number of neighboring cells considered depends on how far the herbivores may move, \( h_{md} \). The effective producer population of a cell is calculated using the actual producer population, the presence of other herbivores and the cost of moving to the cell, \( h_{mc} \times \text{movedistance} \). If other herbivores are present in a cell then the resources will be shared evenly, making the presence of more than one herbivore on a cell improbable with the parameter sets used in the simulations reported here. A level of stochasticity is involved—the final \( h_{ms} \) (herbivore move level of stochasticity) percentage of the effective producer population is randomly chosen before a decision to move is made, as the herbivores do not see the neighboring producer populations with 100% accuracy.

3. Each herbivore eats the given percentage of producer on the new cell, \( h_{pe} \). The cell producer population is reduced and the herbivore resource level is increased, taking into account the trophic efficiency of the herbivore \( h_{te} \). The latter parameter has values of 100% and 20% in the simulations reported here, as described in the text. If two or more herbivores are present in a cell, the cell producer population is still reduced by \( h_{pe} \) and the resources are shared evenly by the herbivores.

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 then do not have sufficient resources to live one more time step (herbivore resource level < \( h_{mt} \)) die of starvation and are removed from the simulation.

5. Any herbivores with sufficient resources to live one more time step and reproduce (herbivore resource level > \( h_{mt} + h_{tc} \)) 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 population of the cell when a decision to move is made.

3 Experimental design

3.1 Increasing move distance

The herbivore maximum move distance (\( h_{md} \)) is one cell per time step for the simulations illustrated in Figure 1. To test the effect of increasing \( h_{md} \) on population means the model was executed for 1000 steps in 100 separate executions for each of \( h_{md} = 1, 2 \) and 3. The data collected were the mean producer and herbivore populations for each of the 100 executions for each level of \( h_{md} \). The remaining parameter values were the same as listed in Section 2 except for the existence of an an edge in these simulations, which was added to avoid a torus effect. The 100 means for producer and herbivore populations for each \( h_{md} \) were then compared using a one-way ANOVA. The assumption of homogeneity of variance was tested using Cochran’s Test, and the multiple comparison procedure used was Student-Newman-Keuls.

3.2 Matrix shape

The default matrix shape is a square, 100 by 100 cells. To test the effect of matrix shape on the population means the model was executed for 1000 steps in 100 separate simulations for each of several different rectangular shapes, each with a total of 10 000 cells. The widths of the rectangular matrix were 6, 7, 8, 9, 10, 15, 20, 25, 32, 55, 77 and 100 cells. The mean populations are presented graphically against matrix width.

3.3 Corridor quality

A corridor between patches of cells which are able to sustain a herbivore population must itself be able to sustain a herbivore population for the time it takes the herbivores to cross. We compare corridors of differing widths, maximum producer population of each cell (\( p_K \)), and producer growth rate of each cell (\( p_r \)). The widths used were 4, 7 and 10 cells, the values of \( p_K \) were 1000, 1500 and 2000 and the values of \( p_r \) 0.025, 0.050 and 0.075.

Figure 3 illustrates corridors in differing states. Figure 3(a) shows the \( p_K \) values in the matrix, with
Figure 3: Corridor quality matrices. (a) Three levels of $p_K$, (b) producers are added to the upper patch and corridor, (c) and (d) herbivores move in the corridor. Cells containing a herbivore are white.

higher $p_K$ values illustrated in the lighter shades. The $p_K$ values here are 0 in the empty areas, 1000 in the upper patch and 2000 in the corridor of width four cells. Figure 3(b) illustrates a corridor of ten cells in width and the initial producer populations before the herbivores are added to the upper patch. In Figure 3(c) the herbivores attempt to cross to the end of the four cell corridor, and in Figure 3(d) the herbivores do reach the end of the corridor, ten cells in width in this case.

These simulations are initiated with a patch of $100 \times 25$ cells with the following changes to the parameter values listed in Section 2: an edge is used ($g_e = 1$), the maximum producer population of each cell $p_r = 0.025$, the maximum producer population of each cell $p_K = 1000$, the initial number of herbivores $h_{p0} = 25$ and the trophic efficiency of the herbivores $h_{te} = 20$. These parameters will sustain a population of just under 20 herbivores indefinitely in this patch. The herbivores are initially placed in this patch only, and have to make their own way into the corridor.

The data collected are the number of steps taken to cross the corridor in each simulation. The simulation stops when the corridor is crossed. For each of the 27 sets of parameter values ($3$ widths $\times 3p_K \times 3p_r$) the simulation is executed 100 times. These data are compared using a three-way ANOVA.

3.4 Edge definition

In the simulations described above involving patches of cells with differing parameters, the transition from one parameter value to another occurs over just one cell boundary. To test the effect of gradual changes of parameter values over boundaries with widths greater than one cell, patches are set up with increasingly fuzzy edges. The model is then executed for 1000 steps in 100 separate simulations using the parameters listed in Section 2.

The parameter which varies over the patch edge in these simulations is the maximum producer population of each cell ($p_K$). Matrices are set up with $p_K = 250, 500, 750$ and 1000 in concentric squares. The edge step widths tested were of 1, 2, 3, 5 and 10 cells for each $p_K$ value. Figure 4 illustrates these matrices with edge step widths of 1, 3, 5 and 10 cells. In all cases the total potential producer
Table 1: Means and standard deviations of herbivore populations by move distance.

<table>
<thead>
<tr>
<th>Move distance h&lt;sub&gt;md&lt;/sub&gt;</th>
<th>Mean ± SD</th>
<th>Percentage herbivore of extinctions population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>58.06 ± 1.39</td>
<td>0.0</td>
</tr>
<tr>
<td>2</td>
<td>51.41 ± 1.50</td>
<td>16.7</td>
</tr>
<tr>
<td>3</td>
<td>50.44 ± 2.18</td>
<td>62.4</td>
</tr>
</tbody>
</table>

population was equal to 3 000 000 units—the total possible producer population with no herbivores present. A matrix with a patch size of 55 × 55 cells, \( p_K = 1000 \) (which results in the same total possible producer population) and a discrete edge was also compared with the fuzzy edge matrices.

The data collected were six sets of 100 mean populations for the herbivores and producers. These were then separately compared using a one-way ANOVA.

4 Results

4.1 Increasing move distance

The variances of the producer and herbivore data were heterogeneous (Cochran’s \( C = 0.45, P < 0.05 \) and \( C = 0.53, P < 0.01 \) respectively). This is not a problem for the interpretation of the ANOVA results because the sample sizes are the same, and this analysis is robust to departures from the assumption of homogeneity of variances for the sample sizes \( (n = 100) \) used in these tests (Underwood 1997). The one-way ANOVA found significant differences between all move distances for producers \( (F_{2,297} = 616.52, P < 0.0001) \) and herbivores \( (F_{2,297} = 576.86, P < 0.0001) \), with an increasing producer population and a decreasing herbivore population as the herbivore maximum move distance \( (h_{md}) \) increases—the negative effect of increasing move distance on the mean herbivore population results in an increase in the mean producer population. Table 1 illustrates this effect for the herbivores—the producers are not listed as their population levels tend to mirror those of the herbivores.

A simulation stops if the herbivore population reaches zero. Table 1 also lists the percentage of unsuccessful attempts to reach 1000 steps. All attempts at \( h_{md} = 1 \) were successful, but as \( h_{md} \) increases so does the risk of extinction. The model was executed until 100 successful attempts were recorded for the statistical procedure.

4.2 Matrix shape

Figure 5 illustrates the mean populations for producers and herbivores plotted against the width of the matrix \( m_w \). As the matrix width falls below 20 the herbivore population falls, accompanied by a rise in the producer population.

Table 2 lists the percentage of unsuccessful simulations for each value of \( m_w \). For widths 8–100, every simulation reached 1000 steps, meaning that in none of these simulations did the herbivores become extinct. Below a width of 8 an increasing number of attempts were necessary in order to reach 100 simulations of 1000 steps.
Table 3: Three way ANOVA summary table of corridor quality simulations. Width of the corridor in cells ($m_w$), maximum producer population of each cell ($p_K$), producer growth rate of each cell ($p_r$).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m_w$</td>
<td>2</td>
<td>1360814</td>
<td>147.23</td>
<td>0.0000</td>
</tr>
<tr>
<td>$p_K$</td>
<td>2</td>
<td>1913309</td>
<td>288.95</td>
<td>0.0000</td>
</tr>
<tr>
<td>$p_r$</td>
<td>2</td>
<td>328903</td>
<td>35.59</td>
<td>0.0000</td>
</tr>
<tr>
<td>$m_w \times p_K$</td>
<td>4</td>
<td>728895</td>
<td>78.86</td>
<td>0.0000</td>
</tr>
<tr>
<td>$m_w \times p_r$</td>
<td>4</td>
<td>28567</td>
<td>3.09</td>
<td>0.0150</td>
</tr>
<tr>
<td>$p_K \times p_r$</td>
<td>4</td>
<td>176817</td>
<td>19.13</td>
<td>0.0000</td>
</tr>
<tr>
<td>$m_w \times p_K \times p_r$</td>
<td>8</td>
<td>17294</td>
<td>1.87</td>
<td>0.0604</td>
</tr>
<tr>
<td>Error</td>
<td>673</td>
<td>9242</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4: Means and standard deviations of the herbivore populations at different edge step widths.

<table>
<thead>
<tr>
<th>Edge step width</th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>17.98 ± 0.56</td>
</tr>
<tr>
<td>1</td>
<td>17.57 ± 0.47</td>
</tr>
<tr>
<td>2</td>
<td>16.31 ± 0.48</td>
</tr>
<tr>
<td>3</td>
<td>15.27 ± 0.45</td>
</tr>
<tr>
<td>5</td>
<td>12.42 ± 0.43</td>
</tr>
<tr>
<td>10</td>
<td>6.05 ± 0.39</td>
</tr>
</tbody>
</table>

4.4 Edge definition

The variances of the producer and herbivore data were heterogeneous (Cochran’s $C = 0.49$, $P < 0.01$ and $C = 0.24$, $P < 0.05$ respectively). Mean population sizes differ significantly between all edge step widths for producers ($F_{5,594} = 1722.47$, $P < 0.0001$) and herbivores ($F_{5,594} = 9281.19$, $P < 0.0001$).

Table 4 lists the mean herbivore population after 1000 steps for each edge step width.

5 Discussion

The graphical model output illustrated in Figure 2 highlights the behavior of the model in ways which are difficult to reproduce on static printed pages. The movement of the herbivores and the destruction and subsequent re-growth of the producers after the herbivores have moved on or suffered local extinctions resembles the local extinction-recruitment cycle described in metapopulation theory (see, for example, Krohne (2001) p126), albeit with transient patches instead of static patches.

This metapopulation behavior is particularly well highlighted as the maximum move distance of the herbivores $h_{md}$ is increased: the metapopulation effect of local extinction-recruitment decreases as the move distance increases and the herbivores are able to move around the matrix in fewer time steps, eventually being able to move to any cell in one time step as $h_{md}$ approaches the larger of the width $m_w$ and height $m_h$ of the matrix. At this stage the effects of space have been removed and individuals may interact across the two-dimensional space. We have reported here the
effect of $h_{md} = 1, 2, 3$—as $h_{md}$ increases the herbivore population decreases and the chances of herbivore extinction increase as the herbivore population peaks and troughs increase in amplitude. This increased amplitude of population fluctuations can be seen by comparing Figure 7(a) with Figure 1, where $h_{md} = 1$. In Figure 7(b) the herbivore population goes extinct with $h_{md} = 3$, which happened in 62.4% of simulations with this level of $h_{md}$. With lower maximum move distances per time step the transient patches of high producer population have more metapopulation effect, and the herbivore population fluctuations and chances of extinction are moderated.

The distance over which individuals may move in one time step is found to affect the stability of the populations in the models of DeAngelis and Petersen (2001), McCauley et al. (1993) and Wilson et al. (1993). These authors report that the higher the mobility of prey or producer organisms, the more stable the producer populations, the converse of our findings with herbivore populations. DeRoos et al. (1991) find that limited mobility in a predator-prey model reduces population fluctuations, although average densities remain unaffected.

In order to observe the behaviour of the model with higher values of $h_{md}$ it is necessary to significantly increase the resources available to the herbivores so that a population may be maintained. Figure 8 shows the graphical output after 1000 steps with $h_{md} = 10$ and the producer growth rate of each cell ($p_r = 0.1$). Although increasing the move distance decreases metapopulation spatial effects and could be assumed to result in a more homogeneous distribution of herbivores, observations of the graphical output show clumping of the herbivores as they are better able to move to the areas highest in producer population.

Decreasing the matrix width $m_w$ also puts pressure on the herbivore population below a consistent lower limit for each set of parameters. Figure 5 indicates that $m_w$ becomes a limiting factor below a value of 20, but above this value this parameter is not the only limiting factor, if it is one at all. As $m_w$ falls below 20 the herbivore population falls, accompanied by a rise in the producer population. Observing the graphical output it is apparent that the herbivores move in two dimensions in the matrix in order to consume sufficient resources. If $m_w$ falls below 20 cells for this set of parameters the herbivores are no longer able to consume sufficient resources in all four directions and the risk of extinction increases, as illustrated by Table 2.

The finding regarding matrix width has implications for corridors between patches of herbivore populations. Our findings regarding corridor quality suggest that we cannot talk of width effect independently of the maximum producer population of each cell ($p_K$), and producer growth rate of each

---

Figure 7: Populations over 1000 steps with move distances of 2 and 3 cells.

Figure 8: Graphical output with a move distance of 10 illustrating clumping behavior.
Table 5: Percentage of failed attempts (extinctions) to reach the end of the corridor in 1000 steps of the simulation at differing corridor widths.

<table>
<thead>
<tr>
<th>Width</th>
<th>Growth rate</th>
<th>Percentage of extinctions</th>
</tr>
</thead>
<tbody>
<tr>
<td>m_w</td>
<td>p_r</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0.025</td>
<td>49.49</td>
</tr>
<tr>
<td></td>
<td>0.050</td>
<td>13.04</td>
</tr>
<tr>
<td></td>
<td>0.075</td>
<td>1.00</td>
</tr>
<tr>
<td>7</td>
<td>0.025</td>
<td>6.54</td>
</tr>
<tr>
<td></td>
<td>0.050</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>0.075</td>
<td>0.00</td>
</tr>
<tr>
<td>10</td>
<td>0.025</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>0.050</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>0.075</td>
<td>0.00</td>
</tr>
</tbody>
</table>

cell \((p_r)\), and that these latter two parameters interact significantly. These statistical findings support our observations of the graphical output—reducing the corridor width reduces the ability of the herbivores to cross the corridor, and increasing one or both of \(p_K\) and \(p_r\) has a positive effect on the ability of the herbivores to cross the corridor. Table 5 indicates a lower limit to corridor width, below which the corridor quality must be raised above that of the patch in order for the herbivores to cross. Note that the corridor width lower limit is different to the matrix width lower limit discussed above because of the differing parameters used in these simulations. Corridor or matrix width becomes a limiting factor below a given value for each set of parameters, and this effect can be moderated by increasing the conditions in the corridor for the herbivores.

These findings are supported by Haddad (1999), who finds that the effectiveness of a corridor increases with corridor width, and that movement rates increase before leveling off as corridor width increases. Haddad also finds that corridor effects decrease as patch size increases, which will be investigated using this model in future research. Laurance and Laurance (1999) also find a lower width limit below which a corridor is not useful for several species of arboreal mammals, this lower threshold differing for the different species of mammals surveyed, and Sieving et al. (2000) find similar results in understorey birds in fragmented forest. Bennett (1999) states that increasing the width of corridors is one of the most effective options for increasing corridor function for several reasons including the resulting reduction of edge effect.

The results of our investigation of edge definition in this model indicate a significant edge effect on the herbivore population levels—all the edge step widths tested resulted in herbivore populations significantly different from each other, the herbivore
population falling as the width of the edge rises. Edge step widths of 0, 1, 2, 3 and 5 cells resulted in simulations reaching 1000 steps without the herbivores becoming extinct. An edge step width of 10 did result in herbivore extinction in approximately 42% of cases. Figures 9 and 10 illustrate a patch with edge step width of 10 cells. The herbivores are concentrated in the centre where the maximum producer population of each cell ($p_K = 1000$) is highest. In the lower right of this central area in Figure 9 the trace of a herbivore is seen—this herbivore died of starvation in this area in which the $p_K$ value is 500. In simulations resulting in extinctions, all the herbivores ventured out into areas of low $p_K$ and died of starvation. Although all these patches with differing edge step widths contain the same total potential producer population, increasing the edge step width, or edge effect, effectively removes producer resources from the reach of the herbivores and so lowers their numbers. An edge step width above a threshold value results in herbivore extinctions.

These findings are supported by Bennett (1999) and Zheng and Chen (2000). Both find greater effects on populations with increasing edge effects, or width of edges. Large edge effects result from the edges extending further into the effective patches, decreasing the usable size of the patch. These effects interact with the size of the patch and the level of contrast between inside and outside the patch. The latter two findings will be tested in this model in future research.

6 Concluding remarks

We have presented a parsimonious individual-based model of producer-herbivore behavior in a two-dimensional space. We find that the model algorithm replicates several behaviors of real systems as reported in the literature. These behaviors include metapopulation local extinction-recruitment cycles and a sensitivity to herbivore move distance, corridor width and quality and edge width effects. We find that some of the model parameters display lower or upper thresholds beyond which they become the limiting factor for the herbivore population, and are often the cause of herbivore extinctions. We suggest that in cases where the behavior of this model is similar to empirical studies of real systems, the algorithm of the model may contribute to mechanistic understanding of the real system.

References


