



Probabilistic cellular automaton: model and application to vegetation dynamics

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Abstract: We offer a new framework for cellular automata modeling to describe and predict vegetation dynamics. The model can simulate community composition and spatial patterns by following a set of probabilistic rules generated from empirical data on plant neighborhood dynamics. Based on published data (Lippe et al. 1985), we apply the model to simulate Atlantic Heathland vegetation dynamics and compare the outcome with previous models described for the same site. Our results indicate reasonable agreement between simulated and real data and with previous models based on Markov chains or on mechanistic spatial simulation, and that spatial models may detect similar species dynamics given by non-spatial models. We found evidence that a directional vegetation dynamics may not correspond to a monotonic increase in community spatial organization. The model framework may as well be applied to other systems.

Abbreviation: CA - Cellular automaton or cellular automata.

Introduction

Markov models have been used in ecology as a tool for describing and predicting vegetation dynamics (Lippe et al. 1985, Orlóci et al. 1993, Baltzer 2000). We refer to Feller (1968) for an exposition of Markov mathematics. Basically, the community state at a future time point $t+1$, given by a vector \mathbf{X}_{t+1} of population quantities, is determined by the community state \mathbf{X}_t at time t multiplied by a known transition matrix \mathbf{P} whose rows add to unity. Each element p_{hi} of this matrix indicates the rate at which population h loses space to population i from time t to $t+1$. A controversial question about the applicability of pure Markov chains in ecology is founded on the basic assumption that the last state record of the system corresponds to a stable state that comes about in the Markov process. Most natural ecosystems continuously change according to variations in the biotic and abiotic environment, and the behavior of organisms reflects these changes (Lippe et al. 1985 and references therein). This fact restricts the predictive power of the Markov chain approach and calls for adjustments in the conceptualization of the model.

Baker (1989) shows cases where different transition matrices are applied to the same data; in this case the

choice of the transition matrix to be used must be modeled. Another approach consists in changing the transition matrix probabilities and making them dependent on exogenous variables such as climate conditions and/or on endogenous variables such as composition; thus the transition matrix is unstable and changes according to these variables. An additional limitation in the Markov chain approach resides in the characterization of the transitory communities between the beginning and the end of the simulation, sometimes very unrealistic if compared to the data collected in the field; this effect is caused by the smoothing of transitions due to the nature of the Markov chain (Baltzer 2000).

Previous studies with the Markov chain in vegetation dynamics (Orlóci and Orlóci 1988, Anand and Orlóci 1997, Orlóci 2000, 2001, Orlóci et al. 2002 and references therein) have revealed the chaotic nature of transition probabilities under natural conditions and have shown that a randomly perturbed Markov chain can give a closer approximation of the natural process than the pure Markov chain.

The aforementioned limitations, however, should not make Markov models unworthy. Baltzer (2000) obtained good results by adjusting Markov chains and concluded that annually measured data give better results than quar-

terly measured data, and that microdata (those data derived from observed transitions on objects such as points) reduce the adjusting error level when compared to macrodata (those data which represent the relative state frequencies – such as species).

De Smidt collected a series of vegetation cover data from 1963 to 1981 on grazed Atlantic Heathland in The Netherlands. The data, published as percentage cover of major species in Lippe et al. (1985), were used in Markov chain modeling by different authors. Lippe et al. (1985) computed transition probabilities from presence-absence of species observed at a large number of points over the 19 years. They did not find a stationary Markov chain due to perturbations (such as climate and occasional insect plagues), strong temporal tendencies following these perturbations, and to the existence of strong spatial interactions. However, with the same data set Orlóci et al. (1993) successfully fit a stationary Markov chain using a new approach that statistically extracted the transition probabilities from species cover percentages. Lippe et al. (1985) obtained the transition matrix directly from points whereas Orlóci et al. (1993) used inference that did not consider the spatially distributed point arrangement that Lippe et al. (1985) have used. Therefore, diverging results were obtained depending on the method used.

With the same De Smidt data (Lippe et al. 1985), Prentice et al. (1987) performed simulations with a previously created spatial model and with parameters obtained from observations on the study area. They also varied the model parameters and observations on the succeeding changes in the community composition could predict possible scenarios resulting from these changes. Based on Prentice et al.'s (1987) results, we can conclude that spatial models could perform as well as non-spatial models and may detect similar species dynamics given by non-spatial models.

Cellular automata (CA) models have been successfully used to simulate complex systems (Wolfram 1983, 2002). A CA model is applicable whenever the system may be discretely represented and described through similar units that interact with their adjacencies. Possible applications lie in the field of plant ecology. Cells (units of the CA) may represent a community with their populations (Moloney et al. 1992), living plants (when occupied) and empty places (without plants) (Jeltsch et al. 1996, Molofsky 1994, Van Hulst 1997, Gassmann et al. 2000) or even plant parts (Colasanti and Hunt 1997). There may be more than one plant species in the simulation; in this case, every species behave according to its own rule set. Through these simulations it is possible to study the system's dynamics (syndynamics, where succession is a par-

ticular case). Perturbations can be applied to verify the effect on the CA configuration in the overall simulation result (Molofsky 1994).

In this paper, we develop a probabilistic CA model to simulate vegetation dynamics based on De Smidt data (Lippe et al. 1985). The model has some resemblance to a Markov chain model with variable transition probabilities given according to the composition. We compare the simulation results with the ones obtained by previous models applied to the same data.

Methods

The model

According to Wolfram (1983), a CA consists of a regular uniform lattice (*array* if in one dimension or *grid* if in two dimensions) of *cells*. The borders of the lattice can be filled with zero values or they may repeat the values in the opposite cells. In the first case, the lattice is denoted as an island; in the latter, it is denoted as a *torus* (or a toroidal lattice). Each cell at a given time point is described by the states of one or more variables. A CA evolves at discrete time steps, with the value of a variable at a cell being affected by the values of the variables at cells in its *neighborhood* on the previous time point. The neighborhood is generally taken to be the adjacent cells around a given cell. The variables at each cell are updated at each time point, based on the values of its neighborhood in the preceding time point, and according to a set of *local rules*. These rules may be deterministic or may involve probabilistic elements or noise (Wolfram 1983). The simplest probabilistic rule is that the value of a cell is to be reversed with a given probability. Ermentrout and Edelstein-Keshet (1993) explained how cellular automata can represent complex differential equations in an attempt to model complex physical and biological phenomena through computer simulations.

In our model, a toroidal grid with 1025 cells arranged in 25 lines \times 41 columns was used to simulate the vegetation dynamics on the basis of De Smidt's data, published in Lippe et al. (1985), from grazed Atlantic Heathland in The Netherlands. These are the same dimensions of De Smidt data points in the study site. At a given point in time each cell is occupied with one of 9 possible states (a plant species or bare ground).

A reason presented by Lippe et al. (1985) for their unsuccessful Markov chain fitting was the existence of strong spatial interactions. These interactions were modeled by Lippe et al. (1985) based on the neighborhood frequency of a given state around every sampling point. This was possible since the data consisted of presence or ab-

sence of species or bare ground in each point in a grid of 1025 sampling points covering a 12 by 20 m plot. Separate linear equations were obtained for each possible state i based on the frequency (maximum 8) of state i around every point and whether state i was already present or not at the point. Thus, a total of 18 equations were fitted. The parameters a and b for the linear equations $P_i = a + bx_i$ for each point state are given in Table 1, where x_i is the neighborhood frequency for state i and P_i is a value between 0 and 1 defining the occupation probability of a point by state i . Based on these equations, we developed a spatial model according to the following rules:

- (1) A cell occupied with a given state h will remain unchanged if a random number drawn in the range 0 to 1 is not larger than the corresponding P_h computed for the cell under this condition (state h present).
- (2) If rule (1) does not hold (the random number is larger than P_h), then the other $q-1$ possible states $j \neq h$ will have the opportunity to occupy the cell. For that, an occupation probability P_j is calculated for every other state $j \neq h$ that is absent in the cell (based on the cell's neighborhood). The m probabilities $P_j > 0$, after adjusted to unit sum and arranged side by side (P_1, P_2, \dots, P_m), define a sequence of intervals

$$(0, P_1], (P_1, P_1+P_2], \dots, \left(\sum_{j=1}^{m-1} P_j, 1\right].$$

A second random number in the interval (0, 1] is drawn which will belong to one of these intervals, defining the state $j \neq h$ to which the cell will change. The interval may include its border limit (shown with a bracket) or exclude it (shown with a parenthesis). The order in which the probabilities P_j are arranged is irrelevant for the definition of the intervals. In case $q = 2$ or $m = 1$, the corresponding state $j \neq h$ will occupy the cell.

In summary, on the basis of different probabilities generated from neighborhood frequencies, the algorithm allows the persistence of the state present in the cell or its changing into the other possible states. The spatial model is a CA because the cell behavior, which is probabilistic, is defined by rules that are variable according to the cell state and to its neighborhood.

The equations for *Juncus squarrosus* (when present) and for "other species" (when absent) may generate negative values (see Table 1). This effect is likely due to a small sample (for *Juncus squarrosus*) and to a high variance (for "other species", which form a heterogeneous

Table 1. Parameters for probability determinations (from Lippe et al. 1985).

Code	State	Presence	Parameters	
			b	a
1	Bare Ground	Absent	0.036	0.044
1	Bare Ground	Present	0.045	0.279
2	<i>Empetrum nigrum</i>	Absent	0.076	0.066
2	<i>Empetrum nigrum</i>	Present	0.040	0.584
3	<i>Calluna vulgaris</i>	Absent	0.054	0.051
3	<i>Calluna vulgaris</i>	Present	0.076	0.321
4	<i>Erica tetralix</i>	Absent	0.040	0.028
4	<i>Erica tetralix</i>	Present	0.060	0.259
5	<i>Molinia caerulea</i>	Absent	0.026	0.002
5	<i>Molinia caerulea</i>	Present	0.051	0.324
6	<i>Carex pilulifera</i>	Absent	0.015	0.008
6	<i>Carex pilulifera</i>	Present	0.100	0.107
7	<i>Juncus squarrosus</i>	Absent	0.023	0.002
7	<i>Juncus squarrosus</i>	Present	-0.294	0.294
8	<i>Rumex acetosella</i>	Absent	0.040	0.002
8	<i>Rumex acetosella</i>	Present	0.052	0.106
9	Other species	Absent	-0.010	0.030
9	Other species	Present	0.122	0.046

group formed by several species with very low cover). To minimize the distortion a zero probability was assigned to these states when P_i was negative.

The initial arrangement of the states in the grid was randomly created according to the initial proportions (year 1963) of the reference work. The simulation routines were programmed in Visual C++ 4.0 and implemented as a Windows application program available at <http://ecoqua.ecologia.ufrgs.br/~atlanzer>. For obtaining final grid configurations, simulations were also performed in Microsoft Excel for Windows with routines programmed in Visual Basic. The time step for each iteration was one year and thus 18 iterations of the model were needed to cover the 1963-1981 interval in one run. In order to get a sample of the possible solutions a total of 100 runs were executed.

Data analysis

For every state, the percentage cover was computed for the whole cell grid using the data generated in each simulation. The maximum and minimum percentage cover at each time point for the 100 simulation runs were taken as limits, which were compared to the observed percentage cover (Lippe et al. 1985) and to the results obtained by Prentice et al.'s (1987) model. Principal coordinates analysis based on Euclidean distances was

performed to compare the results of our model, Lippe et al. (1985) data and Orlóci et al. (1993) Markov relevés.

The final grid configuration was analyzed to test whether it was random or not. Patterns of neighborhood based on the frequencies of the possible states were extracted from the simulation grids at the initial and final time point (18th year). A possible neighborhood pattern is, for instance, a cell occupied by state 1 and surrounded by five cells with state 2 and three cells with state 3 irrespective of their arrangement, and in the grid this kind of pattern will be found with a given frequency. A chi-square statistic was calculated for each run of the model, for the initial (χ^2_{initial}) and final (χ^2_{final}) configuration grid, based on the frequency distribution of observed patterns and expected uniform frequency distribution. The expected distribution for the computation of the chi-square in any of the cases was determined based on the assumption of equal frequencies for all possible patterns. A chi-square statistic was also calculated for each of 100 random grid configurations created with the states having equal expected frequencies; then an average chi-square was computed (χ^2_{RND}). For each CA model simulation χ^2_{final} was compared to χ^2_{initial} and to χ^2_{RND} . Based on 100 simulations, the probabilities $P(\chi^2_{\text{initial}} \geq \chi^2_{\text{final}})$ and $P(\chi^2_{\text{RND}} \geq$

$\chi^2_{\text{final}})$ were calculated. A small probability was interpreted as an evidence of spatial organization.

From probability theory, the total number of possible patterns is

$$pC_{n+p-1}^n = p \frac{(n+p-1)!}{n!(p-1)!}$$

where n is the total number of cells considered in the neighborhood (8) and p is the number of states in the CA (9). Because the total number of possible patterns (115830) was larger than the number of neighborhoods (1025; which is equal to the total number of cells) the number of neighborhoods (number of cells in the grid) was taken as the maximum number of possible patterns.

Results

A typical final simulation grid is displayed in Fig. 1. We can see that states other than 2 (*Empetrum nigrum*) tend to be clumped in groups rather than scattered in the grid. This could be interpreted as a strategy to survive in a matrix dominated by a single state. Forming aggregates the other states reduce the probability of being replaced by the dominant state (2). This pattern resembles the theoretical description given by Vichniac (1984) for one class of voting rules, which are based on the ‘popularity’ of the

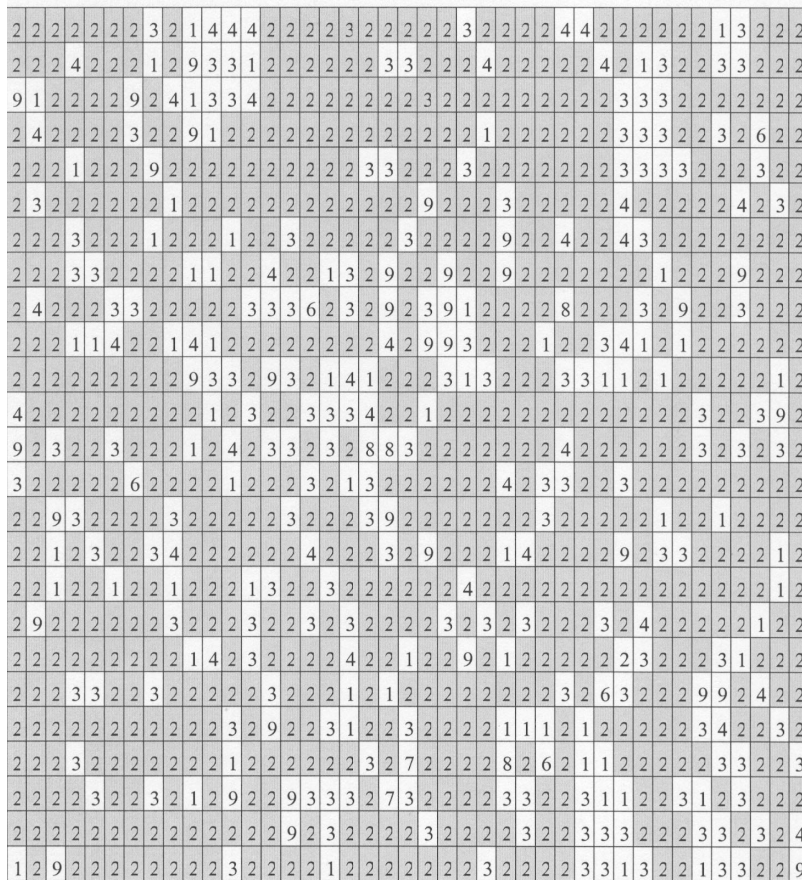


Figure 1. Final grid configuration (year 1981). The most frequent state (2, for *Empetrum nigrum*) is in dark gray. The occurrence of Vichniac’s “surviving minority islands” is apparent in the grid area.

Table 2. Pattern analysis of grid configurations after 10 CA runs. The number of neighborhood patterns decreases from the initial to the final configuration.

Run #	Number of patterns		Chi-Square	
	Initial	Final	Initial	Final
1	363	273	1129.07	1377.06
2	351	290	1162.73	1340.24
3	368	290	1124.23	1341.44
4	360	258	1136.69	1397.92
5	346	313	1176.40	1307.51
6	336	257	1189.33	1405.32
7	372	279	1123.68	1365.93
8	337	261	1207.35	1398.04
9	348	240	1161.43	1446.19
10	320	256	1222.71	1414.32

states in the neighborhood and lead to the occurrence of “surviving minority islands”. However, in our simulations this kind of behavior did not occur in the entire grid area; there were cases where the “surviving minority islands” still occurred but in a less extent.

Pattern analysis of the final grid configuration in Fig. 1 revealed the occurrence of 257 different neighborhood patterns whose frequency distribution is shown in Fig. 2. Other initial and final grid configurations were also analyzed and the number of neighborhood patterns with their corresponding chi-square is in Table 2. We found a negative linear correlation between the number of neighborhood patterns and the chi-square in the simulations, as depicted in Fig. 3, indicating that the chi-square value could

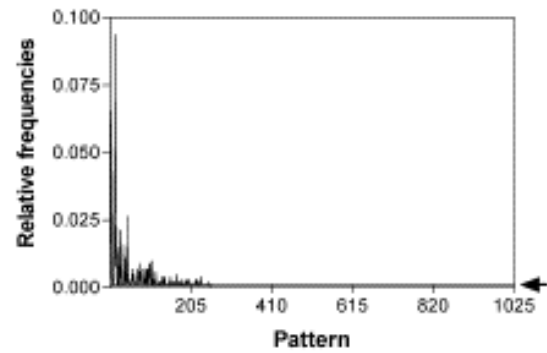


Figure 2. Relative frequencies of detected neighborhood patterns in a final grid configuration (year 1981) simulated by the CA model (Fig. 1). The arrow indicates expected frequency under uniform distribution corresponding to a random grid. Note that the maximum number of neighborhood patterns (1025) was taken as the grid size and it is smaller than the total number of possible neighborhood patterns. Also, the number of detected neighborhood patterns (257) was much smaller than this maximum.

be a good predictor of organization in the grid. It seems that starting from a disordered initial configuration, as spatial organization occurs in the CA simulation the chi-square tends to increase and the number of neighborhood patterns to decrease with time. As a matter of fact, as seen in the dynamics of a single run (Fig. 4), the number of patterns initially tended to increase and then to decrease after a few iterations. The chi-square value changed accordingly, decreasing and then increasing beyond the initial value. Thus, spatial organization did not increase monotonically over time.

The test for spatial organization, based on 100 CA runs, indicated high consistency with a non-random spatial arrangement (Table 3). There was also evidence of

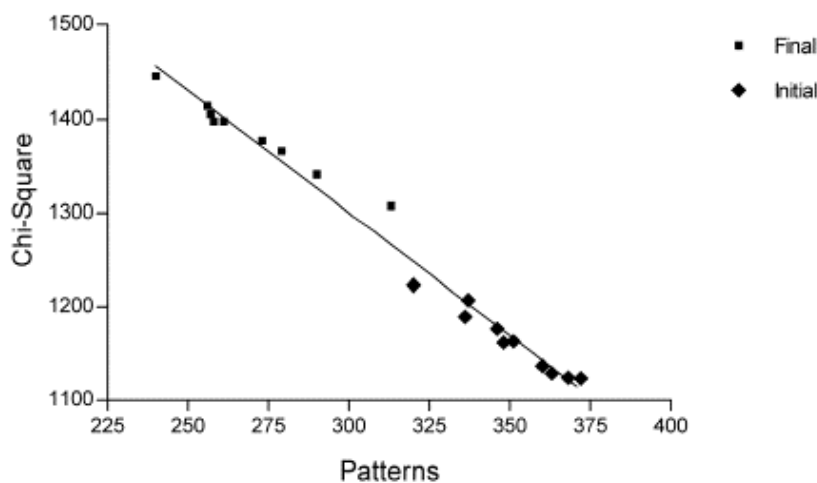


Figure 3. Relationship between the number of detected neighborhood patterns in initial and final grid configurations with their corresponding chi-square values ($r^2=0.9847$). The configurations were generated by 10 runs of the CA model, from initial random configuration with states frequencies given by year 1963 in Lippe et al. (1985).

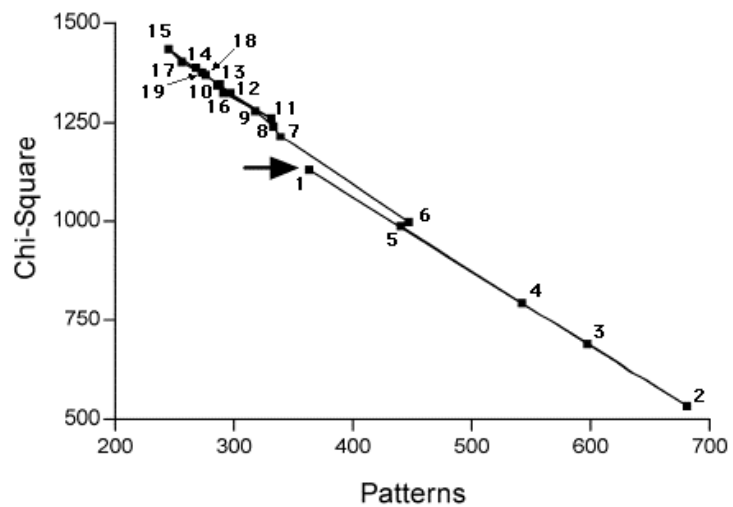
Table 3. Probabilities for the chi-square statistics generated after 100 runs of the CA model. The average chi-square for random grid configurations (χ^2_{RND}) with equal frequencies for the states was 16.76.

Comparison	Probability
$P(\chi^2_{initial} \geq \chi^2_{final})$	0.01
$P(\chi^2_{RND} \geq \chi^2_{final})$	0

Table 4. Euclidean distances between observed relevés (Lippe et al. 1985) and relevés simulated by the cellular automata (CA) model and by Orlóci et al. (1993) Markov chain model. The two models did not differ significantly ($P = 0.71$) in terms of agreement with observed data, based on analysis of variance with randomization test taking years as blocks (Pillar and Orlóci 1996).

Year	Observed x CA	Observed x Markov
1963	185.51	0.00
1964	350.35	108.40
1965	637.02	219.34
1966	216.02	414.64
1967	135.00	157.81
1968	137.10	943.03
1969	219.23	996.42
1970	166.71	104.76
1971	258.78	153.10
1972	188.92	365.32
1973	120.51	117.41
1974	383.39	161.24
1975	274.01	213.07
1976	391.28	251.16
1977	859.37	339.15
1978	359.67	480.89
1979	152.73	289.73
1980	151.84	493.84
1981	173.93	118.43
Average	282.18	311.99

Figure 4. Evolution of a single run, as measured by chi-square and number of neighborhood patterns. The initial configuration, pointed by the arrow, was more ordered than the subsequent grid configurations (all sequentially indicated with numbers up to 18 years) and only after a few iterations the chi-square value increase beyond the initial value.



spatial organization when final and initial configurations were compared.

Fig. 5 depicts simulation results with the CA model in terms of cover percentages. There was overall agreement between simulated and observed (Lippe et al. 1985) data for bare ground and most of the species. For *Calluna vulgaris*, the CA model tended to underestimate while for *Empetrum nigrum* and for “other species” it overestimated the cover. *Empetrum nigrum* shows an irregular behavior, probably due to environmental disturbances, not considered by the CA model. Overall, the CA model mimics reality in a simple but robust way.

In Prentice et al. (1987), the minimum and maximum values in their range included almost entirely the observed cover in the field (not shown, see Prentice et al. 1987). The differences between the two models are mainly in the pattern of maximum and minimum cover values, which were smoother in the CA model.

Fig. 6 depicts the ordination results with the relevés simulated by the CA model together with the observed data of Lippe et al. (1985) and the Markov relevés of Orlóci et al. (1993). By visual inspection, the CA simulated process of vegetation dynamics was clearly directional (Fig. 6a). It appears the Markov chain model had a better agreement with the observed data compared to the CA model agreement but an objective measure of agreement indicated that the two models did not differ significantly (Table 4). The agreement was measured by Euclidean distances for each year using the two ordination axes, which accounted for almost 99% of total variation.

Discussion

The results of the CA model show a trend within a range rather than an exact population amount in a given

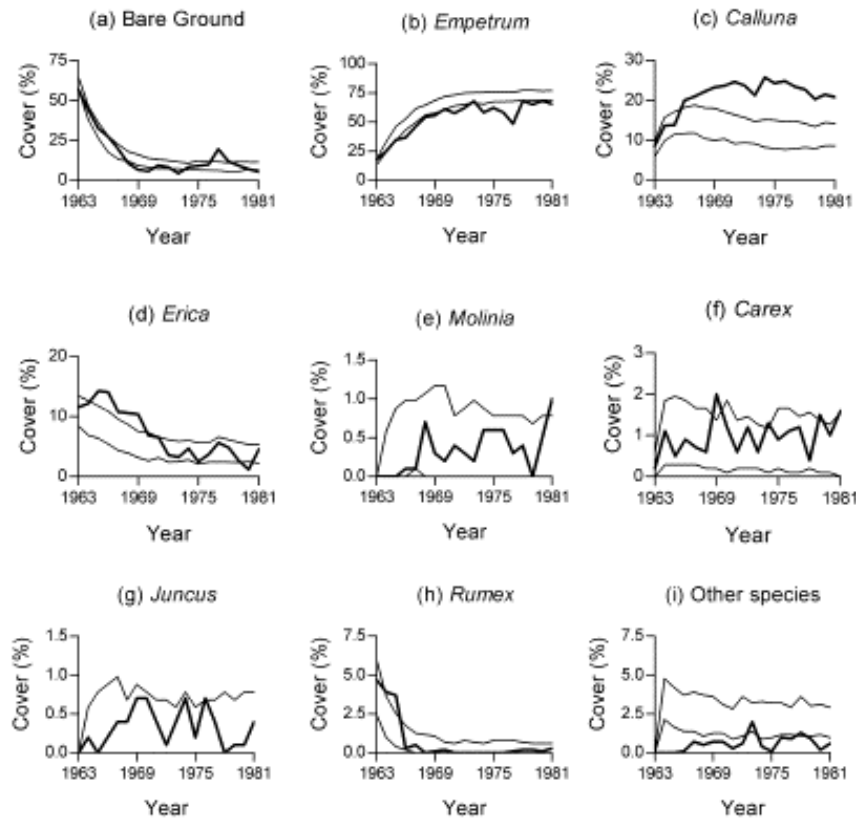


Figure 5. Results of simulations using the probabilistic cellular automata model for the cell states. The maximum and minimum cover percentages in 100 simulation runs are the thin lines and the observed ones (De Smidt data from Lippe et al. 1985) are the thick lines. For every state, the percentage cover was computed for the whole cell grid using the data generated in each simulation.

moment in time contrary to what would be expected in a Markov chain model. Pure Markov chains reach, after several iterations, a final steady composition, which can be represented as a point in a p -dimensional space where p is the number of states. In contrast, the CA and the Prentice et al. (1987) models reach a region of this p -dimensional space, as expected by the range of possible outcomes.

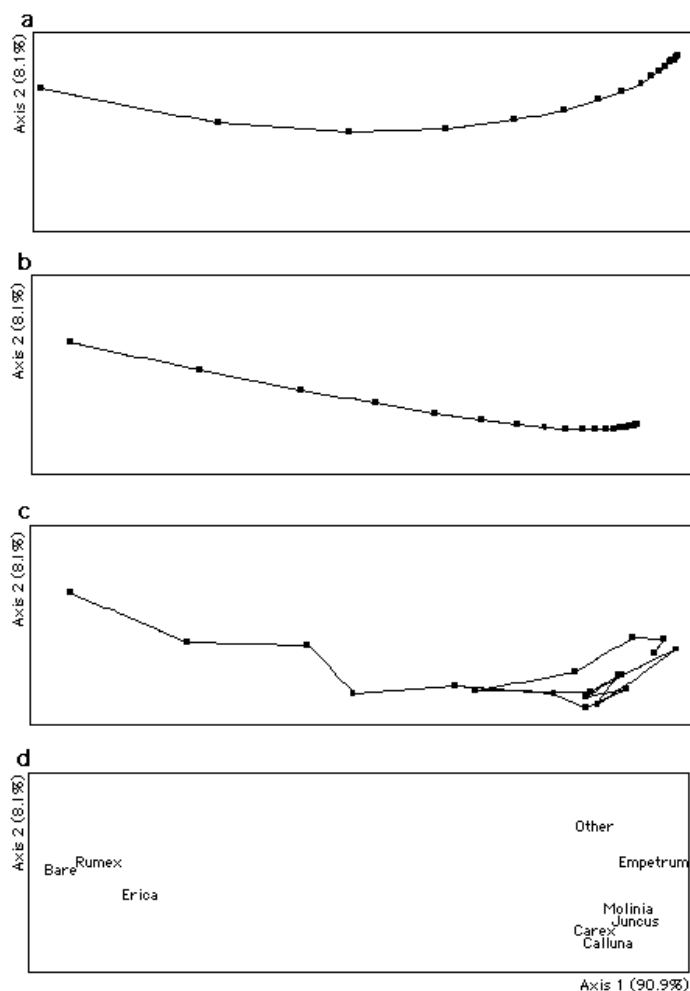
Probabilistic CA are reversible, contrary to the deterministic elementary CA described by Wolfram (1983). In our results, as expected from the random nature of the algorithm, the CA never reached the same final composition. Instead, it was variable around a region in the p -dimensional space. Ecosystem stability depends on external and internal factors and perturbations frequently lead ecosystems to different equilibrium states (Holling 1973). Natural and anthropogenic disturbances may occur occasionally, implying that the same final composition is not achieved after a perturbation. Therefore, probabilistic CA may be useful to model the dynamics of ecosystems based

on the argument that a stable final configuration is not reached. In the CA model several runs are required to find a range of possible outcomes.

It is likely that every possible configuration is reached in the evolution of a probabilistic CA, since the design progressively destroys structures, which would not happen if the rules were deterministic (Wolfram 1983). The destruction of structures does not generate random patterns because the occupation probability is not always 0.5, which is the value proposed by Wolfram (1983) for unpredictable behavior. Though with a small probability, the initial configuration – understood as any grid configuration from which we start examining an ecosystem – may be reached again in the evolution of the CA. This may occur in nature if some factor leads the ecosystem to a previous composition and arrangement.

The probabilistic nature of the present CA model tends to smooth the transitions in composition between transient communities as Markov chain models also do.

Figure 6. Principal coordinates ordination based on Euclidean distances for (a) relevés simulated by the cellular automata model, (b) Markov relevés from Orlóci et al. (1993), (c) observed relevés from Lippe et al. (1985). In graphs a-c the relevés are connected from 1963 to 1981 rightward. In (d) the states are plotted according to their correlation coefficient with the ordination axes after rescaling. The scatter diagrams refer to the same ordination; they are presented separated for better visualization.



Nevertheless, whereas the trajectory in a Markov chain is repeatable for the same initial composition and transition matrix, CA model outcomes vary within a range of possible values as already seen in Fig. 5. The range is smaller if compared to the results of the model in Prentice et al. (1987), though in some cases the CA model was not accurate. Yet, the CA model is simpler than the model described in Prentice et al. (1987). While in Prentice et al. (1987) the model requires information about the parameters establishment rate, maximum diameter and height, growth constant and maximum radial increment for every plant species, the CA model defines probabilistic rules based on empirical linear equations generated from neighborhood frequencies for every species in the raw data.

We point out the possibility of an inadequate use of linear equations as given by Lippe et al. (1985) to explain the spatial interactions. The effects of neighbors are likely to be non-linear, as demonstrated by Goldberg (1987). Improving the fitness of the equations would probably result in a better model performance, reducing the disagree-

ments shown in Fig. 5 for some states, especially for *Calluna vulgaris*.

The CA model we described performed as satisfactory as the Markov chain model described in Orlóci et al. (1993) for the simulation of population quantities. Nonetheless the CA model simulated spatial patterns, which may be useful to study population strategies in the occupation of space. Furthermore, a directional process in the vegetation dynamics may not correspond to a monotonic increase in community spatial organization. The comparisons with previous models applied on the study area reinforce the initial conclusion, we drew from Prentice et al. (1987) results, that spatial models may perform as well as non-spatial models detecting similar species dynamics, with the advantage of generating spatial patterns. Also, there is no reason to believe the CA model framework we present could not be applicable to simulate the dynamics of other systems as well, provided the same kind of description by components is given.

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