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Cellular automaton models of interspecific competition for space — the effect of pattern on process

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Summary

1. Species in plant communities generally shown an aggregated distribution at one or more spatial scales. This, and the fact that competition between sessile organisms occurs chiefly between neighbours, suggests that the spatial configuration of plants should affect the process and outcome of interspecific competition.
2. Cellular automaton models were constructed to simulate the competitive interaction of five grass species, *Agrostis stolonifera*, *Holcus lanatus*, *Cynosurus cristatus*, *Poa trivialis* and *Lolium perenne*, based on experimentally determined rates of invasion.
3. A model with a random initial starting arrangement showed a very rapid loss of species compared to initial arrangements in which species occurred in monospecific bands.
4. Different arrangements of monospecific bands produced quite different results from each other, depending only upon the initial juxtaposition of species in the model community. Non-linear dynamics, with transitory increases followed by decreases in species' abundance, were observed with some starting arrangements. Community change followed trajectories that could not be deduced in any simple manner from a knowledge of pairwise interactions alone. These results suggest that the spatial pattern and configuration of competing species may be just as important as the density and frequency of competitors in determining the outcome.

Key-words: cellular automata, clonal growth, neighbourhood, non-linear dynamics, spatial pattern

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Introduction

Plants and other sessile organisms must secure space in order to obtain access to resources (Harper 1985). When competing organisms are of similar stature (e.g. grassland plants or encrusting modular animals such as sponges and bryozoans), competition occurs primarily between immediate neighbours along the boundaries between them. Recognition of the importance of neighbourhood competition in plant populations has led to the application of intraspecific and interspecific neighbourhood models of competition (e.g. Mithen, Harper & Weiner 1984; Pacala 1986; Pacala & Silander 1990), but these have been aimed mainly at predicting individual performance and population dynamics. Although the models are

spatial, they do not address the important general question of how spatial pattern itself affects process.

Studies of pattern in plant communities have shown that most species are clumped at one or more scales (Greig-Smith 1979), but the consequences of aggregation for vegetation dynamics have scarcely been investigated. Schmid & Harper (1985) grew *Bellis perennis* and *Prunella vulgaris* in competition with one another at a range of densities and spatial arrangements, but found that spatial pattern had no effect on the outcome of competition because, they suggested, *P. vulgaris* was very mobile. Van Andel & Nelissen (1981), Marshall (1990) and Thórhallsdóttir (1990) grew numbers of herb species in hexagonal plots in which species competed with neighbours along common boundaries. These experiments, and others by Harper (1961) and Van Andel & Dueck (1981) that compared the results of interspecific competition in treatments with dif-

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ferent sowing patterns, indicate that the spatial arrangement of competing species can affect their performance, but the consequences of this at the community level have not been fully addressed.

The inclusion of space in competition models introduces two new factors that have been insufficiently explored in model or experimental studies of plant communities until now: the effect of intra-specific aggregation *per se* (Shmida & Ellner 1984), and the influence of initial conditions on the outcome of interspecific competition. These are examined here using cellular automaton models that describe the dynamical behaviour of a system, treating space and time in a discrete fashion (Wolfram 1983, 1984). A cellular automaton uses a regular lattice of cells, the states of which are completely defined by local rules. Each cell may have one of a range of states, for example representing vacant space or occupancy by a particular species or group of species. The local rules apply equally to every cell and determine, at each iteration of the model, what the states of each cell will be as a function of its current state (i.e. which species occupies it) and the state of neighbouring cells (i.e. what the neighbours are). Cellular automata are 'bottom-up models' that generate global behaviour from local rules.

The utility of cellular automata as models of plant populations has been recognized by a number of authors who have used them to achieve the greater realism that a spatial model provides. Cellular automata of various kinds have been used to model clonal growth in single species (Barkham & Hance 1982; Inghe 1989), competition between annual species (Weiner & Conte 1981; Czárán 1989), competition between an annual and a perennial (Crawley & May 1987), gap colonization by annuals (Hobbs & Hobbs 1987), succession (Hogweg *et al.* 1985; van Tongeren & Prentice 1986; Czárán & Bartha 1989), the influence of fire on forest mosaics (Green 1989), wave regeneration in subalpine fir forests (Iwasa, Sato & Nakashima 1991) and weed-spread between farms (Auld & Coote 1981). None of these studies directly addresses the fundamental questions posed in this paper.

Methods

THE MODEL

We used a lattice of 40×40 square cells, each of which could be occupied by one of five grass species. At any time, t , the state of a cell depended upon the state of its four vertical and horizontal immediate neighbours at time $t-1$, as determined by a set of rules that were the same for every cell. The rules were time-invariant and were based upon the observed extent of invasion across boundaries between five grass species grown in hexagonal plots by Thórhallsdóttir (1990). This was the best experimental study of invasion rates we could find in the literature. Table 1, reproduced from Thórhallsdóttir's study, shows the relative biomass of neighbouring species found in plots 18 months after they were originally sown with *Agrostis stolonifera*, *Holcus lanatus*, *Cynosurus cristatus*, *Poa trivialis* and *Lolium perenne*. Because these biomasses were the result of invasion of one species by another, we treated the values in Table 1 as replacement probabilities in our model. This involves the simplifying assumption that invasion and replacement are related in a linear manner, which is likely if biomass is proportional to rooted frequency. Our approach essentially takes the transition matrix used in Markov models of vegetation dynamics (Horn 1975), and restores the spatial dimension that is present in real communities, but is absent from Markov models. The net rates of invasion between species (Fig. 1) are computed from Table 1.

At each iteration of the model, a species i in a cell of the lattice was replaced at random by a neighbouring species j with the probability p_{ij} taken from Table 1, weighted by the number of neighbouring cells containing species j . For example, if the central cell was *Holcus* and one neighbour was *Agrostis*, the probability with which *Holcus* would be replaced by *Agrostis* invading from one side was $0.09 \times 1/4$. If *Agrostis* was present on all four sides of the central cell, the probability of replacement was $0.09 \times 4/4$.

Table 1. Rates of replacement (p_{ij}) used in the cellular automaton models. Species along the top are the native species, and those along the side are the invaders. Numbers are the proportion by biomass of the invader found in the native plot 18 months after the experiment was set up (from Thórhallsdóttir 1990)

Invader	Native species					Sum
	<i>Lolium</i>	<i>Agrostis</i>	<i>Holcus</i>	<i>Poa</i>	<i>Cynosurus</i>	
<i>Lolium</i>	—	0.02	0.06	0.05	0.03	0.16
<i>Agrostis</i>	0.23	—	0.09	0.32	0.37	0.81
<i>Holcus</i>	0.06	0.08	—	0.16	0.09	0.39
<i>Poa</i>	0.44	0.06	0.06	—	0.11	0.67
<i>Cynosurus</i>	0.03	0.02	0.03	0.05	—	0.13
Sum	0.76	0.18	0.24	0.58	0.60	

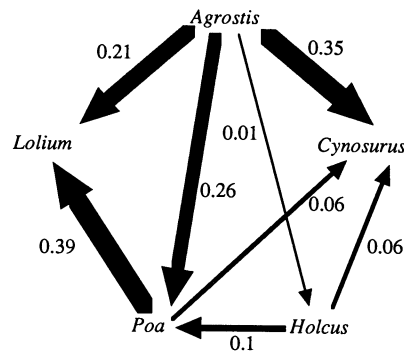


Fig. 1. Net rates of invasion by species ($p_{ij} - p_{ji}$) in Thórhallsdóttir's (1990) experiment, calculated from transitions (p_{ij}) shown in Table 1. Arrows point from the invading species to the invaded species.

EXPERIMENTS WITH THE MODEL

Analytical models (e.g. Shmida & Ellner 1984) suggest that aggregation should delay competitive exclusion. We tested this with a model of a community in which equal numbers of the five species were assigned randomly to cells. The outcome of random initial starting conditions was compared with that of species aggregated in bands (see below).

The second set of experiments explored the effect of altering the juxtaposition of species in models where all species were initially equally clumped and equally abundant. Species were arranged in horizontal bands of equal width (Fig. 2a), varying only the order of the species from the top to the bottom of the plane. Three arrangements of species were ranked down the plane: the most invasive species (*Agrostis*) at the top, followed by species ranked so they are least invasive from above (Fig. 2a: *Agrostis*, *Holcus*, *Lolium*, *Cynosurus*, *Poa*), the most invasive species (*Agrostis*) at the top, followed by species ranked so they are least able to invade their upper neighbours (Fig. 2b: *Agrostis*, *Lolium*, *Cynosurus*, *Holcus*, *Poa*), species ranked by general invasiveness (row totals in Table 1) minus general invasibility (column total in Table 1) (Fig. 2c: *Agrostis*, *Holcus*, *Poa*, *Cynosurus*, *Lolium*).

Each model was run five times. All the effects described in Results occurred in all replicates, except when mentioned otherwise. Spatial effects were produced that can only be satisfactorily represented by photographs, but the numbers of cells occupied by each species in each iteration was recorded and can be used as a summary of the numerical consequences of the spatial processes taking place in the model.

Results

Three of five species went extinct very rapidly in the models with a random initial arrangement of species

(Fig. 3). The two survivors, *Agrostis* and *Holcus*, were the same as the species that survived for the longest period in all of the aggregated models, although the minor species lasted much longer in these (Fig. 4).

A typical pattern of changing species abundance resulting from the arrangement in Fig. 2(a) was as follows. *Poa* and *Agrostis* both increased for the first 150 iterations, and then *Poa* declined to extinction and *Agrostis* rose to dominance (Fig. 4a). *Holcus* was still present at a frequency of about 15% at iteration 600, although it was declining slowly. Figure 4(a) exhibits non-linear, humped trajectories for *Lolium* as well as *Poa*. These non-linearities are a consequence of the particular configuration of species in Fig. 2(a), because they were absent (Fig. 4b) from the trajectories of the same species competing with the different arrangement shown in Fig. 2(b). A comparison of the sequence of events in Fig 4(a) and (b) shows that the different species' trajectories in these two models results from the different juxtapositions of the major species *Agrostis* and *Holcus*. In Fig. 2(a), the spread of *Agrostis* was limited by the presence of *Holcus*, until it was able to break its way through the middle of the *Holcus* band to reach the rest of the plot. Before this happened, *Poa* spread at the expense of its first and second neighbours, *Cynosurus* and *Lolium*, but afterwards all three of these species were rapidly eliminated by *Agrostis*. After *Agrostis* had broken through the band of *Holcus*, *Holcus* also began to decline more rapidly because it was now attacked by *Agrostis* from two sides and the middle.

Just as in Fig. 2(a), *Agrostis* and *Holcus* were neighbours in Fig. 2(c), but the arrangement of the less-competitive species in the region beneath *Holcus* was different, with *Poa* instead of *Lolium* as its immediate neighbour on the lower side. This difference had a dramatic and unforeseen effect. In this arrangement, *Agrostis* was unable to break through *Holcus* because *Holcus* spread rapidly into *Poa*, forming a broad, impenetrable barrier that *Agrostis* could not nibble its way across. Initially the spread of *Holcus* caused a decline in *Poa* frequency (Fig. 4c), but *Poa* spread into the areas occupied by its neighbours *Lolium* and *Cynosurus*. For a period between iterations 100 and 200 in the run of the model illustrated in the Fig. 2(c), the rate of spread into this new space exceeded the rate attrition by *Holcus*, so that *Poa* actually increased and even became more abundant than *Agrostis*. Once its weaker competitors' space had been fully occupied by *Poa*, it began to decline under competition from *Holcus*. In other replicates of this model (not shown) the rate of attrition of *Poa* by *Holcus* was faster than the rate at which *Poa* invaded its more-vulnerable neighbours and *Poa* did not show a temporary rise in frequency, although it did move position down the plot.

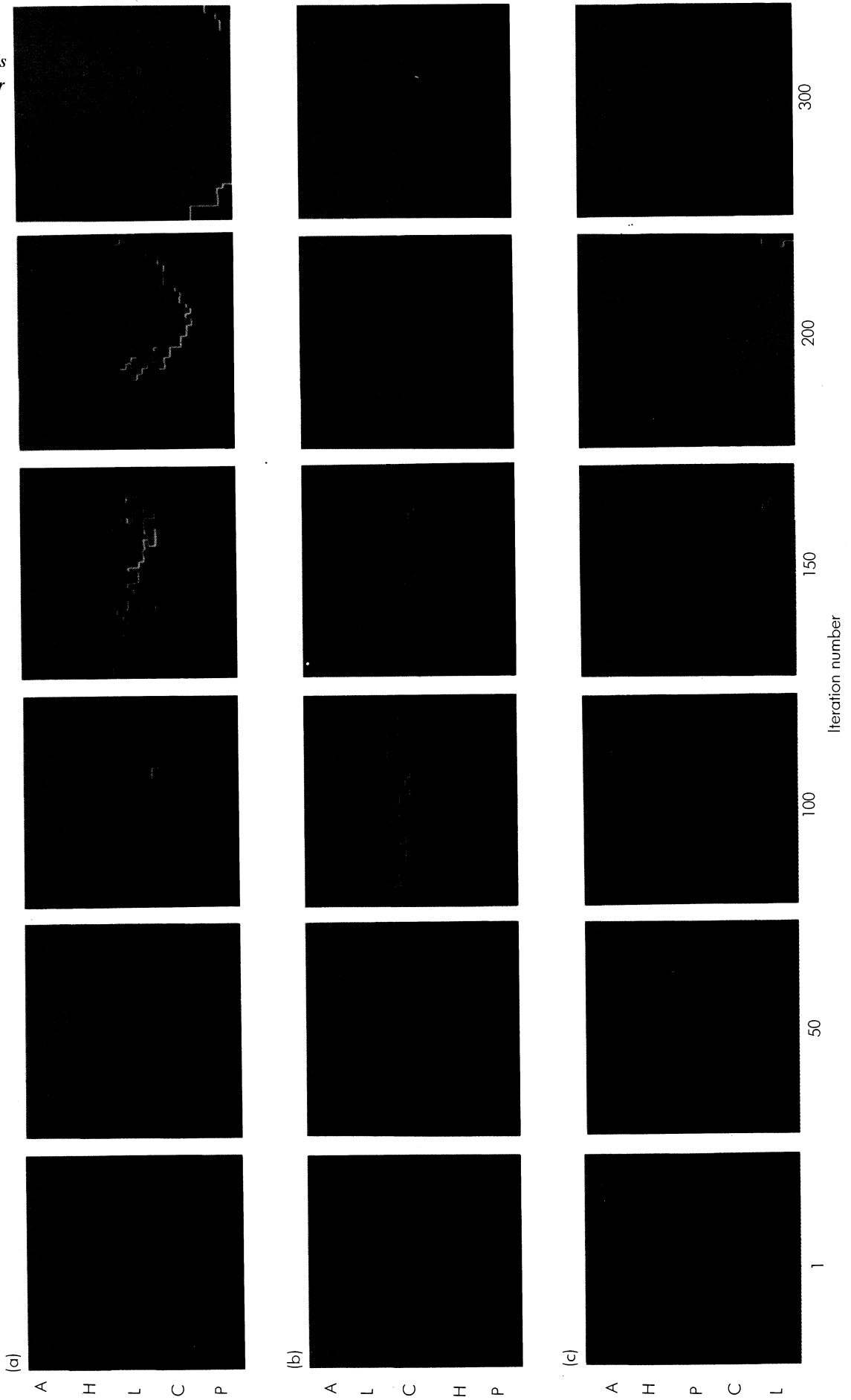


Fig. 2. Initial arrangement of *Agrostis* (yellow), *Holcus* (green), *Lolium* (red), *Cynosurus* (dark blue) and *Poa* (light blue) in the aggregated model and species' distributions at iterations 1, 50, 100, 150, 200, 300; (a) *Agrostis*, *Holcus*, *Lolium*, *Cynosurus*, *Poa*; (b) *Agrostis*, *Holcus*, *Poa*; (c) *Agrostis*, *Holcus*, *Poa*, *Cynosurus*, *Lolium*.

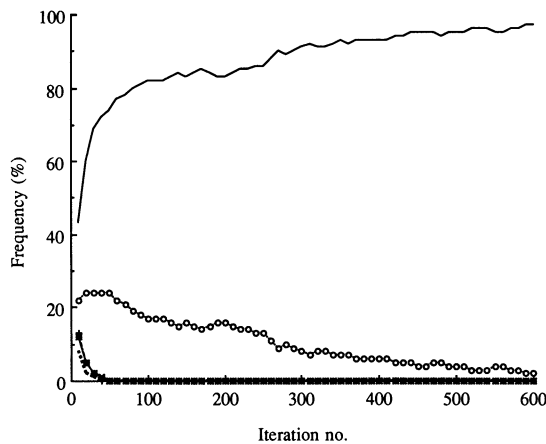


Fig. 3. Abundances of *Agrostis* (—), *Holcus* (—○—), *Lolium* (.....), *Cynosurus* (—×—) and *Poa* (—+—) over time in the model with a random starting arrangement of species.

Discussion

The automaton with a random initial starting arrangement of species is a reasonable model of the spatial arrangement used in standard competition experiments. The fact that extinction of inferior competitors was so much more rapid with this starting arrangement than with aggregated arrangements suggests that most competition experiments greatly over-estimate the importance of competition in field communities, where interspecific aggregation is the norm. Aggregation has a dramatic effect in reducing the rate at which stronger competitors are able to exclude weaker ones (Ives 1988a,b; Rosewell, Shorrocks & Edwards 1990). The existence of aggregation introduces other spatial variables into the dynamics of a community because the configuration of patches and the juxtaposition of species may have strong effects on community composition in the medium term.

Agrostis and *Holcus* were the two strongest competitors in Thórhallsdóttir's experiments and there was ultimately a battle for dominance between them in our models. However, the transitory dynamics of the community were very different, depending upon the configuration of species placed between or adjacent to the ultimate opponents. Comparison of the behaviour of *Agrostis* and *Holcus* in the arrangements shown in Fig. 2(a) and (c) demonstrates that the relationship between two dominants, even when adjacent to one another, can be totally altered by the presence of a third species, and that this effect can long outlast the existence of the third species in the community. The implication for real communities is that these 'ghosts of competition past' (Connell 1980) cannot be distinguished from other causes of community pattern because neither cellular automata nor the spatial processes they simulate can be run backwards.

The interactions between species in our models,

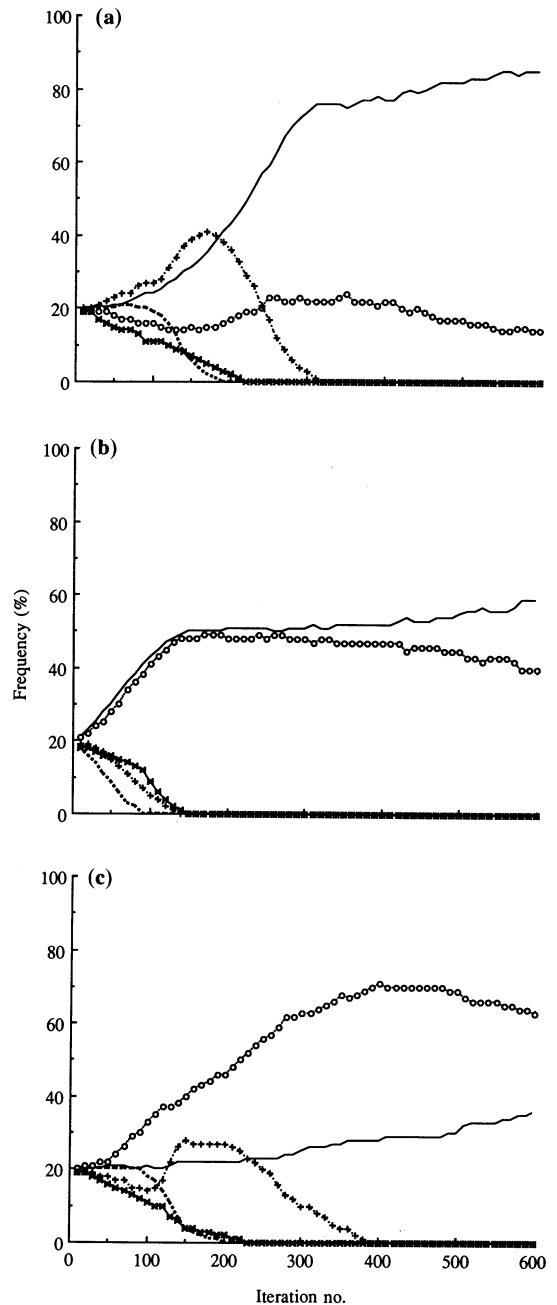


Fig. 4. Abundances of *Agrostis* (—), *Holcus*, (—○—) *Lolium* (.....), *Cynosurus* (—×—) and *Poa* (—+—) over time in the models shown in (a) Fig. 2a, (b) Fig. 2b and (c) Fig. 2c.

although depending on the pairwise relationships between species, cannot be deduced in any simple manner from the replacement values in Table 1. These values represent low-level rules of community dynamics, but the inclusion of space in the model introduces higher-level rules which, in some circumstances, produce non-linear dynamics. The initial spatial arrangement of species determines *when* different species encounter each other, and how much space each occupies when contact is made. For example the initial configuration of species shown in Fig. 2(a) survives until approximately iteration 77. Changes are slow with this arrangement

of species because net movements between adjacent species are low (Fig. 1). When *Agrostis* breaks through the *Holcus* band at iteration 77, it meets *Lolium*, against which it is a strong competitor. At iteration 98, *Poa* penetrates the *Cynosurus* band and meets *Lolium*. Both these events produce new interfaces between species that are much less evenly balanced than the starting arrangement, and this speeds up the subsequent rates of change, causing *Agrostis* and *Poa* to expand rapidly. When *Agrostis* and *Holcus* are the only two species remaining, further change is very slow because the difference in their invasion rates is only 1%. In Fig. 2(b) and (c), change in these species is further retarded by the relatively linear interface between them at iteration 300, compared to the more complex boundary in Fig. 2(a).

Associations between plant species are generally interpreted as the product of environmental heterogeneity (e.g. Kershaw 1973). Where the physical environment is patchy and species do not compete with each other, they may occur together because they share a requirement for certain conditions, or because they share a tolerance of certain conditions. The ability of competing species to coexist in positive association is usually taken to imply a complementarity of resource use. All of these explanations place the causes of association in the autecological relationship between a plant species and its physical environment. A quite different interpretation is possible. This is that patterns of association between species originate from the dynamics of interaction between them. Intraspecific aggregation can provide a refuge for poor competitors (Shmida & Ellner 1984), but it has not been widely realized that interspecific association between competitors of low rank may also provide a refuge and delay or even avert competitive exclusion.

Our model communities were kept deliberately simple so that the effects of spatial arrangement would be clear. We do not, of course, suggest that species occur in bands in most real plant communities, nor that plants are as aggregated or patches as monospecific as they are in our model. However, without making these simplifying assumptions this model, like any model, would have been self-defeating because it would have been as difficult to interpret the model as it is to understand the real world. The effects we have shown are a function of the values in Table 1, but they can only be discovered by simulation. The purpose of this paper was to test our model with real parameter values. Because the values in Table 1 were determined empirically by Thórhallsdóttir (1990), the model is certainly as relevant to real communities as the experiment which generated its parameters. We are in the process of collecting other data from field experiments, and future theoretical research will systematically explore the parameter space of such models.

We believe that these results provide the strongest argument yet that spatial distribution must be considered just as important as competition coefficients, density and the frequency of competitors in determining competitive outcome. This implies that a change in the methodology of competition experiments is needed, at least where these involve clonal perennials.

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