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Neighbourhood effects in forests: implications for within-stand patch structure

LEE E. FRELICH*, SHINYA SUGITAT, PETER B. REICH*, MARGARET B. DAVIS† and STEVEN K. FRIEDMAN*

*University of Minnesota, Department of Forest Resources, 1530 N. Cleveland Ave. St.Paul, MN 55108 USA; and †University of Minnesota, Department of Ecology, Evolution and Behaviour 1987 Upper Buford Circle, St.Paul, MN 55108 USA

Summary

1 MOSAIC, a spatially referenced Markov model was used to show how interactions among trees in a neighbourhood may influence the patch structure of forests. A series of two-species simulations were conducted with neighbourhood strength ranging from neutral (chances of species replacing each other independent of neighbourhood composition) to strong (chance of replacement for each species proportional to neighbourhood composition), and with neighbourhood sizes including 1–50 neighbours.

2 Neighbourhood strength was positively correlated with the degree of patchiness. Very high neighbourhood strength is necessary to form mono-specific patches composed of hundreds of individual trees. Intermediate neighbourhood sizes (5–12 neighbours) led to the most distinct patches where individuals were arranged so that contact between species was minimized.

3 Neighbourhood effects alone are unlikely to lead to large areas (several ha) dominated by one species. However, simulations showed that neighbourhood effects can augment small differences in the environment, resulting in large mono-specific patches.

4 Simulations with 4 and 5 species indicated that groups of species can interact to form spatially distinct communities, starting from a random mixture on a uniform environment. This implies that neighbourhood effects may be responsible for some unexplained variability in studies that attempt to relate environmental parameters to forest composition.

5 Patch structures that develop due to neighbourhood effects are usually not recognized by current vegetation classification schemes or by forest managers, and this lack of recognition could lead to the loss of certain natural spatial structures on forested landscapes.

Keywords: community assembly, neighbourhood effects, patch formation, spatial pattern


Introduction

Spatial aspects of forest dynamics, such as the development and maintenance of mono-dominant patches within mixed-species forest stands, and the rules that govern these processes, have been a major topic of ecological research. Within a local area under the same macroclimate, the development of spatial patterns is determined by three major factors: disturbance regime (fire and wind frequency, etc.), the physical environment (soil texture and nutrient status, drainage, slope and aspect), and biotic factors or neighbourhood effects. In the temperate forest region, there are a large number of published works that concentrate mainly on either disturbance (e.g. Heinselman 1973; Henry & Swan 1974; Sprugel 1976; Cwynar 1977; Raup 1981; Runkle 1981; Romme 1982; Lorimer 1983) or physical environment (e.g. Curtis 1959; Peet & Loucks 1977; Spies & Barnes 1985; Pastor & Broschart 1990; Whitney 1990; Pastor et al. 1982, 1984) or a combination of these (e.g. Foster 1983; Whitney 1986; Foster & King 1986; Jonsson 1990; Kohyama 1993; Mladenoff et al. 1993; Bray et al. 1994; Mann et al. 1995) as the cause of spatial patterns in forests. Many studies have also looked at how biotic factors affect succession of temperate
forests or how they influence forest/nonforest boundaries (e.g. Horn 1971; Bormann & Likens 1979; Abrams & Scott 1989; Wilson & Agnew 1992; Milne et al. 1996). Some studies have looked at the influence of biotic factors on within-forest development of patches (Hibbs 1982; Mladenoff 1987; Pastor et al. 1987; Boettcher & Kalisz 1990; Frellich et al. 1993; Pacala et al. 1996). However, we are not aware of any studies that considered how patch shape, size and other features within forest stands are affected by tree-by-tree interactions. The overall goal of this paper is to examine these within-stand patch formation processes.

It seems logical to examine the implications that biotic neighbourhood effects have for spatial structure of forests, since it is necessary to know how each of the important factors works in isolation before attempting synthesis of multiple causal factors. We attempt to look at neighbourhood effects by means of the MOSAIC simulation, a simple spatially referenced Markov model that was designed to predict how different types of neighbourhood interactions between species affect the spatial characteristics of tree distribution at the stand level (1–10 ha) (Frellich et al. 1993). The distance that neighbourhood effects extend out from a tree or clump of trees, the strength of neighbourhood effects and other factors can be manipulated. MOSAIC is the point-based analogue to a cellular model; there are no grid cells and instead each tree is represented by an x–y coordinate. In MOSAIC, transition probabilities depend on the species composition of the neighbourhood, which is defined as all trees within a certain number of metres (usually 5–10 m in northern temperate forests) of a dying tree. Thus, unlike the traditional Markov model, transition probabilities can change from place to place within a stand, and can also change over time within one neighbourhood as well if the species composition of the neighbourhood changes. MOSAIC falls near the simpler end of a gradient of forest dynamics models of varying complexity, ranging from a nonspatial Markov model that projects the future proportion of each species in a stand, based on tree-replacement probabilities (Waggoner & Stephens 1970; Horn 1971), to spatially explicit gap neighbourhood models that simulate seed rain, light, nutrient dynamics, future succession and stand development and biomass (e.g. LINKAGES (Pastor et al. 1987) and SORTIE (Pacala et al. 1996)). The original results in this paper are all derived from simulations; although we compare the simulations to data from published forest studies where appropriate.

For purposes of this paper, neighbourhood effects in forests are defined as any process mediated by canopy trees that affects the replacement probability by the same or other species at the time of canopy mortality. We define neighbourhood effects in relation to overstorey dominant species or groups of species. Positive neighbourhood effects are processes that promote replacement by conspecific individuals; negative effects are processes that prevent conspecific replacement; and neutral effects are processes that neither favour nor disfavour conspecific replacement. In general, neighbourhood effects may include seed rain, stump and root sprouting, alteration of the physical or nutrient status of the forest floor to favour or disfavour germination and establishment of a given species, and the influence of the canopy on local temperature, humidity and light levels. The MOSAIC model simulates generic neighbourhood effects without specifying their nature, and the spatial patterns that develop could occur in forests with any of the above mentioned mechanisms. The mechanism of neighbourhood effects in a given forest (i.e. why and how they occur) is the subject of ongoing research and will be the subject of future papers.

OBJECTIVES AND HYPOTHESES

The objectives of this study are: (i) to show how neighbourhood effects of varying strengths (from neutral to strongly positive) and sizes (including few to many neighbours within a neighbourhood) affect the patch structure of forests, given scenarios where all other factors are equal; (ii) to show how differences in the environment that influence neighbourhood relationships may affect community patch structure; and (iii) to demonstrate how neighbourhood effects allow assembly of alternative communities in a multispecies forest within a uniform environment.

The first two objectives will be addressed by testing three hypotheses regarding the long-term development of spatial patterns in forests, using two-species simulations.

_Hypothesis 1._ A positive relationship exists between strength of neighbourhood effects and degree of patchiness (more patchiness indicated by a larger proportion of the area occupied by patches comprising many individuals of the same species) in a mixed-species forest. Strong positive neighbourhood effects should allow mono-specific patches or stands of each species to form; neutral neighbourhood effects should allow persistence of mixed-species stands. To address this issue we ran a series of simulations of a two-species mixture where both species have equal neighbourhood effects ranging in strength from neutral to strongly self-positive.

_Hypothesis 2._ A negative relationship exists between neighbourhood size and the degree of patchiness in a mixed-species forest. If neighbourhood effects are extremely local, then it should be easier for a given neighbourhood to be dominated by one species, which would lead to replacement by that same species. Thus, small neighbourhoods should lead to propagation of patches to relatively large sizes, while large neighbourhoods should lead to mixed-species stands. To address this we ran simulations of two-species mixtures with positive neighbourhood effects strong
enough to cause mono-dominant patch formation (determined during testing of H1), and varied
neighbourhood size to include from 1 to 50 neighbours that influence replacement probabilities for the two
species.

**Hypothesis 3.** Environmental differences influence the patch size and shape. If the environment is not
uniform, then neighbourhood relationships between the same two species are likely to be different on the
two slightly different adjacent environments (Frellich et al. 1993), leading to different size of patches of each
species on each environment. Vegetation ecologists have long wondered whether differences in the
environment and/or interspecific relationships that are too small to detect in most field studies can cause
a large difference in patch structure. We attempt to address this question by simulating a hypothetical
30 m-wide lake effect, and varying the degree to which the lake effect enhances the strength of neigh-
bourhood effects of one species in a two-species mixture.

If mono-specific patches can form when two species have strong neighbourhood effects (Frellich et al.
1993), then it is a logical extension that groups of species can form patches, with two or more species
mixed together within each patch. Thus, simulations with 4 or 5 species, where an initial random mixture of
species separates into two communities, were used to demonstrate the pattern of neighbourhood inter-
actions among species that allows assembly of such alternative communities (third objective of the paper).

**Methods**

**MOSAIC SIMULATION**

The main mathematical procedure in MOSAIC is to calculate a vector that represents the probability that
each species in the forest will replace a dying tree in a given neighbourhood. This species replacement vector
(SRV) has dimension $n \times 1$ ($n =$ number of species), and sums to 1.0 (i.e. there is a 100% chance that a
tree of some species will replace the dying tree, which is at the centre of the neighbourhood):

$$SRV = \text{NRM}(NV),$$

where NRM is the neighbourhood relationship matrix, of dimension $n \times n$, a matrix that expresses the
probability that each species will be replaced by itself if the neighbourhood is entirely occupied by
that species; and NV is the neighbourhood vector, of dimension $n \times 1$, that contains the proportion of trees
of each species in the neighbourhood surrounding the
dying tree.

A numerical example will help clarify the calculation of the SRV vector. Suppose that the NRM
for a given forest with two species is as follows:

**Matrix 1**

<table>
<thead>
<tr>
<th>Replacement trees</th>
<th>Species 1</th>
<th>Species 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>0.9</td>
<td>0.1</td>
</tr>
<tr>
<td>Species 2</td>
<td>0.1</td>
<td>0.9</td>
</tr>
</tbody>
</table>

And the NV is:

**Matrix 2**

<table>
<thead>
<tr>
<th>Neighbourhood composition</th>
<th>Species 1</th>
<th>Species 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>0.70</td>
<td>0.30</td>
</tr>
</tbody>
</table>

Then SRV is $(0.9)(0.7) + (0.1)(0.3)$ for species 1, and $(0.1)(0.7) + (0.9)(0.3)$ for species 2:

**Matrix 3**

<table>
<thead>
<tr>
<th>Probability of replacement by</th>
<th>Species 1</th>
<th>Species 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>0.66</td>
<td>0.34</td>
</tr>
</tbody>
</table>

This process is repeated throughout the forest for the
neighbourhood surrounding each tree at the time it
dies. The NV is calculated by selecting all trees within
a specified radius of the dying tree, the NRM is con-
stant for a given simulation, but can be adjusted to
simulate different scenarios. Note the diagonal of
NRM indicates the probability that each species will
replace itself if the entire neighbourhood is occupied
by conspecifics – in this case 90%. These would be
strong positive neighbourhood effects. Neutral neigh-
bourhood effects would be represented by a NRM of:

**Matrix 4**

<table>
<thead>
<tr>
<th>Replacement trees</th>
<th>Existing canopy tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>Species 1</td>
</tr>
<tr>
<td>Species 2</td>
<td>Species 2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species 1</th>
<th>Species 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>0.5</td>
</tr>
<tr>
<td>Species 2</td>
<td>0.5</td>
</tr>
</tbody>
</table>

In this case, each species would always have a 50% chance of replacing each dying tree regardless of
neighbourhood composition.

**SIMULATIONS RUN WITH MOSAIC**

A variety of simulations designed to address our hypotheses were completed. For each scenario, three
replicates were run to ensure that results were reliable. All of the simulations started with an equal number
of each species present. For each tree, a random number
generator was used to assign initial $x$ and $y$ co-
dinates, regardless of species. The spatial dispersion
each of species was initially random, both relative to
other members of the same species and other species. Thus, the simulations show whether neighbourhood effects alone can cause spatial patterns and other community patterns to develop.

The following specifications were used for all simulations: plots were 25 ha in size (500 × 500 m), and had a density of 400 trees per ha. To ensure that there was no significant boundary effect, a buffer of extra forest around the 25-ha plot, equal in width to one neighbourhood radius, was carried through the simulations. Canopy-tree mortality is 0.0% per decade up to age 90, 2.5% per decade for canopy trees 91–175 years old, and 10% per decade for trees older than 175 year. The resulting age distribution is similar to that in old-growth forests of the upper Great Lakes Region (Frelich et al. 1993). Previous experience with MOSAIC indicates that spatial pattern development starts to occur within several hundred years, and reaches an asymptote after about 2000 years. Therefore, simulations were run for 3000 years to make sure that at least 10 tree generations elapsed, that initial conditions disappeared and that patches reached their ultimate development.

Hypothesis 1 was tested by running two-species simulations with neighbourhood strengths of 0.5, 0.8, 0.9, 0.95, 0.975 and 1.0. With a neighbourhood strength of 0.5, the two species replace each other at random (neutral neighbourhood effects), and at 1.0, the probability of species 1 replacing the dying tree is equal to the proportion of that species in the neighbourhood, so that at 100% dominance in a given neighbourhood all other species can be excluded. Neighbourhood radius was held constant at 10 m.

Hypothesis 2 was tested by running two-species simulations with neighbourhood radii of: 2.5 m, 5.0 m, 10.0 m, and 20.0 m, which corresponds roughly to 1–50 neighbours included in the neighbourhood. Neighbourhood strengths were held constant at 1.0.

Hypothesis 3 was tested by running two-species simulations with neighbourhood strength held constant at 1.0 and neighbourhood radius held constant at 10 m. A square 4-ha ‘lake’ (200 × 200 m) was centred within the 25-ha, 500 × 500 m plot. Surrounding the lake was a 30-m wide buffer zone in which species number 1 was initially given advantages \( z \) of: 0.01, 0.05, 0.10, 0.25, 0.50, 0.75, 1.0, 2.0, 4.0, and 8.0. Advantage \( z \) (eqn 2) is the ratio of replacement probability of species 1 to species 2 in the case where species 1 has an advantage, divided by the same ratio for the case where the two species are competitively equal. The ratio in the numerator, where species 1 has an advantage, is always greater than the ratio in the denominator, therefore subtracting 1 from the division of the two ratios leaves us with just the proportional advantage for species 1:

\[
P'_{\text{Species 1}} = \frac{a}{1 + a}
\]

Where \( P'_{\text{species 1}} \) and \( P'_{\text{species 2}} \) are the replacement probabilities of species 1 and 2 without advantage, and \( P_{\text{Species 1}} \) and \( P_{\text{Species 2}} \) are the replacement probabilities of species 1 and 2 within the zone with the advantage for species 1. Then,

\[
P_{\text{Species 1}} = \frac{a}{1 + a}
\]

where \( a \equiv (P_{\text{species 1}}/P_{\text{species 2}})(1.0 + z) \); when \( P_{\text{species 2}} = 0.0 \), \( P_{\text{species 1}} \) and \( P_{\text{species 2}} \) are defined as 1.0; also, \( P_{\text{species 2}} = 1.0 - P_{\text{species 1}} \).

When applied, this formula makes the biggest difference in neighbourhoods that have approximately equal numbers of each species, and a minimal difference in neighbourhoods that are already heavily dominated by one species (Fig. 1). For example, if species 1 and 2 each had 50% of the trees in a given neighbourhood, and the advantage \( z \) was 0.50, then the probabilities of species 1 and 2 being successful would be 0.60 and 0.40, respectively (0.6 = 50% more than 0.4, hence the 50% advantage), as opposed to the 50:50 probabilities if one species was not given an advantage (Fig. 1). If species 1 already had 90% of the neighbourhood trees, then its probability of successfully replacing a dying tree under an advantage \( z \) of 0.50 would be 0.93 and the probability for species 2 would 0.07, as opposed to the 0.9 and 0.1 probabilities with no advantage for species 1 (Fig. 1). After running the simulations, it became clear that \( z > 1 \) does not have any additional effect (because all trees within the lake-effect zone are replaced by the species with the advantage), so that only those runs in the range \( z = 0.01–1.0 \) are shown in this paper.

Assembly of communities (objective 3) was demonstrated by running two simulations, designed to allow groups of species to work together, to sort themselves
into communities even when no individual species have strong neighbourhood effects. First, a 4-species system was run with the following NRM matrix:

### Matrix 5

<table>
<thead>
<tr>
<th>Replacement tree</th>
<th>Existing canopy trees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sp. 1</td>
</tr>
<tr>
<td>Sp. 1</td>
<td>0.5</td>
</tr>
<tr>
<td>Sp. 2</td>
<td>0.5</td>
</tr>
<tr>
<td>Sp. 3</td>
<td>0.0</td>
</tr>
<tr>
<td>Sp. 4</td>
<td>0.0</td>
</tr>
</tbody>
</table>

In this matrix, species 1 and 2 can replace each other at random, and if the neighbourhood is all species 1 and/or 2, then species 3 and 4 have no chance of entering the neighbourhood. The same happens with species 3 and 4. Thus, even though no one species has strong neighbourhood effects, the species should be able to work together as groups to exclude another group, and the random mixture of 4 species should sort into two communities, each with two species randomly mixed within the community.

The second simulation involves a five species forest, in which a neutral species is included — one which can replace any other species regardless of neighbourhood composition. The five species can sort into two communities, one with species 1, 2 and 3, and one with species 3, 4 and 5. Species 3 can be a component of either community:

### Matrix 6

<table>
<thead>
<tr>
<th>Replacement tree</th>
<th>Existing canopy tree</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sp. 1</td>
</tr>
<tr>
<td>Sp. 1</td>
<td>0.5</td>
</tr>
<tr>
<td>Sp. 2</td>
<td>0.4</td>
</tr>
<tr>
<td>Sp. 3</td>
<td>0.1</td>
</tr>
<tr>
<td>Sp. 4</td>
<td>0.0</td>
</tr>
<tr>
<td>Sp. 5</td>
<td>0.0</td>
</tr>
</tbody>
</table>

GIS ANALYSES OF PATCH STRUCTURE

ARC-INFO software was used to tessellate stem maps generated by MOSAIC into Thiessen polygons, which represent the canopy space occupied by each tree. The polygon boundaries for each tree are the perpendicular bisectors of line segments drawn at equidistant positions between each neighbouring tree. All polygons that share one or more sides with another polygon of the same species are then merged to form mono-specific patches (Fretlich & Reich 1995). Patch statistics calculated included mean patch size, patch perimeter, shared perimeter between two species, and fractal dimension, D, which is a measure of complexity of patch shape ranging from 1.0 to 2.0 (Clarke & Schweizer 1991). In addition, 5- and 10-m buffers around the perimeter of each patch were applied in the neighbourhood strength and neighbourhood size series of experiments to determine the proportion of area occupied by patch interiors.

**Results**

STRENGTH OF NEIGHBOURHOOD EFFECT

The degree of patchiness and the strength of neighbourhood effects are positively correlated (Fig. 2a–f), showing Hypothesis 1 to be correct. Strong reciprocal positive neighbourhood effects with 2 species developed patches which tend to minimize contact between species. Although the average patch size and patch shape do not change much in response to changes in neighbourhood strength (Fig.3a,b), the distribution of patch sizes does. Large drops in shared boundary between the two species occur as neighbourhood strength increases, indicating that a few very large patches form when neighbourhood strength is very high (Fig.2e,f, 3c). Interior patch area with both 5 m and 10 m buffers increases dramatically between neighbourhood strengths of 0.9 and 1.0 (Figs 2 and 3d).

NEIGHBOURHOOD SIZE

The hypothesized monotonic relationship between neighbourhood size and degree of patchiness does not occur. Instead, there is a peak in patchiness — indicated by relatively large average patch size, low shared perimeter, high proportion of patch interior area — at the 5-m neighbourhood radius, followed by a dramatic decline in patchiness at larger neighbourhood size (Fig.4, 5a,c,d). Fractal dimension reaches its minimum at the 5-m neighbourhood radius, indicating that patches are more compact than with other neighbourhood sizes (Fig.5b). The real determinant in the model of how patches form is the number of trees that each neighbour interacts with. Given the density used for the MOSAIC simulations, this works out to the following: 0.8 neighbours (r = 2.5 m), 3.1 neighbours (r = 5 m), 12.6 neighbours (r = 10 m), 28.3 neighbours (r = 15 m), and 50.3 neighbours (r = 20 m) (Fig. 5). If a neighbourhood has 50 trees, it will be much more difficult to ensure that all 50 are one species than if there 3 or 12 neighbours, thus if replacement depends on 50 trees, self replacement cannot be assured as often, and large patches will not develop.

SIMULATED LAKE EFFECTS

Regarding Hypothesis 3, a significant change in spatial pattern around the ‘lake’ is observed with relatively slight advantages to one species (ε = 0.05 or more). The percentage of lake perimeter bordered by the advantaged species, and area occupied within the 30-m buffer around the lake both increase mono-
Fig. 2 Output of the MOSAIC simulation for the neighbourhood strength series of experiments with two species. Neighbourhood strength (NS) ranges from 0.5 (each species has an equal probability of replacing the other regardless of neighbourhood composition) to 1.0 (probability of replacement is proportional to neighbourhood composition). All MOSAIC maps shown were chosen randomly from the 3 replicates. Each map is 500 × 500 m.

tonically and reach an asymptote of nearly 100% at advantage z of 0.5 (Fig. 6). Percentage of the total area of the forest occupied by the advantaged species also increases monotonically and reaches an asymptote at z = 0.5, but the asymptote is only 60% (not shown). Thus, the advantaged species is not able to exclude the other species from the 25-ha plot. In fact total dominance by the advantaged species never extends more than 40 m from the lake, 10 m greater than the 30-m buffer around the lake.

COMMUNITY SORTING/ASSEMBLY SIMULATIONS

The simulations demonstrate that spatially separated communities can arise from a random mixture of species with certain types of neighbourhood interactions, and boundaries between communities can arise at chance locations on a uniform environment. The random mixture of species does sort itself into communities in both the 4- and 5-species experiments.
Neighbourhood effects in forests

(Fig. 3a,b). A group of species can act as ‘one’ species with 1.0 neighbourhood strength, in fact, the spatial pattern when species 1 and 2 and species 3 and 4 are considered as two groups, is the same as for the two species simulation with 1.0 neighbourhood strength (cf. Figs 2f and 7). In the 5-species mixture, two communities form spatially distinct patches, just as in the 4-species mixture. The main difference is that the fifth species occurs in a random spatial pattern within both communities.

Discussion

NEIGHBOURHOOD EFFECTS VERSUS OTHER CAUSES OF PATCH FORMATION

The simulations in this paper, together with spatially explicit models incorporating mechanistic neighbourhood effects (Pastor et al. 1987; Pacala et al. 1996), and field studies of alternative forest types that have apparently developed on similar and adjacent parent material (Davis et al. 1994) show that biological feedbacks can form and sharpen boundaries within forests, just as they do between forest and non-forest vegetation types. The simulations with 10-m neighbourhood radius and strength of 0.95 or 1.0, are similar to conditions found in an empirical field study where sugar maple (Acer saccharum) and hemlock (Tsuga canadensis) each have strong self-positive (and reciprocal negative effects against each other) neighbourhood effects that help to form and maintain mono-dominant patches (Frelich et al. 1993). The types of feedbacks may be different for interior-forest patch formation than for forest-nonforest patch formation. For example, clumps of trees in otherwise open environments can cause increased soil moisture, allowing patches of forest to form in environments otherwise too dry for trees (see review of subject by Wilson & Agnew 1992). In contrast, within-forest patch formation – although influenced by moisture – is likely to be more strongly reinforced by differences in litter quality that affect germination and early establishment (Davis & Hart 1961; Beatty 1984), nitrogen or other nutrient availability (Pastor et al. 1982, 1984), or degree of shade cast (Canham et al. 1994; Pacala et al. 1996).

The lake effect series of simulations in this paper suggest that minor differences in the environment that result in a change of 5% or more in probability of recruitment, acting over a long time period, can have a major effect on patch structure of the forest. Many field studies do not have sufficient sample size or precision to detect a 5% difference in recruitment, nor a small difference in variables such as nitrogen mineralization rate or water availability, and even if they could, it would not be clear whether the observed differences caused two patches to form, or were the result of the two patches’ effect on the environment. Reciprocal transplant experiments in forests would have to continue for several decades to show whether a slight difference in the environment facilitates long-term success of a given species in occupying the canopy by capturing gaps.

Unfortunately, there are no good palaeoecological proxies for parameters such as nitrogen mineralization rate that could be used to see if differences existed prior to differentiation of patches in studies of
Fig. 4 Maps (500 × 500 m) showing output of the MOSAIC simulation for the neighbourhood size series of experiments with two species. Neighbourhood radius (NR) ranges from 2.5 to 20 m.

long-term forest dynamics. Instead, fossil pollen data can show how long two current patches have been in existence, and whether they were different stand types prior to formation of the current patches. For example, pollen data from Sylvania, Michigan, USA, suggest that eastern hemlock invaded white pine (Pinus strobus) stands c. 3400 years BP, whereas hardwoods, such as sugar maple and basswood (Tilia americana) became dominant in intervening places (Davis et al. 1994). These data indicate the importance of preceding patch types, which could have been influenced by differences in physical environment, for patch formation by new species.

We suggest that differences in communities may exist due to environmental differences that are too small to measure or detect in the field using typical forest ecology methods. Therefore, there will often be a large proportion of unaccounted for variability in community composition in cases where we try to relate the environment to composition.
**Neighbourhood effects in forests**

**Fig. 5** Graphs of patch statistics for the neighbourhood size series of experiments. (a) average patch size (m²); (b) fractal dimension $D_f$; (c) shared perimeter between the two species (m × 1000); and (d) percentage of plot occupied by patch interiors, using 5 m and 10 m buffers around patch edges (m²).

### Neighbourhood effects and classification in forest communities

How a forest is classified has a major impact on management, both in natural areas and in commercial forests. The types of spatial patterns that develop from neighbourhood effects are not recognized by current classification systems. Under the proposed new National Vegetation Classification System currently being developed and implemented across the United States (Federal Geographic Data Committee 1996), patches of vegetation must be 0.5 ha in size to be classified as different communities. Thus, a forest with conifer and hardwood patches as shown in Fig. 2f, would be divided into three communities: those patches of either species larger than 0.5 ha would be delimited as separate communities and the remainder would be considered a mixed community. It is still debatable among ecologists whether a pattern such as that in Fig. 2f should be referred to as a mosaic of communities or a patchy community. A functional classification would suggest that the stand in Fig. 2f functions as a mosaic of communities and should be classified as such.

If managers of commercial forests are to manage to maintain the spatial structure and function of natural communities, then a stand classification system where an area such as Fig. 2f is classified as a mosaic within one stand is preferable. The charge to the manager would then be to manage to maintain the mosaic. In the USA, it is common to delineate stands with a common management history, and base the 'cover type' designation on the species with the majority or plurality of basal area. Thus, if Fig. 2f represented a real stand, it would be classified as a species 1 or species 2 stand, depending on which of the species came out over 50% upon stand inventory. The tendency is then to apply a silvicultural technique to regenerate the whole stand to one species. If successful, this would lead to a landscape dominated by monospecific blocks, not a mosaic like that in Figs 2 and 7. By the same token, if the block is classified as a mixed stand, rather than a mosaic, then silviculturalists will apply techniques to regenerate a mixture throughout, rather than a mosaic. To maintain the types of spatial structures shown in Figs 2 and 7, a stand would best be both classified and managed as a mosaic.

In restoration efforts, patch structures need to be taken into account even on a fairly uniform environment. Often, when patchy forests are logged they then regenerate to a monodominant stand of pioneer species such as aspen (Populus tremuloides). However, a careful habitat typing at a fine spatial scale would detect the former existence of patches, which could be restored rather than regenerating the entire area to one species.

### Conclusions

We make the assumption that neighbourhood effects can be an important force in structuring the forest. In order to hold all conditions constant except for strength and size of neighbourhood effects, we set up the simulations with symmetric matrices (except the lake-effect series) and identical mortality rates among species, so that (somewhat unrealistically) all species are competitively equal. One cannot prove that neighbourhood effects are important using the simulations,
since they are all that are allowed by MOSAIC simulations, but one can show how changing them will change the system – in this case, spatial structure and patch formation. For example, the overall pattern when looking at a range of neighbourhood strengths and sizes, is that average patch size and shape change very little. Size distribution of patches changes, however, so that with strong neighbourhood effects and an optimum number of neighbours, a few relatively large patches form. The largest few patches are very important for determining the characteristics of the mosaic. At the same time, the simulations show that it is not likely that neighbourhood effects alone will cause formation of mono-specific patches many hectares in size. Large solid patches of one species require some enhancement of neighbourhood strength by the environment, as the lake-effect simulations showed. Also, neighbourhood effects may
maintain patches that form for other reasons, such as when a species with strong neighbourhood effects invades after a disturbance. Thus, the simulations give insight into causes that should be considered when studying development of alternative communities adjacent to one another in the field.

Do patterns of relationships among species like those in the species sorting/community assembly simulations exist in nature? Forested landscapes composed of a few species with strong reciprocal neighbourhood effects and several other species with neutral neighbourhood effects have been shown to exist in several temperate forest regions (Sokal & Oden 1978; Runkle 1981; Frelich et al. 1993). Such scenarios
have also been simulated for hemlock-beech forests in Connecticut (Pacala et al. 1996). Even in the case with two heavily dominant tree species, such as the sugar maple–hemlock mosaic in Sylvania, Michigan, different mixtures of herbaceous plants (Davis et al. 1994), fungi (Christensen 1969), and lichens and mosses live in the different patches, so they are different biological communities. The challenge for ecologists at this point is to find out whether forests dominated by species with strong neighbourhood effects are widespread, and to assess the relative importance of abiotic (environment, disturbance) and biotic (neighbourhood interactions) factors in determining the diversity of communities on the landscape.

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