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REVIEW

Advances in spatial, individual-based modelling of forest dynamics

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Abstract
Many individual-based models of forest dynamics lack spatial complexity. Although, in certain cases, spatially simple models may not be substantially inferior to spatially complex models, advances in vegetation science indicate potential weaknesses, particularly the lack of consideration of propagule availability in horizontal space, and varying patch (or canopy gap) dimensions. Models with vertical and horizontal spatial complexity can address these issues, but, thus far, evidence that they outperform patch (or gap) models is limited. Comparison of projections from models that differ only in their spatial complexity is needed to address the effects of propagule availability in space, spatial pattern of canopy tree mortality, and spatial resolution.

Keywords: Canopy gap model; Forest dynamics; Forest succession; Landscape; Simulation; Spatial pattern.

Introduction

A fundamental question in forest dynamics theory pertains to the amount of spatial detail required in the study of stand and landscape dynamics. Arguments against a simple reductionist approach (e.g. O'Neill et al. 1986) are balanced by a search for 'details that matter' (Pacala & Deutschman 1995). In forest dynamics research, the level of spatial detail sufficient for modelling is not fully resolved (Reynolds et al. 2001; Mailly et al. 2003). All individual-based simulation models of forests share an emphasis on capturing the performance of individual trees, but they vary greatly in their degree of spatial complexity (Bugmann 2001). Some investigators have employed comparatively detailed consideration of forest canopy structure and light regimes (e.g. Pacala et al. 1993). Others have avoided such spatial complexity and have adhered to parsimonious models with discrete canopy gaps or patches as the fundamental spatial unit (cf. Shugart 1984; Botkin 1992).

Here we examine the level of spatial detail used to simulate tree performance and the dynamics of forest structure and composition. What, if anything, is gained by adding spatial complexity? How much complexity is effective in the study of forest stands and landscapes? How can the performance of models with contrasting spatial complexity be compared? What aspects of spatial, individual-based forest modelling are promising areas for further development?

Modelling ecological forest dynamics

Spatiotemporal scope and applications

Like all ecosystems, forests undergo changes brought about by endogenous and exogenous processes (Bormann & Likens 1979; White 1979; Oliver 1981; Sprugel 1991). Change may operate on very long time scales because the lives of trees and the forest growth cycle (*sensu* Whitmore 1982) may last several centuries or more. Given the rarity of comprehensive long-term data on vegetation dynamics, simulation modelling is a useful means of inference on long-term dynamics. Also, the use of quantitative models to project forest response to human and natural influences is essential to effective management and conservation planning. Used in tandem with empirical observations, computer models are excellent tools. When combined with other approaches, they can aid in prediction and explanation of changes in complex systems. Models are particularly useful in pointing out weaknesses in our understanding of ecological systems and in pointing out which system components are most important; they provide new perspectives and insights that may lead to the development of testable hypotheses.

Computer modelling of ecological forest dynamics has involved a wide diversity of approaches over the

last three decades (Shugart 1984; Shugart & Smith 1996). Many approaches have been entirely non-spatial or place only weak emphasis on spatial processes (e.g. Waggoner & Stephens 1970; Sullivan & Clutter 1972; Solomon 1974; Suzuki & Unemura 1974; Horn 1975). These models apply changes at the level of trees or patches to project the dynamics of essentially homogeneous stands or landscapes. Models that are suitable for spatial simulation of ecological landscape processes include LANDIS (Mladenoff & He 1999) and LANDSIM (Roberts 1996), but these stand- and landscape-level models cannot address detailed spatial dynamics of forest structure within stands, and so we do not consider them here.

Among individual-based simulators, spatial complexity ranges from weak (e.g. Botkin et al. 1972) to moderately strong (e.g. Pacala et al. 1993) (Table 1). Only a few of these simulators feature explicit representation of three-dimensional space, and they tend to be relatively new models.

Individual-based simulation models of forest dynamics

Individual-based models simulate the performance and fate of individual organisms in ecological systems (Huston et al. 1988; DeAngelis & Gross 1992; Judson 1994). The individual-based approach holds that the properties of a system 'are derived from the properties of its parts and the relations between them' (Lomnicki 1988). Our review concentrates on models in which the performance of each individual is simulated and a set of individuals is taken to represent the dynamics of the system (the i-state configuration models; Metz & Diekmann 1986). The overall dynamics of the forest depends on the combined dynamics of the set of trees simulated.

Individual-based models are successful for several reasons (Judson 1994). First, information on the biology and life history of individuals is often available, facilitating model parameterization. Second, the breadth of information that is generated by individual-based models is sufficient to address a wide range of problems from individuals to ecosystems. The literature abounds with examples, from population structure and dynamics, to biomass and nutrient dynamics (Bormann & Likens 1979; Shugart 1984; DeAngelis & Waterhouse 1987; Huston et al. 1988; Botkin 1992; Shugart & Smith 1996; Bugmann 2001). Finally, individual-based models are particularly effective at time scales of decades to millennia (Solomon et al. 1981; Botkin 1992), an area where traditional modelling, using aggregative and analytic techniques, has proven difficult (Horn et al. 1989).

These are the primary reasons for the widespread application of forest 'gap models' (*sensu* Shugart 1984). Some aspects of early gap models (e.g. JABOWA & FORET) may need revision or replacement, however (Botkin 1992). Certain processes may require more spatial detail than that of early gap models. To what degree the lack of spatial detail, once considered a 'brilliant' (Prentice 1994) simplification with 'power and elegance' (Bossel 1991), hinders progress is unclear. With advances in computer power, spatial simplification may no longer be advantageous in many cases.

Most ecological simulation investigations to date emphasize tree species composition rather than spatial structure of forests. However, given that forest structure and composition are interrelated, the utility of spatial models may not be limited to purely spatial issues. They may also be superior to non-spatial models in the simulation of compositional dynamics.

Models lacking three-dimensional spatial complexity

Forest gap models simulate the ingrowth, growth and mortality of a collection of individuals (trees) on a gap-sized patch of land (typically < 0.1 ha; Shugart 1984). Spatial considerations of most gap models developed prior to 1985 are limited to the vertical dimension, because relative heights of trees play a role in competition for light (Table 1; Fig. 1a, b). FORET (Shugart & West 1977) is a good example; it leaves the locations of individual trees within the patch unspecified. The availability of resources is assumed to be horizontally homogeneous within each patch.

Early versions of gap models simplify considerations of vertical canopy structure to such an extent that it cannot be simulated effectively in some cases. For example, in JABOWA and FORET, tree crowns are simulated as a horizontal plane at the top of each tree (Fig. 1b). This approach can produce unsatisfactory results in tall coniferous forests (Prentice 1994). To address this problem Prentice & Leemans (1990) developed FORSKA, which incorporates more detail on the vertical distribution of shading leaf area by adding crown depth (Fig. 1c). Enhanced canopy structure leads to greater accuracy of simulated vertical structure, particularly in tall coniferous forests (Leemans & Prentice 1987, 1989; Prentice & Leemans 1990; Leemans 1992; Lindner et al. 1997).

Models emphasizing horizontal interactions among trees are quite common. For example, FOREST, a multi-species model with horizontal spatial structure (Table 1), has been applied in temperate forest ecosystems (Ek & Monserud 1974). Although the model can provide information on vertical structure, competition among trees is based largely on horizontal interactions.

Table 1. Selected examples of individual-based, multispecies forest models with spatial considerations.

Model	Year*	Angle(s) of insolation	Tree crown dimensions	Tree coordinates	Horizontal space resolution	Patch interactions**	Horizontal seed dispersal	References
JABOWA	1972	Vertical	Height	None	None	None	None***	Botkin et al. (1972)
FOREST	1974	None****	Height, depth & width	Cartesian plane	Individual tree	Competition & dispersal	Non-random	Ek & Monserud (1974)
FORET	1977	Vertical	Height	None	None	None	None***	Shugart & West (1977)
ZELIG	1988	Vertical	Height	None	Patch	Competition	None***	Smith & Urban (1988)
FORSKA	1990	Vertical	Height & depth	None	None	None	None***	Prentice & Leemans (1990)
SPACE	1991	Vertical	Height	Cartesian plane	Individual tree	Competition	Random	Busing (1991)
SORTIE	1993	Multiple	Height, depth & width	Cartesian plane	Individual tree	Competition & dispersal	Non-random	Pacala et al. (1993)
FIRE-BGC	1996	Vertical	Height, depth & width	None	Patch	Dispersal	Non-random	Keane et al. (1996)
FORMOSAIC	1998	None	None	Cartesian plane	Individual tree	Dispersal	Non-random	Liu & Ashton (1998)
TROLL	1999	Multiple	Height, depth & width	Cartesian plane	Individual tree	Competition, dispersal & mortality	Non-random	Chave (1999)
DRYADES	2000	Vertical	Height & depth	Cartesian plane	Individual tree	Competition & dispersal	Non-random	Mailly et al. (2000)
PICUS	2001	Multiple	Height & depth	None	Patch	Competition & dispersal	Non-random	Lexer & Honninger (2001)

* = Approximate year of initial description is provided; model characteristics may have evolved since then.
** = Types of interactions among neighbouring patches of trees are listed.
*** = Ubiquitous availability of seeds of all species is assumed. Seedling species eligibility for ingrowth is based on patch conditions. In certain models (e.g. FORET), seedlings are randomly selected from the pool of eligible species.
**** = Competition effects are based largely on horizontal overlap among tree crowns.

Ecological studies using FOREST show that horizontal considerations such as seed dispersal and the size of forest islands have implications for forest dynamics in fragmented landscapes (Johnson et al. 1981; Ranney et al. 1981). FORMOSAIC is a tropical forest model developed for studies of horizontal spatial dynamics of a species-rich community (Liu & Ashton 1998; Table 1). Parameterized largely from long-term field data at a 50-ha site, the model reveals that forest landscape composition and structure can influence the dynamics of stands. For example, seed dispersal from surrounding areas is shown to affect species richness of the focal stand. These two-dimensional models have not been applied as widely as one-dimensional models partly because they generally require much more data for parameterization (Dale et al. 1985).

How well do ecological models lacking three-dimensional complexity perform? In most published studies the predictions of gap models match trends evident in field data (Shugart & West 1979; Doyle 1981; Shugart 1984; Botkin 1992). Nevertheless, some authors note inaccurate distributions of tree diameters and heights in JABOWA, FORET and initial versions of ZELIG (Leemans 1992; Prentice 1994; Vanclay & Skovsgaard 1997; Bugmann 2001). Unfortunately, evaluation of models is often limited to a few aspects of dynamics at a limited number of sites. To remedy this, Bugmann (2001) proposed a "careful combination of sensitivity analyses, qualitative examinations of process formulations, and quantitative tests of gap models or selected submodels against various kinds of empirical data." The empirical data may include potential natural vegetation, data from forest stands of known age, composition time series from pollen data, tree rings, and long-term studies. In addition, the projections of several independent models can be compared. Ideally, such comparisons involve forests with extensive data from empirical studies (e.g. Bugmann et al. 2001).

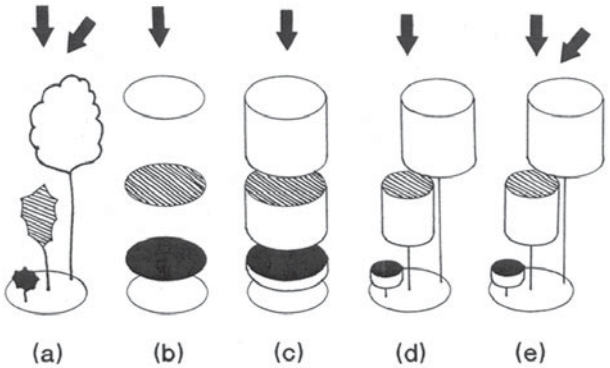


Fig. 1. Vertical and horizontal spatial considerations of ecological forest simulators shown in relation to an actual forest patch. The range of spatial detail in light competition routines employed is shown in order of increasing complexity. Individual illustrations represent (**a**) an actual forest patch; (**b**) a model with simple vertical competition for light (e.g. JABOWA and FORET); (**c**) a model with crown depth added (e.g. FORSKA); (**d**) a model with horizontal locations of individuals added (e.g. DRYADES); and (**e**) a model with multiple angles of insolation added (e.g. SORTIE). Arrows at the top of each illustration indicate the general direction(s) of incoming light. Two arrows indicate multiple light angles. See Table 1 for further information on the simulators illustrated.

Models with three-dimensional spatial complexity

One key to including spatial detail in forest models is the concept of neighbourhood effects (Harper 1977; Mack & Harper 1977), also referred to as 'zones of influence' (Opie 1968; Bella 1971; Berger & Hildenbrandt 2000) or 'fields' (Wu et al. 1985). Foresters have focused primarily on the growth rates of individual trees as a function of crowding by neighbouring trees (Spurr 1962; Opie 1968; Bella 1971; Hegyi 1974; Martin & Ek 1984; Tome & Burkhart 1989; Holmes & Reed 1991). Plant ecologists have also considered neighbourhood effects on growth, survival and reproduction of individuals spanning a variety of plant life forms from annual herbs to trees (Mack & Harper 1977; Ford & Diggle 1981; Weiner 1982, 1984; Silander & Pacala 1985; Lieberman et al. 1989; Taylor & Aarssen 1989).

Most neighbourhood competition formulas for trees fall into one of three major categories: (1) models with fixed neighbourhood radii and no inter-tree distance weighting of competition; (2) models with distance weighting of competition; and (3) tessellation models based on polygonal areas defined by the locations of neighbours around a focal tree (Czaran & Bartha 1992). A wide range of above-ground attributes has been used to estimate the competitive effects of neighbours. These include neighbourhood tree density, neighbourhood basal area, area of crown overlap, volume of crown overlap, tree diameters, tree heights and various combinations of these dimensions (Lorimer 1983a; Dale et al. 1985; Daniels et al. 1986; Ford & Sorrenson 1992). Few studies have given direct consideration to below-ground interactions (Stohlgren 1993; Hauhs et al. 1995). Ford & Sorrenson (1992) asserted that distance-dependent calculations based on crown structure (e.g. Hamilton 1969; Mitchell 1975; Biging & Dobbertin 1992) are useful in modelling competition. However, they have not been widely tested because the measures of crown structure required have rarely been made (but see Cole & Lorimer 1994; Pretzsch et al. 2002).

Alternative, process-based approaches to modelling competition in space are becoming more common (Ford & Sorrenson 1992). Rather than relying on formulas or indices of competition, which typically use available space as an indicator of resource availability, resource depletion processes can be simulated explicitly. Process-based models incorporating this approach are: (1) gap models that consider competition processes; (2) tree models that consider physiological processes (Bossel 1991; Norby et al. 2001). Models concentrating primarily on competition often have low resolution in horizontal space (Table 1). For example, ZELIG (Smith & Urban 1988), derived from FORET, tracks the location of gap-sized patches in a stand, although the locations of trees within patches are still unknown. This interacting-patch structure design is commonly applied in spatial modelling of forest stands and landscapes (e.g. Keane et al. 1996; Malanson 1996; Kohler & Huth 1998; Lexer & Honninger 2001). Higher resolution was achieved in SPACE (Busing 1991), which tracks the location of individual trees in a stand.

A merging of the approaches of Busing (1991) and Prentice & Leemans (1990) with explicit consideration of horizontal and vertical structure has been accomplished in the simulation of a tall coniferous forest of

British Columbia (Mailly et al. 2000) (Fig. 1d). The three-dimensional structure of this model results in diminished local dominance of large trees, which, in contrast to some earlier gap models, allows subordinate trees to persist within the neighbourhood of a large tree. Pacala et al. (1993) have used a similar, but somewhat more complex, approach in a southern New England forest (Fig. 1e).

SORTIE (Pacala et al. 1993) uses an individual-based design inspired by forest gap models (Pacala et al. 1993; Liu & Ashton 1995). New algorithms are used to simulate regeneration, growth and death processes of individual trees. Most notably, a complex routine that considers seasonal and daily movements of the sun is used to calculate light regimes beneath forest canopies (Table 1). The typical simulation area is an entire forest stand (e.g. 1-9 ha; Pacala et al. 1993; Deutschman et al. 1999). Specific locations of trees in horizontal space and the positions of tree crowns in three-dimensional space are known. Seed dispersal in horizontal space is modelled as a function of the locations and sizes of established, conspecific adults. SORTIE is touted for its attention to interspecific variation in tree growth and mortality, and for its comparatively rigorous calibration with field data at a given locale (Pacala et al. 1993, 1996). The model was designed so that field measurements of finer-scale processes drive projections of community dynamics.

Investigation of the long-term effects of spatial factors in forest dynamics has only begun. Many authors have stressed a need for more spatial modelling work (e.g. Shugart et al. 1988; Horn et al. 1989; Urban et al. 1991; Czaran & Bartha 1992; Glenn-Lewin & van der Maarel 1992; Liu & Ashton 1995; Pacala et al. 1996; Lexer & Honninger 2001), but few have provided specific objectives and approaches. In the following discussion, we suggest directions, objectives and means toward progress in spatiotemporal modelling of forests.

Issues in spatial modelling

Assumptions

Models can help us understand the roles of life histories, site history, disturbance, and other environmental factors in vegetation dynamics (Glenn-Lewin & van der Maarel 1992). They may also be useful in determining the relative contributions of deterministic and stochastic factors underlying dynamics. One approach to the study of forest dynamics is to develop a generalized model that can be easily parameterized to simulate dynamics in many different forests (Shugart 1984; Urban et al. 1991). A generalized model of this sort facilitates comparison of dynamics among forest systems and the fundamental processes that drive them. However, models that can be tied closely to field data may be particularly valuable in pointing out the significant factors driving changes in a given ecosystem (Glenn-Lewin et al. 1992; van der Maarel 1996).

Careful comparison of model assumptions and projections to pertinent empirical data is necessary (Gates 1993; Pacala et al. 1993; Robinson & Ek 2000; Keane et al. 2001; Wyckoff & Clark 2002). Evaluations of this nature will lead to better models and to a better understanding of vegetation dynamics. The validity of assumptions concerning spatial issues is addressed below.

Canopy gap dynamics

A critical assumption of Shugart's (1984) approach, and that of Botkin et al. (1972), is that a set of gap-sized patches, simulated independently, collectively represents a forest. Patch size is a critical parameter in simple gap models (Shugart 1984), but once set, it is not varied during a simulation, which precludes the simulation of certain phenomena related to gap size. For example, gap-size partitioning, whereby pioneer species tend to be excluded from smaller gaps (Whitmore 1982) cannot be simulated explicitly. A generalized theory of vegetation patch dynamics holds that patch size influences dynamics (Pickett 1980; Pickett & White 1985; Glenn-Lewin & van der Maarel 1992). So the simulation of a wide range of patch sizes might be desirable. Spatially complex models, tracking individual tree locations, are able to simulate variable patch sizes and associated edge effects (Busing 1991; Pacala et al. 1993; Chave 1999; Dube et al. 2001). For example, spatially enhanced gap models (Busing 1995; Mailly et al. 2000) show that endogenous changes in structure (e.g. canopy tree size) during forest development can influence disturbance patterns, including gap size, and that large canopy trees characteristic of late-successional stands can create larger gaps, allowing the persistence of pioneer species.

Although the gap dynamics concept has generality, it is an abstract simplification of actual forest dynamics (Lieberman et al. 1989). First, it is not well suited to forests lacking a closed canopy. Even in closed-canopy forests, gaps are not uniform in size, shape and orientation. Some gaps are filled by lateral growth rather than recruitment and vertical growth (Runkle & Yetter 1987). Others are not filled at all (Spies et al. 1990). The duration of gap and non-gap phases can vary greatly. In some cases, variation in gap frequency and duration

may be more important than gap-size variation in influencing the success of species differing in their light requirements (Canham 1989). Finally, gaps need not be directly overhead to influence the light regime and the growth of understorey stems (cf. Hunter & Barbour 2001). These issues are ignored in most models with constant patch (or gap) size. Models with higher spatial resolution can simulate these phenomena. Certainly, they provide more detailed information on physical structure and the spatial distribution of species (e.g. Moravie & Robert 2003).

Tree regeneration and recruitment limitation

Simulation of tree regeneration is a difficult problem (Bugmann 2001; Fulton & Harcombe 2002). Three potential weaknesses have been identified (Price et al. 2001). First, the various stages of regeneration from dispersal to establishment are often aggregated into one step. Second, assumptions of universal availability of propagules and environmental homogeneity are common. Third, effects of animals and pathogens are often ignored. Field studies suggesting that propagule availability can be patchy, and concentrated near parent trees contradict the second assumption (Ribbens et al. 1994; Reader et al. 1995). This patchiness can have strong implications for community composition and diversity (Clark et al. 1999; Hubbell et al. 1999). However, to what degree explicit simulation of propagule availability in space and time improves model projections of forest community dynamics is unclear. It has been suggested that propagules of most species are abundant, so the local composition of propagule pools does not have a strong influence on community dynamics (Shugart 1984; Bugmann 1994). However, this view is contradicted by the finding of Urban & Shugart (1992) that dominance of a species at a site could be reinforced by seed production of local adults. Also, Clark & Ji (1995) found that models assuming unlimited supplies of propagules were likely to overestimate species availability. In the latter case, the authors suggested that high availability was mitigated by the presence of highly competitive species that restrict recruitment of other species. In this case, a model assuming unlimited propagules might give the right results, but for the wrong reasons.

In general, the nature of recruitment limitation in forests is poorly understood and requires further empirical study as well as modelling analysis. Comparative studies using spatial, individual-based models are needed to further elucidate the effects of propagule abundance and dispersal. A minimum requirement of dynamic vegetation models is the ability to detect when propagules of a species are likely to be absent from a site and to limit regeneration accordingly.

Tree growth, competition and mortality

In JABOWA, tree growth was based on the fundamental physiological process of photoproduction minus respiration (Botkin et al. 1972). More elaborate process-based models of tree growth have been used (Sievanen et al. 1988; Moore 1989; Prentice & Leemans 1990; Friend et al. 1993; Williams 1996; Weishampel & Urban 1996; Weinstein et al. 2001). In all of these models it is assumed that the interaction of trees at the gap- or patch-level is sufficient to model tree competition and growth (but see Bossel & Krieger 1991).

Much empirical evidence supports the assumption that spatial competition formulas do not necessarily outperform non-spatial formulas (Opie 1968; Daniels et al. 1986; Lorimer 1983b; Tome & Burkhart 1989; Wimberly & Bare 1996). However, much of this evidence comes from tree plantations (Daniels 1976; Martin & Ek 1984) or thinning studies (Wimberly & Bare 1996) in which the spatial distribution of trees is regular and competition for resources is diminished. In other cases, models using distance-dependent competition indices are superior to their non-spatial counterparts in projecting tree growth (Pukkala 1989; Tham 1989; Mailly et al. 2003).

The value of spatial detail in modelling growth appears to depend on the structure of the forest and on the species involved. It may be especially important in mixed stands (Biging & Dobbertin 1992) or in irregular stands with marked clustering (Pretzsch 1995). In mixed stands, interactions between trees are more complex than in mono-species forests because of differences in crown sizes and form, leaf area density and rooting pattern.

Mortality is another process requiring attention. Even if models with low spatial resolution are sufficient to generate reasonable tree growth rates, they may be unable to generate population and community patterns effectively because mortality is modelled incorrectly. For example, Huston (1992) noted that gap- or patch-level simulators do not produce realistic thinning curves for developing stands. However, simulators with horizontal spatial considerations can (Busing 1991, 1995). Furthermore, comparisons of actual and simulated spatial pattern suggest that models with detailed consideration of inter-tree distance effects on competition generate more realistic horizontal dispersion patterns of surviving trees than those without distance-weighted competition (Busing 1999).

In addition to the effect of spatial pattern on mortality, the pattern of mortality may also be important because it affects stand dynamics. For example, simulators with horizontal detail show that when simulated disturbance patches are small and isolated, the recruitment of pioneer species is minimal (Busing 1995; Mailly et al. 2000; Coates et al. 2003). By contrast, highly clumped mortality of canopy trees, creates large disturbance patches that enhance levels of pioneer species (Busing 1995; Coates et al. 2003). Even when overall disturbance severity (e.g. basal area loss) is equal among regimes, only a large-patch regime substantially enhances pioneer species importance (Busing 1995).

Based on the discussion above, we recommend a few fundamental improvements to the spatial simulation of tree growth, competition and mortality. First, the capacity for slow growth and persistence of certain subordinate trees, including those in the shaded understorey, should be accommodated. Enhancing growth and persistence of subordinate trees does not necessarily involve spatial enhancements in the horizontal dimensions (e.g. FORSKA; Prentice & Leemans 1990; Leemans 1992). However, given that nearby openings can enhance the growth and persistence of understorey trees, some horizontal spatial structure is likely to improve the accuracy of modelled competition effects on understorey trees (e.g. Mailly et al. 2000).

Second, a range of patch sizes is desirable because of the potential effects of gap size on composition. At first glance, this would seem to require horizontal spatial structure with resolution at the scale of small gaps or higher. However, it is possible that patch-size effects can be approximated by models with a larger, fixed patch size (ca. 0.1 ha) and little or no interaction among patches. In such models, a patch is usually occupied by several codominant canopy trees rather than a single dominant tree (as is the case in early gap models), and severity of disturbance depends on the fraction of canopy trees killed. A large-gap response occurs only when all canopy trees on a patch are killed. How effective patch models with codominant trees might be in comparison with spatially intensive models has not been evaluated rigorously. Nonetheless, it is clear that models with one canopy tree per patch and no interactions among patches cannot generate the variety of responses to disturbance size and pattern captured by more complex models (Urban et al. 1991).

Spatial resolution and scaling

Clearly, the individual-based framework is well suited to spatially explicit modelling, even at the scale of community- and ecosystem-dynamics over very large areas (Acevedo et al. 1995; Levin et al. 1997; Shugart 1998; Moorcroft et al. 2001). The question is whether or not the inclusion of spatial detail in simulations of interactions among trees improves simulation projections at other spatial scales. In some cases, it does. For example, when Pacala & Deutschman (1995) eliminated all horizontal heterogeneity in their stand-level SORTIE simulations the simulated forest had atypically low biomass and diversity. However, in subsequent work, Deutschman et al. (1999) tested various model versions that considered spatial locations of individual trees, but differed in spatial complexity of the light regime. In this case community dynamics did not differ substantially among model versions. The authors concluded that averaging at the gap level or 'at even broader scales, say blocks of neighbouring trees, would continue to provide adequate detail, but it remains true that some level of spatial detail regarding light regimes is essential.'

In similar investigations, comparisons of gap model simulations with and without spatial interaction among gap-sized patches have revealed potential limitations of the independent-patch approach used in JABOWA and FORET. For example, compositional dynamics generated by FORET and ZELIG diverged when large-gap disturbances were introduced into the simulations (Urban et al. 1991). ZELIG, with spatial interaction among patches, was able to detect larger gap sizes and respond with a marked increase in shade-intolerant trees. FORET, with no interaction among patches, could not, and produced only a mild increase in shade-intolerants. The ZELIG prediction is supported by empirical data from forests incurring repeated large-gap disturbances (Busing 1995).

From these simulation experiments we conclude that some consideration of spatial heterogeneity in the horizontal dimensions is beneficial for modelling stand dynamics. Sufficient horizontal resolution appears to lie between the neighbourhood (or canopy gap) patch and the individual tree. Further comparative studies among model versions with gap- or patch-level spatial resolution and versions with higher spatial resolution are needed to clarify the issue of relevant spatial detail.

Conclusions

Evidence to date suggests that: (1) models without three-dimensional spatial complexity can capture many aspects of forest compositional dynamics; (2) a potential weakness in this regard is their inability to capture the effects of disturbance patch size on species composition; (3) another potential weakness is their inability to simulate patchy dispersal of propagules; and (4) three-dimensional information such as crown depth and inter-tree distances can improve the accuracy of forest structural dynamics including thinning, spatial dispersion, and size distributions of trees and patches. Areas requiring additional work include spatial availability of propagules, spatial patterns of mortality, and spatial interactions among competing trees. Can tracking the location of each individual and accounting for detailed spatial interactions among neighbours (e.g. inter-tree distances) lead to improved simulation of individual tree growth and mortality? Does accurate simulation of individual tree growth really matter, or do patch-level aggregations suffice? Obviously, the answers to these questions will depend on the problem addressed. If the goal is to simulate small-scale spatial phenomena then spatial detail is essential. However, at larger spatial scales, the sensitivity of such projections to spatial complexity of the model is only beginning to be explored. Comparison of model projections from simulators differing only in their spatial complexity (e.g. Urban et al. 1991; Deutschman et al. 1999) is a viable approach.

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