MINI-REVIEW

Spatio-temporal development of forests − current trends in field methods and models

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We present a critical review of current trends in research of spatio-temporal development of forests. The paper addresses (1) field methods for the development of spatially-explicit models of forest dynamics and their integration in models of forest dynamics, (2) strengths and limitations of traditional patch models versus spatially-explicit, individual-based models, and (3) the potential for moment-based methods in the analysis of forest dynamics. These topics are discussed with reference to their potential for solving open questions in the studies of forest dynamics. The study of spatio-temporal processes provides a link between pattern and process in plant communities, and plays a crucial role in understanding ecosystem dynamics. In the last decade, the development of spatially-explicit, individual-based models shifted the focus of forest dynamics modelling from the dynamics of discrete patches to the interactions among individual organisms, thus encapsulating the theory of "neighbourhood" dynamics. In turn, the stochastic properties and the complexity of spatially-explicit, individual-based models gave rise to the development of a new suite of so-called moment-based models. These new models describe the dynamics of individuals and of pairs of individuals in terms of their densities, thus directly capturing second-order information on spatial structure. So far, this approach has not been applied to forests; we indicate extensions needed for such applications. Moment-based models may be an important complement to spatially explicit individual-based models in developing a general spatial theory of forest dynamics. However, both kinds of models currently focus on fine scales, whereas a critical issue in forest dynamics is to understand the interaction of fine-scale processes with coarser-scale disturbances. To obtain a more complete picture of forest dynamics, the relevant links and interactions between fine-, intermediate-, and coarse-scale processes ought to be identified. Intensive links between modelling work and field studies designed across different scales are a promising means to create a new perspective on forest dynamics.

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Studies of forest dynamics, i.e. of the changes of forest composition and structure over time, have received much scientific attention since the early concepts of forest succession by Cowles and Clements (Cowles 1899, Clements 1916 cited in Glenn–Lewin and van der Maarel 1992). The spatio-temporal development of forests may be described as changes of tree populations due to birth and colonization, growth, and death of trees. This biotic development is driven by disturbance events set on a stage of a spatially heterogeneous environment (White 1979, Pickett and White 1985, Spies and Turner 1999).

Spatio-temporal processes involve the development of spatial patterns over time, thus providing a link between pattern and process in plant communities, and playing a crucial role in understanding ecosystem dynamics. An important cornerstone in the study of spatio-temporal dynamics was Watt's synthesis "pattern and process in the plant community" (Watt 1947). He described plant communities as a mosaic of patches in different phases, with an orderly time sequence of phases at a given place. Watt's (1947) findings from his long-term field studies were extraordinarily influential during the second half of the last century (Leibundgut 1959, van der Maarel 1996). In particular, Watt's identification of phases in the dynamics of beech forests laid the foundation for the concept of gap-phase dynamics, which has become a dominant theme in forest ecology (Urban and Shugart 1992). Research on gap-phase dynamics originally focused on ecosystems in humid climates, where natural disturbances were generally of low intensity and small spatial extent (Brokaw 1985, Runkle 1985). At the same time, scientists working in more xeric ecosystems were documenting the pervasive role of coarse-scale disturbance by fires in structuring the spatio-temporal dynamics of entire landscapes (Lertzman et al. 1998).

These two lines of inquiry were united through the development of a theory of patch dynamics, in which the spatio-temporal dynamics of the system were described through a demographic analysis of the birth, growth, and death of patches rather than of individual organisms (Levin and Paine 1974, Shugart and West 1977, Urban 1990, Belsky and Canham 1994, Weishampel and Urban 1996). In its basic form, the theory treats ecosystems as mosaics of discrete and internally homogeneous patches created by disturbance events, embedded in a relatively uniform "matrix". Through succession, disturbance patches gradually fade into the background matrix. This approach has now been applied to a wide range of terrestrial and aquatic ecosystems, ranging from tropical savannas to coastal sea-grass communities (Loucks et al. 1985, Sousa 1985, Dayton et al. 1994, Botts 1997, Ramage and Schiel 1999, Jensen and Bell 2001). It has also had wide application in conservation biology (Pickett and Thompson 1978, Shugart and West 1981, White 1987, Baker 1992). As a first approximation, patch dynamics provide an apt and useful conceptual model for many ecosystems and landscapes.

The reason why Watt (1947) treated plant communities as a mosaic of patches was pragmatic: he found it "impractical" to describe communities in "terms of their characters" (the individual plants) and "their spatial relations to each other". More than 50 years after Watt's (1947) seminal paper, advances in spatial ecology allow for quantifications of both, the effects on and the responses of individual plants to their local spatial structure (Pacala 1997). The importance of local processes in plant interactions and of their effects on community dynamics is now widely acknowledged (Silander and Pacala 1985, Tilman 1994, Lehman and Tilman 1997, Amarasekare 2003, Murrell and Law 2003), giving rise to the development of a neighbourhood-oriented perspective in plant community dynamics (Stoll and Weiner 2000, Purves and Law 2002a). In forest dynamics, recognition of neighbourhood processes has so far mainly been in terms of the growth response of target trees to surrounding competitors (Biging and Dobbertin 1992, Stoll et al. 1994, Soares and Tomé 1999, Ledermann and Stage 2001). The community response to neighbourhood interactions, however, has rarely been characterised. Consequently, forest dynamics research faces major challenges (i) to describe vegetation development and spatial structures; (ii) to identify the relevant processes that generate spatial structures, e.g. disturbances, dispersal, species interactions, or herbivory; and (iii) to understand the consequences of the so generated spatial structures for community dynamics. The third challenge entails integrating processes acting at different scales, e.g. by studying the interaction of fine-scale neighbourhood processes with coarser-scale disturbances. To better understand the complex interplay of these processes and of their different intensity in driving forest dynamics in different systems and, within systems, at different temporal and spatial scales, forest ecologists

have collected a variety of empirical information. This includes information on disturbance regimes (Lorimer 1984, Pickett and White 1985, Lorimer and Frelich 1989, Duncan and Stewart 1991, Veblen et al. 1994, Parshall 1995, Villalba and Veblen 1997, Mast et al. 1998, Fischer et al. 2002) and on biotic processes and life-history traits of tree species in relation to heterogeneous habitats and disturbances (Runkle 1981, Lusk and Smith 1998, Lavorel and Chesson 1995, Lertzman 1995, Lehmann and Tilman 1997).

At the same time, the need for a comprehensive representation of the complex processes and their potential for simulation called for the application of computer models. The conceptual shift in forest dynamics described above, from the patch to the individual, was paralleled by the development of models of ecosystems dynamics. Starting from patch models, rapid advances in computing power over the past 20 years have led to a proliferation of spatially explicit individual-based models (DeAngelis and Gross 1992, Judson 1994, Grimm 1999). These models allow some degree of mechanistic realism to be incorporated into the modelling of neighbourhood interactions. Most recently, developments in moment-based methods in discrete and continuous space have sought to bridge the gulf between oversimplified, analytical mean-field models and highly complex, individual-based simulation models. Moment-based methods enable analysis of the non-linear, spatially localized, stochastic processes that underlie biologically generated spatial patterns (Pacala and Levin 1997, Dieckmann and Law 2000). Yet, with the exception of a pair-approximation model on a spatial lattice (Iwasa 2000), such approaches have not yet been applied to forest dynamics.

Although the need for intensive integration of empirical and modelling approaches is increasingly acknowledged (Jeltsch and Moloney 2002), examples of such integration in forest dynamics research are still rare. This also applies to the large body of spatial ecological theory which remains poorly tested by empirical methods (Murrell et al. 2001, Amarasekare 2003).

In this review we first present an overview of current field methods for studying biotic processes and disturbances. We stress the importance of including spatial processes in studies of forest dynamics and present two different modelling approaches that incorporate a neighbourhood-oriented perspective on forest dynamics by discussing, in turn, spatially-explicit, individual-based models and a new class of moment-based models. We particularly emphasize the latter family of models, because, so far, they have hardly been applied to forest dynamics studies and are not as well known to the ecological community. We suggest ways to strengthen the link between ecological theory and forest dynamics studies and discuss options for better integrating em-

pirical work and modelling in addressing future challenges in forest dynamics research.

Field methods

There are three basic approaches available for collecting information on change of forests with time: retrospective (e.g. "historical" photographs, pollen records), prospective (e.g. permanent sample plots), and space-for-time approaches (e.g. chronosequences). In the absence of long time series on permanent sample plots (PSPs), retrospective methods and chronosequences are most frequently used for studies of forest dynamics. The use of chronosequences requires the existence of similar sites, a precondition which is hard to meet. Pickett (1991) mentioned the suitability of space-for-time substitutions for getting insight into trends in life-history types, the order of dominant species, stages of succession, and regional differences. Which approach is the most appropriate depends mainly on the studied ecosystem, the research question, the available data, and also on the spatial scale of the studied processes. The formulation of a research question and the subsequent design of a field study always include a decision about grain and extent, even if not explicitly stated. The selection of the appropriate scale for the research question in mind is probably the most crucial decision that has to be made beforehand. However, such a decision is not always straightforward, particularly when the scale of the studied process is unclear.

Models of spatio-temporal processes rely heavily on empirical data that characterize the following processes in both space and time: (i) colonization (seed production, seed dispersal, and germination requirements), (ii) growth (growth potentials, competitive relationships), and (iii) death (mortality rates). Below, we briefly review field methods for collecting empirical data for these demographic processes and for characterizing disturbance regimes.

Colonization

Phenological observations and seed traps provide basic information on minimum diameters (or age) of maturation, flowering patterns, as well as the timing, frequency, and quantity of seed production for many species. More difficult to obtain is quantitative information on dispersal distances and patterns of dispersed seeds. Seed rain studies usually estimate seed production and dispersal from randomly placed seed traps in forest stands or in open areas using some regular orientation of seed traps around or adjacent to the potential seed source (Clark et al. 1999). This is based on assumptions on the origin of seeds in the trap which may bias the

results (Nathan and Mueller-Landau 2000). More precise predictions of seed dispersal patterns can be gained through the development of mechanistic models of seed dispersal (Nathan and Mueller-Landau 2000, Nathan et al. 2001). A second approach is to measure distance and distribution of already germinated seeds. Inverse modelling approaches using maximum-likelihood estimation were successfully used to estimate distribution and numbers of recruits relative to the distribution of parent trees in a stand (Ribbens et al. 1994). Problems with all these methods arise in dealing with far dispersers and stochastic (extreme) events that transport seeds over long distances, but may be very important for the survival and distribution of a particular species. Mechanistic models that couple seed release with aerodynamic processes are the most promising approach to derive dispersal distances of wind dispersed seeds of far dispersers (Greene and Johnson 1993, Clark et al. 1999, Jongejans and Telenius 2001, Nathan et al. 2001, 2002, 2003). While these models describe the movement of seeds from point sources, Cousens and Rawlinson (2001) showed that both the shape of plant canopies and the position of seeds within canopies influence the shape of seed shadows, particularly for species with short dispersal distances. More complexity is added when considering secondary dispersal or differential seed deposition patterns on different microsites, caused by different roughness of surfaces or preferences of zoochorous dispersed seeds (Nathan and Mueller-Landau 2000). Methods using already germinated seeds simultaneously account for non-random seed distribution and germination requirements, such as availability and distribution of safe sites, but the underlying processes are then very difficult to interpret.

Growth

In many models growth is included as the potential growth for an individual tree relative to its size and reduced by a competition factor, the latter being estimated based on the distance to neighbouring trees (Wykoff and Monserud 1987) or through direct light measurements (Pacala et al. 1993). The potential growth rate of a species is relatively easy to obtain using standard methods of growth and yield research, e.g. height-growth curves developed from stem analysis of top-height trees of even-aged stands (Heger 1968, Carmean and Lenthall 1989, Chen et al. 1998). However, actual growth varies from year to year mainly due to age (and size) related growth pattern, climate fluctuations, and changes in the light environment due to disturbances. Growth measurements on seedlings, saplings, and mature trees on permanent plots, in relation to measurements of local resources, provide the best source

of data for characterizing the response of species to resource variation. This can also include the feedback of neighbouring trees on resource availability. In the absence of long-term data, the use of tree rings to measure past growth along resource gradients provides a means for quantifying species-specific growth-responses (Pacala et al. 1994).

Mortality

Mortality is best studied in PSPs as they follow tree and cohort development through time, thus measuring mortality directly. In the absence of PSPs, dendrochronological methods can provide estimates of past mortality rates (Dynesius and Jonsson 1991). Alternatively, growth–mortality relationships for various tree species can be established using growth as an indicator of tree vigour and thus of mortality risk (Kobe et al. 1995, Wyckoff and Clark 2000, Gratzer et al. 2004).

Disturbance regimes

Depending on the system and type of disturbance, methods to reconstruct disturbance history include (1) descriptions and measurements of change in forest horizontal structure (Tanaka and Nakashizuka 1997, Valverde and Silvertown 1997), (2) age structure analysis (Duncan and Stewart 1991, Quigley and Platt 1996), and (3) dendroecological reconstructions of fire histories and gap creation events (Lorimer and Frelich 1989, Brown and Swetnam 1994, Cherubini et al. 1996, Nowacki and Abrams 1997, Villalba and Veblen 1997). A variety of methods have been developed for quantifying interactions between different types of disturbances (Fischer 1992, Veblen et al. 1994) and between weather patterns and disturbance events (Villalba and Veblen 1997, 1998, Mast et al. 1998), especially for forest fires and insect outbreaks. Except for studies using charcoal records and pollen data (Calcote 1995, Long et al. 1998), most of these methods are limited in the time domain, as they cannot provide information on events dating back to before the last stand-replacing disturbance. Limitations in space are imposed by the extent and grain of the study and the data available for the reconstruction. These limitations must be made explicit since disturbance regimes can only be defined for a particular area. Consequently, results obtained through such studies are only valid at the observed scale, while, e.g. extrapolating results to larger scales will underestimate coarse-scale disturbances (Wimberly et al. 2000).

Models of forest dynamics

Patch models

The numerous patch models available in the literature can be sub-divided into two major categories:

- Finite state automata (Shugart 1998) or state-transition models classify vegetation on a given patch into a finite number of states and assign transition probabilities from one state to another, depending on the presence of a system-driving operator. The most common operator in these models is the passage of time, but others can readily be considered, for instance, disturbances such as fire (Kessel and Potter 1980, Gullison and Bourque 2001).
- Individual tree models keep track of the birth, growth, and death of each individual tree on the simulated patches (Botkin et al. 1972, Shugart and West 1977, Kienast 1987, Leemans and Prentice 1989, Bugmann 1994). The earliest of these models were developed in forestry to predict the growth of forest stands (Newnham 1964).

Most patch models based on individual trees follow the concept of the JABOWA model pioneered by Botkin et al. in the 1970s. The model was originally developed as part of the Hubbard Brook ecosystem study in the north-eastern forests of the US to explain species composition and succession at sites along an altitudinal gradient under current climate (Botkin et al. 1972, Botkin 1993). The key assumptions of JABOWA are:

- The forest consists of many small patches of land each 0.01–0.1 ha in size which is approximately the area an adult individual tree can dominate. On the one hand this allows for an individual to achieve maximum size, on the other hand the death of a single large tree significantly influences the light regime at a patch.
- No interaction among the simulated patches is considered (i.e. the forest is either envisaged as a mosaic of independent patches or the simulated patches are taken to be independent samples from the entire forest).
- The position of each tree on a simulated patch is unknown. Horizontally, the model assumes homogeneous competition throughout the entire patch.
- All leaf biomass of each simulated tree is located at the top of the tree in an infinitely thin layer.

Over the years, there have been many modifications to the original model formulation. For comprehensive reviews see Bugmann (2001), Keane et al. (2001) and Price et al. (2001). Because of the relative ease of parameter estimation, numerous models were developed for a diverse range of ecosystems, including models for alpine tundra (Humphries et al. 1996) and prairie (Coffin and Lauenroth 1990). A major reason for ongoing model development and application is the need for individual-based simulators of vegetation change sensitive to climate, to assess the likely impacts of global climate change on forest composition and structure. Several review papers questioned the applicability of classical gap models for research on impacts of climate change due to erroneous scaling assumptions and misleading parameterization schemes (Loehle and LeBlanc 1996, Schenk 1996). Besides attempts to add more physiological realism with particular emphasis on a more mechanistic representation of carbon fixation and allocation (Friend et al. 1993, Prentice et al. 1993, Bugmann et al. 1997), model variants were developed that consider spatial interaction between patches. Amongst the earliest of these spatially explicit model variants was the ZELIG-model (Smith and Urban 1988, Urban 1990) where the patches are arranged on a rectangular grid corresponding to a total area of up to several hectares. Such model variants are useful for examining seed dispersal and other landscape processes that involve spatial interactions between patches, such as fire and insect outbreaks (Lexer and Hönninger 2001).

Spatially explicit individual-based models

Spatially explicit, individual-based models (SEIBs) such as ZELIG (Urban et al. 1989), and SORTIE (Pacala et al. 1996), shift the focus from dynamics of discrete patches to interactions among individual organisms, and allow a more detailed treatment of environmental heterogeneity at a variety of spatial scales.

Specifically, models such as ZELIG, which operates within the patch model paradigm of homogeneous competition within patches, and SORTIE, where dynamics evolve as a result of local dispersal and local competition, treat forests as sets of individual trees rather than as mosaics of discrete gaps. In changing the focus, these models encapsulate an emerging theory of "neighbourhood" dynamics, in which fine-scale spatial interactions regulate the demography of component tree species (Pacala et al. 1996). The specific mechanisms for these spatial processes take many forms:

- Seed dispersal and seedling recruitment are highly localized processes for many forest trees. Estimates of the mean seed and seedling dispersion distances away from parent trees are less than 20 m for many temperate tree species (Ribbens et al. 1994, Clark et al. 1998, LePage et al. 2000), although longer distance dispersal is also important (Greene and Johnson 1993, Clark et al. 1999). Stand structure and the presence of gaps within a stand also

influences effective seed dispersal distances (LePage et al. 2000).

- The spatial distribution and abundance of tree seed predators can be strongly influenced by the spatial distribution of seed sources (particularly of large-seeded tree species), with potentially significant effects on patterns of tree seedling establishment (Schnurr et al. 2002, Schnurr et al. 2004).
- The activity of even large herbivores such as white-tailed deer (*Odocoileus virginianus*) may be influenced by fine-scale spatial variation in both soil nutrient availability and the abundance and nitrogen content of saplings that form a critical winter food source (Tripler et al. 2002).
- Resource competition between sessile plants is clearly a spatial process. In the case of competition for light, the geometry of both solar radiation and plant canopies interacts with the spatial distribution of individuals to determine the availability of light to individuals in a forest (Canham et al. 1994, 1999). There is a large literature on tree competition based on phenomenological analyses of the distance to, size, and species of neighbouring trees (Bella 1971). Non-spatial models are often effective in describing relatively uniform and even-aged stands, but spatial models provide distinct advantages in more heterogeneous stands (Lorimer 1983).
- Tree species vary significantly in their effects on soil chemistry and soil nutrient availability (Zinke 1962, Finzi et al. 1998). The effects of mixtures of different tree species are not necessarily additive (Finzi and Canham 1998). When species effects are non-additive, non-spatial models are likely to either overestimate or underestimate average resource conditions within a stand.

The shift to SEIB models has been facilitated by the development of new methods of examining field data, in which measurements of environmental factors (e.g. light) and critical demographic rates (e.g. recruitment, growth, and mortality) are analyzed in terms of the spatial distributions of neighbouring trees and of physical environmental factors (Canham et al. 1994, 1999, 2004, Pacala et al. 1994, Ribbens et al. 1994, Kobe et al. 1995, LePage et al. 2000), as outlined in the section on field methods above. These methods allow a tight linkage between the models and the parameterization of these models based on field data, thus allowing quantification of uncertainty in both parameter values and model predictions (Pacala et al. 1996).

The shift to a neighbourhood perspective has also had important implications for analysis of forest disturbance regimes. Past studies of wind disturbance have tended to focus on the extremes of a gradient in windstorm severity, from very small, isolated treefall gaps with discrete edges (Brokaw 1985, Runkle 1985), to large,

catastrophic disturbance in which most canopy trees are felled (Canham and Loucks 1984, Peterson 2000). It is becoming increasingly clear that the wind disturbances which most frequently drive forest ecosystem dynamics in many temperate and tropical forests falls in between these extremes (Walker et al. 1991). Intermediate-severity storms (e.g. hurricanes, typhoons, extra-tropical cyclones, severe thunderstorms) create a wide range of damage across large regions, as a result of heterogeneity in topography and the meteorology of the storm event (Boose et al. 1994, Peterson and Pickett 1995), and because of variation among species and tree sizes in susceptibility to mortality or damage from winds of a given severity (Zimmerman et al. 1994, Canham et al. 2001). The extremely heterogeneous patterns of canopy disturbance created by these events are very difficult to incorporate in traditional patch models or theories. Patch dynamic models (Levin and Paine 1974) have traditionally used patch size as a metric of the magnitude of disturbance effect. This becomes untenable for intermediate-severity storms, in part because of the difficulty of identifying discrete edges to patches, but more fundamentally because it ignores the pronounced heterogeneity at a wide range of spatial scales that is so distinctive in intermediate-severity disturbance events.

Moment-based models

SEIB models have two properties, stochasticity and complexity, that cause difficulties when trying to extract succinct ecological predictions from these models. Stochasticity stems from the fact that – at the level of the individual – colonization, growth, and death are random events: in the corresponding models, no two realizations of a spatio-temporal process, based on different sets of random numbers, will give the same results. This can be instructive, for example, in estimating the expected natural range of variability in a finite-sized plot. But stochasticity also hides the underlying ecological signal, unless a great many realizations are carried out to obtain reliable averages. The complexity of SEIB models is evident from the intricate mechanisms they often try to incorporate, as noted above. Given the scope for incorporating such complexity, investigations by different groups of scientists will almost always differ in at least a few structural details, making it difficult to compare results and to assess reliably the structural stability of SEIB models (Grimm 1999).

These considerations motivate the development of theory in which the deterministic ecological signal embedded in SEIB models is itself the state variable, and in which mechanistic detail is subsumed by standard model components (Bolker and Pacala 1997, Law and Dieckmann 2000b). So-called moment-based models are a promising step in this direction, and are currently

being developed by translating earlier work in statistical physics into the context of biological populations of interacting individuals. The models jointly deal with the dynamics of the density p_i of individuals of type i, and of the density of pairs p_{ij} (r) of individuals of type i and j that are situated a distance r apart in space (types i and j could represent species for instance, or states such as size classes, or both). These densities are the first two moments of a spatial distribution of individuals, calculated by integration over the spatial distribution. The pair density is a member of a class of second-order statistics widely used in spatial pattern analysis (Dale et al. 2002, Wiegand and Moloney 2004); other related statistics include Ripley's K, the semi(co)variance, and the spatial covariance (Ripley 1977, Burrough 1995). One can think of moment-based models as stepping from the static description of spatial pattern to the dynamics of how spatial structures changes over time. Since the density of individuals lies at the core of nonspatial ecological theory, moment-based models contain the traditional nonspatial theory of population dynamics as a special case.

Since the original work on moment-based models in physics had focused on lattices, it was natural that lattice-based ecological models, the so-called pair approximation models, were also developed first (Matsuda et al. 1992). These models describe the densities p_{ij} of ij pairs where j is in a neighbourhood (of constant size z) of i on a lattice; there is no dependence on r in this case as all individuals in the neighbourhood are equivalent. Since the density of individuals can be obtained from the density of pairs by summing over partners, $p_i = \Sigma_j p_{ij}$, the former need not to be treated separately. To describe the dynamics $\frac{d}{dt} p_{ij}$ of pair densities, the pair approximation assumes that the densities of triplets with a focal individual i can simply be expressed as $p_{ijk} = p_{ij} p_k$. This can be interpreted by saying that the pair approximation only traces spatial correlations among neighbours and that, accordingly, any correlations of higher order or at longer distance are ignored. Despite this simplification, pair approximation models have been applied successfully to a fairly wide spectrum of ecological settings (Harada and Iwasa 1994, Satō et al. 1994, Harada et al. 1995, van Baalen 2000) and so far provide the only moment-based models that have been applied to forests (Iwasa 2000).

Individual trees, however, do not grow naturally on neatly arranged lattices, and therefore it is helpful to extend moment-based methods to spatial patterns given by collections of points in continuous space (Bolker and Pacala 1997, Dieckmann and Law 2000, Law and Dieckmann 2000a). Moment-based models in continuous space can be based on different assumptions about how to express the density of triplets p_{ijk} (r_{ij}, r_{jk}, r_{ki}) in terms of pair densities. Such assumptions are called "moment closures" and have recently been investigated in some detail (Dieckmann and Law 2000, Murrell et al. 2004). They are all based on the idea that the dynamics of triplet densities equilibrate more quickly than those of pair densities, such that, after a short transitory period, pair densities are sufficient to characterize the spatial structure of a system. While this time scale separation is often justified, certain spatio-temporal processes may defy such simplification, especially when containing long-range spatial structures.

Moment-based models in continuous space typically involve so-called dispersal and interaction kernels. As noted earlier, dispersal kernels are already well established in forest ecology and simply describe the probability density with which a seed of type i ends up at distance r from its parent. In animal ecology, a dispersal kernel can also be used to describe the movement of individuals throughout their life. An interaction kernel c_{ij} (r) weighs the impact of an individual j on an individual i over a spatial distance r. Such impact may lead, for example, to decreased growth or fecundity, or to increased mortality. Integrating the weights c_{ij} (r) over all distances r, we recover the interaction coefficients $\tilde{a}_{ij} = \int_0^\infty c_{ij}(r) \, 2\pi r dr$ of traditional ecological models such as the Lotka–Volterra model of competition (Begon et al. 1996). By contrast, for spatially structured populations the interaction coefficients are given by $a_{ij} = \frac{1}{p_i p_j} \int_0^\infty c_{ij}(r) p_{ij}(r) \, 2\pi r dr$ and, importantly, thus turn out to directly depend on the pair densities p_{ij} (r) that serve as the state variables of moment-based models in continuous space. An interaction kernel thus allows for summing over all interacting pairs in a neighbourhood with the appropriate weights and thus formally brings such sums into a description of the spatio-temporal population dynamics. By defining SEIB models in terms of dispersal and interaction kernels and by then studying the resultant dynamics of pair densities, moment-based models help to establish a more canonical modelling platform. This is likely to aid the systematic comparison of results between models of different systems.

Moment-based models can account for two types of corrections relative to nonspatial models (Dieckmann and Law 2000). First are correlation corrections, arising from the non-random distribution of individuals, as measured by pair densities. The traditional non-spatial models do not consider spatial correlations, which implies $p_{ij} = p_i p_j$ and thus $a_{ij} = \tilde{a}_{ij}$. Once some spatial structure is present, $a_{ij} - \tilde{a}_{ij}$ is different from zero and measures corrections resulting from the spatial correlations present in the ecological pattern. A second type of improvement – ignored by non-spatial models but potentially captured by moment-based models – are fluctuation corrections. These arise from the fact that, even in a hypothetical, infinitely large habitat, the number of individuals in a local neighbourhood is finite and varies from one neighbourhood to another, with the

result that different individuals are bound to experience different local environments. Unless the ecological responses of individuals to densities in their neighbourhood are linear – which rarely will be the case – their response to the average local environment then differs from their average response to the different environments. In particular canopy structure and asymmetric competition for light are likely to induce such nonlinearities in the response of individuals to their local environment. Moment-based models can capture these potentially large differences through fluctuation corrections.

There still exists an appreciable gap between sufficiently realistic models of forest dynamics and models currently amenable to theoretical analyses. Three extensions could strengthen the utility of moment-based models for studying forest dynamics:

- The most important extension needed is systematic incorporation of size structure in moment-based models. With such additional structure, pair densities take three arguments, p_{ij} (s_i, s_j, r), and describe the densities of pairs formed by individuals of species i and size s_i with individuals of species j and size s_j at distance r. The study of competition kernels has already gone some way towards analyzing these dependencies on size and distance (Biging and Dobbertin 1992, Stoll et al. 1994, Soares and Tomé 1999, Ledermann and Stage 2001, Purves and Law 2002b), but their effects on population dynamics have still to be explored.
- A second important extension will be the incorporation of heterogeneities in local environmental conditions e. This can be achieved through the introduction of extra pair densities into moment-based models, p_{ie} (r) for density-like environmental factors (like nutrient concentrations) or p_{ie} (e, r) for other factors (like temperature; Law et al. 2001).
- Thirdly, disturbances could be implemented in moment-based models by describing the signature of their impact on pair densities. Depending on their frequency of occurrence, such disturbances can be incorporated in moment-based models either as a continuous deterministic flow or through discrete stochastic events.

Perspectives and conclusions

The role of SEIB models

SEIB models in forest ecology have been a great success: they overcome the often artificial spatial discreteness of patch models, respect the discreteness of individuals, and encourage a mechanistic representation of factors determining vital rates. It was through the development of SEIB models that the importance of neighbourhood

processes for forest dynamics was demonstrated (Pacala and Deutschman 1995, Kubo et al. 1996, Pacala 1997, Jeltsch and Moloney 2002, Purves and Law 2002a,b). The neighbourhood-oriented perspective adopted in SEIB models thus provides a general framework for studying and understanding forest dynamics by overcoming key limitations of traditional non-spatial models. However, SEIB models are computationally demanding and thus limited to stand scales. For applications at coarser scales, spatially explicit patch models are currently the only feasible modelling approach at hand (Bugmann 2001).

The application of SEIB models helped to identify a number of fine-scale neighbourhood processes as driving forces for tree-population dynamics. However, while some of these processes – e.g. seed dispersal (Chave 1999, Clark et al. 1999, Pastor et al. 1999, Bleher et al. 2002) and competition for light (Canham et al. 1994, 1999, Chave 1999) – are well described and readily included, other pattern generating processes – like plant–soil feedback or interaction with herbivores – are still only rarely included in tree population models, even though they are empirically well documented (Binkley and Giardina 1998, Van Breemen and Finzi 1998, Pastor et al. 1999). Thus, if one of the major challenges in understanding forest dynamics remains the identification of important pattern-generating mechanisms at different spatial and temporal scales (Levin and Pacala 1997, Parker and Pickett 1998), SEIB models through their close linkage with field studies, provide a promising route for this endeavour, because of their rich potential for exploring the consequences of intricate spatial interactions.

The potential of moment-based models

The promise of moment-based models lies in their canonical structure and greater mathematical tractability. As an alternative to including ever more mechanistic detail, moment-based models may be a good complement to SEIB models in developing a general spatial theory of forest dynamics. Yet, the extensions needed for moment-based models to reflect some specific features of forest dynamics are by no means trivial: for instance, incorporating size dependences, environmental heterogeneities, and spatial disturbances pose many interesting challenges for theorists and empiricists. Even with the simplification that moment-based models allow, there will be intricate couplings of variables in the dynamics. While it would be unrealistic to expect general analytical mathematical insights from such models in the immediate future, numerical analyses are readily feasible.

Yet, whenever a wide range of complex ecological mechanisms is to be considered simultaneously, or when a tactical match with the quantitative details of a

particular ecosystem is required and sufficient data is available for model parameterisation, individual-based models are likely to prove superior because of their essentially unlimited flexibility. In other cases, moment-based models may offer a useful middle ground.

Links between field studies and models

Even with more models developed and parameterised, empirical studies will remain fundamental to progress in understanding forest dynamics. Both SEIB and moment-based models have stimulated recent empirical work in forest dynamics by highlighting the need for quantifying certain mechanistic assumptions about, e.g. competition and dispersal. The development of new methods of analysis of field data is largely triggered by the current gaps in our knowledge, which become evident in the process of parameterising the corresponding models. Still, information on resource–mortality and resource–growth responses, as well as on dispersal distances, is missing for many tree species around the world (Chave 1999, Gratzer et al. 2004). Such information is not only necessary for modelling forest dynamics but also for its own right and for applications in forest management.

Future interactions between models and field work will go far beyond the traditional unidirectional way of data collection for model development and parameterisation. It is already clear now that models will become a more integral part of studies on forest dynamics: models will be used for hypothesis generation before empirical studies are devised and carried out, for assessing the grain and extent of empirical studies adequate for capturing essential properties of the ecological processes under investigation, and for extrapolating results of empirical studies to longer time scales. It will thus be fruitful to explicitly plan for the interaction between empirical and modelling work by identifying the desired connections in advance, allowing for bi-directional feedback and continuous progress.

One of the crucial problems in understanding forest dynamics is the frequent lack of adequate data for validating model results. Long-term ecological studies ought to fill this gap by capturing slow phenomena, rare events, as well as subtle and complex processes (Pickett 1991). To achieve this in the context of forest dynamics, long-term ecological studies will have to extend over decades.

On the interaction of fine scale neighbourhood processes with coarser scale disturbances

A critical issue in forest dynamics is to understand the interaction of fine-scale neighbourhood processes with coarser-scale disturbances. In the section on field methods we presented state-of-the-art methods for analyzing disturbance regimes. All of the presented approaches struggle with temporal and spatial limitations (Lertzman and Fall 1998). At least the former limitation can be overcome by using spatially explicit models. So far, however, only few attempts in this direction have been undertaken (Wiegand et al. 1998, Canham et al. 2001, Ménard et al. 2002).

By linking a neighbourhood-oriented perspective on forest development with an approach from disturbance ecology, Dubé et al. (2001) bridged the gap between these two realms of investigating forest dynamics. They characterized canopy gaps according to a species' light requirements and could thus move beyond the (practically useful but theoretically often unjustified) geometrical characterization of gaps or expanded gaps. This can be seen as an extension of the neighbourhood perspective towards disturbance ecology. Most studies simulating disturbances are based on simply removing trees of different diameters (Menard et al. 2002), even though this practice ignores the specific characteristics of disturbance events. In general, disturbances vary not only in size but also greatly differ in severity and residuals (Turner et al. 1998): they therefore leave "fingerprints" in the landscape that are specific to the characteristics of the disturbance (disturbance agents and intensity) but also depend on species- and structure-specific susceptibilities to the disturbances. Models of disturbances might have to consider these species-specific feedback mechanisms (the creation of micro-sites and the response of regeneration to these spatial heterogeneities and to the presence of surviving seed trees) in order to capture the essential effects of disturbances on forest dynamics.

If also interactions between disturbances are to be considered, even more complexity has to be added to models. Such complexity across scales requires strategies for dealing with scaling issues. The most promising way of addressing this would be an application of hierarchy theory (Pattee 1973, Allen and Hoekstra 1992, Ahl and Allen 1996). The theory is based on the assumption that ecological systems exhibit a loose vertical and horizontal coupling in structure and function and are thus highly decomposable. Such a loose coupling allows for distinguishing between different hierarchical levels (vertical) and sub-systems (horizontal) at the same vertical level (Parker and Pickett 1998, Wu 1999, Wu and David 2002). However, whether or not coupling in nature typically are sufficiently loose to justify such simplification currently remains an open empirical question.

Both SEIB models and moment-based methods in continuous space are working on fine spatial scales. To obtain a more complete picture of forest dynamics, and to move towards a general theory for the spatio-temporal developments of forests, all relevant links and interactions between processes at fine, intermediate, and coarse spatial scales must be identified and understood.

Field studies designed across different scales, in conjunction with models describing the spatio-temporal development of forests, would seem to offer the most promising means for creating a new perspective on forest dynamics.

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