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Aggregation of Individual Trees and Patches in Forest Succession Models: Capturing Variability with Height Structured, Random, Spatial Distributions

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Individual based, stochastic forest patch models have the potential to realistically describe forest dynamics. However, they are mathematically intransparent and need long computing times. We simplified such a forest patch model by aggregating the individual trees on many patches to height-structured tree populations with theoretical random dispersions over the whole simulated forest area. The resulting distribution-based model produced results similar to those of the patch model under a wide range of conditions. We concluded that the height-structured tree dispersion is an adequate population descriptor to capture the stochastic variability in a forest and that the new approach is generally applicable to any patch model. The simplified model required only 4.1% of the computing time needed by the patch model. Hence, this new model type is well-suited for applications where a large number of dynamic forest simulations is required.

***Key Words*: forest succession; individual based model; stochastic model; patch model; aggregation; structured population; model simplification; spatial distribution.**

INTRODUCTION

The dynamics of populations are determined by birth, death, the change in the state of individuals, and the interactions between them and also by exogenous events such as disturbances. Individuals differ with respect to their properties or states, such as size or age, they may experience spatially heterogeneous living conditions, such as nutrient supply, and they may also be affected differentially by random events, i.e. by demographic or environmental stochasticity (Turelli, 1986). These differences among indi-viduals lead to a variability in the population which can strongly influence its overall dynamics (Koehl, 1989; May, 1986).

Individual-based, stochastic models are one approach to account for this variability, since they describe explicitly the processes and interactions of the individuals and also include random events, e.g. the death of one particular organism. Thus, they have the potential to describe the dynamics of entire populations realistically (Grimm *et al.*, 1996; Murdoch *et al.*, 1992), i.e., close to what can be observed in nature, and to give insight into the mechanisms of community dynamics (McCook, 1994; Shugart, 1984).

In describing the dynamics of forest populations and communities, the individual based patch (or gap) model approach has a long tradition. It reaches back to the development of JABOWA (Botkin *et al.*, 1970; Botkin *et*

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al., 1972a; Botkin *et al.*, 1972b) and its successors like FORENA (Solomon *et al.*, 1981), FORET (Shugart and West, 1977), FORECE (Kienast, 1987), FORSKA (Leemans and Prentice, 1989), ZELIG (Urban *et al.*, 1991), SIMA (Kellomäki *et al.*, 1992), and the models FORSUM (Kräuchi and Kienast, 1993) and FORCLIM (Bugmann, 1994; Bugmann, 1996; Fischlin *et al.*, 1995).

A patch model uses Monte Carlo simulations to describe the stochastic dynamics of individual trees or cohorts of trees on many small patches at a specific site. These patches have the approximate size of the canopy area of one dominating tree (about 1/12 ha). The concept is based on two fundamental assumptions: **(1)** Interactions among trees occur only locally and population densities on these small areas are too small to average out stochastic effects in the tree dynamics (Drury and Nisbet, 1973; Remmert, 1991; Watt, 1947). **(2)** Usually, birth and death are treated as intrinsicly stochastic processes. Consequently, the resulting forest succession is a stochastic process which accounts for the stochastic variability in forests (Shugart and West, 1979).

Besides the advantage of including variability, the basic idea of patch models to simulate single trees is straightforward and easy to comprehend. Much effort and expertise have been put into the accurate formulation of the model equations and the identification of the model parameters. Patch models have been tested and applied under various conditions (Bugmann, 1994; Bugmann and Fischlin, 1996; Bugmann and Solomon, 1995; Lischke *et al.*, 1998; Kellomäki *et al.*, 1992; Prentice, 1986; Shugart and Prentice, 1992; Solomon *et al.*, 1981). Thus, they are considered as reliable models in studying and projecting forest dynamics.

However, forest patch models, together with other stochastic individual based models have several disadvantages. They are not well suited to be analysed mathematically, partly because they are often only defined as an algorithm or a computer code and not in a mathematically closed form. Analytical equilibrium and stability analysis is practically impossible for models of this type. Moreover, to obtain sound results, many variates have to be sampled from the stochastic processes described by such a model (Bugmann *et al.*, 1996). Typically, these Monte Carlo methods require large computing times, which renders the model ungainly for applications where many or long simulation runs are required.

We asked whether it is possible to derive from such an individual based model a simpler, faster, and mathematically better tractable model, which produces similar results for the expected values of the overall dynamics.

One obvious solution is to aggregate individuals into a hierarchically higher level (O'Neill *et al.*, 1986), such as (sub)populations described by densities and to replace the random variates of the process rates resulting from the Monte Carlo simulation by average rates. Such an approach belongs to the class of problems which deals with the aggregation of components of ecological models from a lower to a higher hierarchical, temporal, or spatial level (Auger and Roussarie, 1994; Cale and Odell, 1979; Gard, 1988; Gardner *et al.*, 1982; Iwasa *et al.*, 1989; Murdoch *et al.*, 1992).

A crucial question in this context is: What is the minimal level of aggregation required to incorporate the intrinsic variability of a forest? Obviously, it can not just be the averaged trees of each species, since trees and their living conditions differ and "the average of the solution of an equation, in general, is not the solution of the averaged equation" (Hornung, 1996). Thus, how can we "...consider the effects of patchiness, which not only affect the statistical variability but have a profound effect on the nature of the dynamic interactions." (Steele, 1989)?

Examples for aggregating tree individuals to subpopulations are the model FLAM by Fulton (1991) which was derived from an individual based forest patch model, and the canopy layer model FORMIX(2) by Bossel and Krieger (1991, 1994). In these models trees of similar height are combined to height or developmental stage classes. However, both models are still based on Monte Carlo simulations in order to include variability: Birth and death, in FLAM also growth, are formulated as random events, and both models simulate the dynamics on many patches.

In this paper we present a new type of forest dynamics models, resulting from the aggregation of a forest patch model, which also uses an explicit height structure, i.e., assumes the forest consists of several discrete height layers (discs). In this respect the approach is similar to structured population models (Metz, 1986), which have also been applied to forests (Karev, 1994; Kohyama, 1992; Pacala and Deutschman, 1995). The new concept of this model type is to take into account the stochastic variability in a forest by horizontal distributions of tree densities, which replace the distinct patches and the random variates of the Monte Carlo simulation used in patch models. One example is the distribution based climate driven forest model DISCFORM, which we aggregated from the forest patch model FORCLIM (Bugmann, 1994; Bugmann, 1996; Fischlin *et al.*, 1995), hereby taking advantage of the expertise contained in the latter model.

MATERIAL AND METHODS

The Patch Model ForClim

ForClim is a forest patch model, which can be generally used where the needed species parameters are available. It was developed to study the influences of a changing climate on forests in the northern temperate and boreal zone, and particularly in the European Alps.

We focus on the submodel ForClim-P (version 2.4.0.2), which uses as input the expected values of bioclimatic variables, e.g., drought stress or day-degree-sum, calculated in advance by the submodel ForClim-E from inter-annual means, standard deviations and correlation coefficients of monthly temperature and precipitation.

ForClim-P simulates the stochastic dynamics of tree cohorts for any number (e.g., 30 for Central Europe; see legend of Fig. 3) of different species usually on 200 patches which are assumed to be independent of each other. These patches represent different realisations of the stochastic process running at a specific site. We interpret these realisations in the following as different patches of a forest area with spatially homogenous soil and climatic conditions. The model follows the fate, i.e., establishment, growth, and death, of every single tree cohort. All processes depend explicitly on climate and on the available light intensity at the tree top. Birth and death are formulated stochastically, i.e., as probabilities for each cohort, that individual trees are born or die. Since the focus of the model is on the successional dynamics of forests, population genetics are neglected. Furthermore, establishment occurs from a constant seed pool, which is independent from the parent population density.

Simulation Environment

The new model DisCForM was implemented and developed with the interactive part of the simulation environment RAMSES[2] (Fischlin, 1991). To improve the performance of the implementation (Doud, 1993; Löffler, 1995), we optimized the code by evaluating time and state independent expressions in advance, outside the integration loop. For comparison, simulations of DisCForM and ForClim-P were run on a SUNserver MP630 (40 MHz) under RASS (Thoeny *et al.*, 1994), the batch simulation server of RAMSES.

Sites and Forest Data

The simulations of both models were run for 1200 years with a yearly time step. Input included the same constant bioclimatic and edaphic data from seven climatically different sites in Switzerland (Table 1).

For the colline, upper montane, and subalpine vegetation belt, represented by the sites Bern, Davos, and St. Gotthard, respectively, we compared qualitatively the simulated equilibrium species compositions to data of species compositions (Fig. 3d), compiled from the First Swiss National Forest Inventory (WSL, 1997), which consists 0.05 ha sample plots on an 1-km grid. In Switzerland the majority of the forests are managed. In order to include only plots in forests as close to natural as possible and to obtain still a reasonable sample size we, therefore, restricted the evaluated sample plots to all those, where the last management was longer than 25 years ago and regeneration was natural. To take into account only plots with similar conditions, plots from 50 m below to 50 m above the altitude of the sites from surrounding regions (Table 2) were included; the regions had to be chosen rather large to increase the sample size. The plots were split according to the estimated age of the surrounding stands, i.e., whether they were likely to represent rather an early or an intermediate successional state (stand age <80 or $\geqslant 80$ years). For stands of mixed developmental state stand age was not available; we assumed them to correspond to the mixed age structure of the shifting-mosaic climax (Bormann and Likens, 1979; Remmert, 1991). Table 2 shows the numbers of plots in the three age classes. Wood biovolumen was estimated (Kaufmann, 1996) from stem diameter at breast height (DBH) for all trees with DBH > 12cm and multiplied by species specific density factors (Knigge and Schulz, 1966; Lakida *et al.*, 1995; Niemz, 1993; Trendelenburg and Mayer-Wegelin, 1955) to obtain biomass in dry weight, same as in the models.

TABLE 1

Characteristics of Sites Used to Test the Forest Models DisCForM and ForClim-P

Site	Elevation (m.a.s.l.)	Annual mean temperature (°C)	Annual precipitation sum (cm)
Locarno	379	11.8	184.6
Sion	542	9.7	59.7
Bern	570	8.4	100.6
Huttwil	639	8.1	128.7
Davos	1590	3.0	100.7
Bever	1712	1.5	84.1
St. Gotthard	2090	−0.07	216.2

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[2] RAMSES can be downloaded by anonymous ftp from ftp.ito.umnw.ethz.ch (Internet address: 129.132.80.130). For information s. homepage at URL http://www.ito.umnw.ethz.ch/SysEcol.

TABLE 2

Characteristics of Swiss National Forest Inventory Plots (WSL, 1997) Included in the Evaluation of Near-Natural Forest Composition: sites, vegetation zones represented by the sites, regions included in evaluation, and number of plots of different stand ages

Site	Vegetation belt	Swiss regions included in evaluation	Numbers of plots of stand age (years)			Number of species in equilibrium			
			<80	$\geqslant 80$	mixed	FC	DF_D	DF_V	Data
Bern	Colline	Jura, Central Plateau, Prealps	9	14	8	10	2	16	7
Davos	Upper montane	Alps	9	15	31	5	2	8	5
St. Gotthard	Subalpine	Alps	2	6	20	3	1	3	3

Note. Number of species with biomass $>1\%$ of total biomass in equilibrium of simulations with ForClimm-P (FC), DisCForM without variability (DF_D) and with variability (DF_V), and in the mixed age plots of the NFI (Data).

Similarity Index and Run-Time Measurment

As a quantitative measure of similarity between the results (x and y) of the two models we took the similarity index S (Bugmann, 1994; Cormack, 1971; Wolda, 1981) and extended it to time series by

$$S = 1 - \frac{\sum_i \sum_k |x_{i,k} - y_{i,k}|}{\sum_i \sum_k (x_{i,k} + y_{i,k})} \tag{1}$$

with k running over all species and i over the entire simulation period, encompassing transient and steady state behaviour. Computing times were measured by recording start and end time of each simulation.

Data of Tree Dispersions

For the evaluation of spatial tree distributions we used the data of an extensively managed larch forest in Samedan, which is located in the Upper Engadine, Swiss Alps (Baltensweiler and Rubli, 1984). These data are given as DBH and position of each tree on a profile consisting of 14 quadratic plots, each with a size of about 100m^2. The tree density n ($1/100\text{m}^2$) in each plot, the mean tree density $\bar{n}$, and the empirical distribution of the tree density over all plots were determined separately for each of four DBH-classes (0–17.9cm, 17.9–35.7cm, 35.7–53.6cm, and 53.6–89.3cm). The DBH was transformed into height by using the empirical allometric relationship (Ker and Smith, 1955)

$$H = 137 + \frac{2(H_{\max} - 137)}{DBH_{\max}} \cdot DBH - \frac{(H_{\max} - 137)}{DBH_{\max}^2} \cdot DBH^2$$

with the maximum height $H_{\max}$ and maximum DBH $DBH_{\max}$, which are for larch equal to 52m and 1.85m, respectively (Bugmann, 1994). This leads to the height classes 0–10m, 10–19m, 19–26m, and 26–38m.

Then we tested by a χ^2 goodness of fit test (significance levels $\alpha = 0.01$, 0.05, 0.1, 0.2) the hypotheses $H_{0,1}$ and $H_{0,2}$, that the empirical distributions in the distinct height classes can be described by a Poisson distribution and by the positive part of a Normal distribution with both mean and variance equal to $\bar{n}$.

DERIVATION AND STRUCTURE OF DISCFORM

In a first attempt to aggregate the patch model, we modelled tree populations deterministically both with and without height structure. Because those models could not reproduce the patch model's population dynamics, but yielded forests with too few species in the equilibrium, we concluded that the stochastic variability between patches cannot be completely ignored.

The only interaction between trees modelled explicitly in ForClim-P, as in many other forest patch models, is the inter- and intraspecific competition for light. The light available for each tree is reduced by the shade of all trees above its top (Fig. 1a); the leaves of the trees are assumed to be concentrated at their tops. This means that the actual height structure, i.e., the height distribution of the tree tops in a patch at a certain time, determines the vertical light gradient in this patch.

The tree tops in ForClim-P are not only distributed vertically. Whereas in each single patch all trees are assumed to be located at the same position, tree densities differ between patches due to the stochastic model formulation. This corresponds to a horizontal distribution of trees of a certain height over all patches. The spatial,

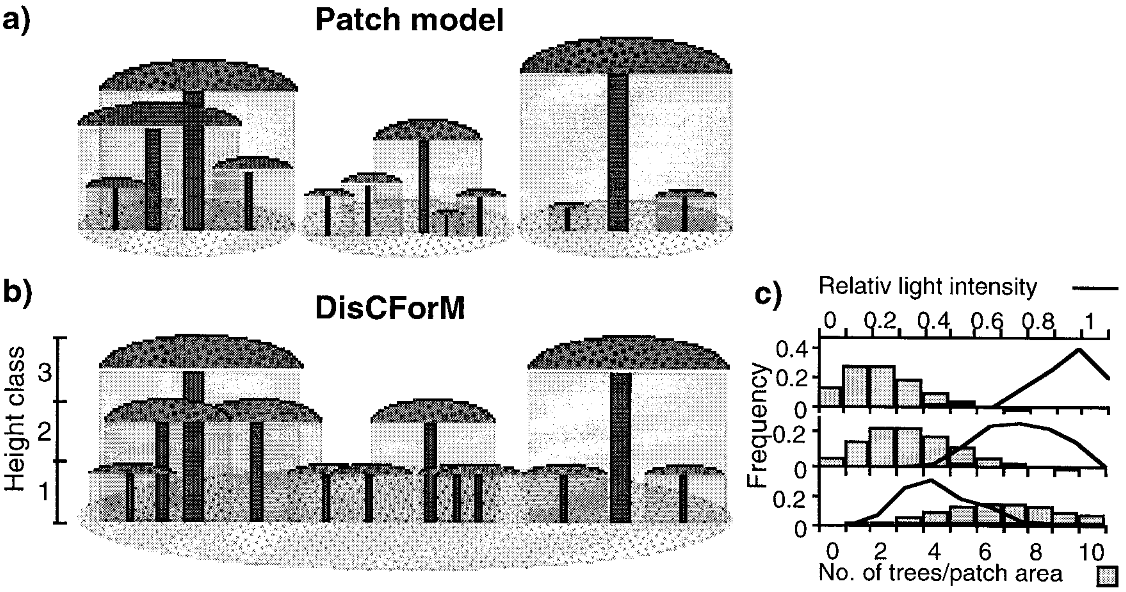

FIG. 1. Distribution of trees and light in a forest, as simulated by a conventional forest patch model and the new model DisCForM. In both cases the leaves are assumed to be concentrated at the tree top. The grey areas portray the shading by the canopy: (a) In a conventional forest patch model individual tree dynamics produce a continuous vertical distribution of tree heights and light within each distinct patch; (b) In DisCForM the patches are lumped together to form a forest, which consists of a stack of discrete height classes ("forest discs," here three height classes are shown). Within each forest disc, trees and the available light are distributed horizontally; (c) Density functions of tree population densities, (grey columns) and the available light (solid black line), in three forst discs as modelled by DisCForM. Within these discs the tree dispersion is assumed to be random and is modelled with a Poisson distribution.

i.e., vertical and horizontal, and temporally changing distribution of tree tops determines the spatial distribution of light (Fig. 1a) and influences tree to tree competition for light throughout the forest.

The new model DisCForM focuses on the temporal dynamics of these spatial tree and light distributions (Fig. 1b). The spatial distributions are represented by frequency distributions (Fig. 1c) of the density of tree tops per unit area and of the light intensity at a certain height.

The main differences between DisCForM and a patch model are: (1) The continuous height distribution of the trees is replaced by a discrete height structure. (2) The entire forest is simulated at once in each time step. The spatial distribution of trees per unit area is modelled by the assumption that in each time step all trees of a certain height are distributed randomly over the forest, which results in a Poisson distribution. Consequently, it is no longer feasible nor desirable to trace the fate of individual trees or cohorts.

With these assumptions and the process functions and parameter values of ForClim-P we get the following distribution based, height structured population dynamics model (a summarisation of the symbols is contained in Table 3):

$N_{s,i}$ is the average population density per patch area of trees of species s in the height class i in the entire forest. The rate of change of $N_{s,i}$ at time t (Eq. (2)) is determined by death $D_{s,i}$ (Eq. (3)), growth $G_{s,i}$ (Eq. (4)) and birth $B_{s,i}$ (Eq. (5)). Trees grow into height class i from height class $i-1$ ($G_{s,i-1}$) and leave height class i by outgrowing ($G_{s,i}$). Birth (Eq. (5)) is restricted to the lowest height class ($i=0$). These processes depend not only on state but they are also driven by time dependent input variables, namely temperature, precipitation and nitrogen. For easier reading we omit all explicit notation of time dependence in the following equations:

$$\frac{dN_{s,i}}{dt} = \underbrace{-D_{s,i}}_{\text{death}} + \underbrace{G_{s,i-1} - G_{s,i}}_{\text{growth}} \underbrace{+B_{s,i}}_{\text{birth}} \tag{2}$$

$$D_{s,i} = (\mu_{const,s} + (1 - \mu_{const,s}) \cdot \bar{\mu}_{s,i}) \cdot N_{s,i} \tag{3}$$

$$G_{s,i} = \frac{\bar{\gamma}_{s,i}}{h_{i+1} - h_i} \cdot N_{s,i} \tag{4}$$

$$B_{s,i} = \begin{cases} 0, & i > 0 \\ \bar{\beta}_s, & i = 0. \end{cases} \tag{5}$$

The species specific death, growth, and birth rates $\bar{\mu}_{s,i}$, $\bar{\gamma}_{s,i}$, and $\bar{\beta}_s$ are the expected values of the light dependent rates , $\mu_{s,i}(l)$, $\gamma_{s,i}(l)$, and $\beta_s(l)$ (for the specific formulation of the rates cf. Appendix 1). Since light

TABLE 3

Symbols Used

Symbol	*Meaning*	*Unit*
t	Time	year
h_i	Height of lower boundary of height class *i*	m
s	Species index	
$N_{s,i}$	Average population density of species *s* in height class *i* (per unit area)	m^{-2}
$D_{s,i}$	Dying trees of species *s* in height class *i*	$\mathrm{m}^{-2}\,\mathrm{year}^{-1}$
$G_{s,i}$	Trees of species *s* growing from height class *i* to height class $i+1$	$\mathrm{m}^{-2}\,\mathrm{year}^{-1}$
$B_{s,0}$	New saplings of tree species *s*	$\mathrm{m}^{-2}\,\mathrm{year}^{-1}$
$\bar{\mu}_{s,i}, \bar{\gamma}_{s,i}, \bar{\beta}_s$	Expected values of mortality, growth, and birth rates with respect to light intensity	year^{-1}, $\mathrm{m\,year}^{-1}$, $\mathrm{m}^{-2}\,\mathrm{year}^{-1}$
$\mu_{s,\mathrm{const}}$	Constant mortality of species *s*	year^{-1}
$\mu_{s,i}(l)$	Stress induced mortality of species *s* at light intensity *l* in height class *i*	year^{-1}
$\gamma_{s,i}(l)$	Per tree growth rate of species s at light intensity *l* in height class *i*	$\mathrm{m\,year}^{-1}$
$\gamma_{s,i,max}$	Maximal diameter increment of species *s* in height class *i*	$\mathrm{m\,year}^{-1}$
$\omega_{s,i}$	Diameter to height increment conversion factor	—
C_s	Climate dependence of growth of species *s*	—
$g_{1,s}, g_{2,s}, g_{3,s}$	Species parameters for light dependence	—
$\beta_S(l)$	Birth (establishment) rate of species *s* at light intensity *l*	$\mathrm{m}^{-2}\,\mathrm{year}^{-1}$
$l_{\beta\mathrm{crit},s}$	Critical light intensity for establishment of species *s*	—
$\beta_{max,s}$	Maximal establishment rate of species *s*, climate dependent	year^{-1}
$f_Y(y)$	Probability density function of random variable *Y*	—
L_i	Light in height class *i* (fraction of full light); random variable	—
$X_{s,j}$	Population density of species *s* in height class *j*; random variable	m^{-2}
ζ	unit area (set to usual patch size, $833\mathrm{m}^2 = 1/12\mathrm{ha}$)	m^2
$a_{s,j}$	Specific leaf area of trees of species *s* in height class *j*	m^2
LAI_i	Leave area index in height class *i*; random variable	—
α	Extinction coefficient (set to 0.25)	—
$\mu_{LAI_i}, \sigma_{LAI_i}$	Mean and standard deviation of leaf area index in height class *i*	—

intensity is a random variable, these expected values are calculated with the probability density function f_{L_i} of light intensity L_i in height class *i* by

$$\bar{\varphi} = \int_{-\infty}^{\infty} \varphi(l) \cdot f_{L_i}(l)\, dl = \int_0^1 \varphi(l) \cdot f_{L_i}(l)\, dl$$
$$\text{with} \quad \varphi = \mu_{s,i}, \gamma_{s,i}, \beta_s. \tag{6}$$

In order to be able to use (6) we have to determine the light density function f_{L_i}.

An essential assumption in our approach is that all trees of each species *s* in each height class *j* are randomly distributed over the patches, which for the tree population densities $X_{s,j}$ leads to a Poisson distribution with the mean $N_{s,j}$. Thus, the tree dispersion in each height class is independent of all other height classes. The Poisson distribution is then approximated by a Normal distribution with the same mean $N_{s,j}$ and the standard deviation $\sqrt{N_{s,j}}$.

Particularly for small means of a Poisson distribution this seems to be a crude approximation. Yet, tests with random numbers drawn from Poisson distributions with various parameters and from corresponding normal approximations which were truncated at zero and scaled to the area of one, indicated that the approximated distributions were satisfactorily similar in position and shape to the original ones. Additionally, the distribution of a linear combination of two Poisson distributed random variables was similar to the truncated normal distribution, which was obtained by first approximating the two Poisson distributions by Normal ones, then determining the Normal distribution of the linear combination of the two random variables, and then truncating and scaling this distribution.

This allows the following transformations:

Given a tree density of species *s* in height h_j of $X_{s,j}$ trees per unit area ζ (size of one patch) and a species and height specific, constant leaf area $a_{s,j}$ per tree, the leaf area index LAI_i in height class *i* is a random variable defined by

$$LAI_i = \frac{\sum_{j>i} \sum_s X_{s,j} \cdot a_{s,j}}{\zeta} \tag{7}$$

Since LAI_i in height class i is a linear function of the normally distributed tree densities $X_{s,j}$ in all height classes above class *i*, it is also normally distributed with the parameters

$$\mu_{LAI_i} = \frac{1}{\zeta}\sum_{j>i}\sum_{s} N_{s,j}\cdot a_{s,j},$$
$$\sigma_{LAI_i} = \frac{1}{\zeta}\sqrt{\sum_{j>i}\sum_{s} N_{s,j}\cdot a_{s,j}^{2}}. \tag{8}$$

With the full light intensity ($=1$) above the topmost height class and a the extinction coefficient of leaves, the light L_i which is transmitted down to height class *i* is described by $L_i = e^{-\alpha\cdot LAI_i}$. Thus, a certain light intensity L_i in height h_i is reached by the leaf area index LAI_i, which fulfils

$$LAI_i = -\frac{\ln(L_i)}{\alpha} \tag{9}$$

Using transformation (9), the light density function f_{L_i} can be expressed by the density function of the leaf area index f_{LAI_i} which is a normal distribution with the parameters μ_{LAI_i} and σ_{LAI_i} (Eq. (8)).

If $f_Y(y)$ is the density function of a random variable Y at a specific realisation y and X is another random variable $X = h(Y)$ with a unique function h and with the density function f_X, then $f_Y(y)$ can be expressed by $f_Y(y) = f_X(h(y))\cdot|dh(y)/dy|$ (Fisz, 1980). Hence,

$$f_{L_i}(l) = f_{LAI_i}\left(-\frac{\ln(l)}{\alpha}\right)\cdot\frac{1}{l\cdot\alpha}. \tag{10}$$

The density function f_{L_i} is scaled to 1 by $\int_0^1 f_{L_i}(l)\,dl \overset{!}{=} 1$ to partly compensate the errors introduced by replacing the Poisson by not truncated Normal distributions.

In the implementation light intensity was discretized into 10 light classes ξ, to be able to compute light dependent rates once in advance for accelerating the code. In this discrete formulation (6) turns to

$$\bar{\varphi} = \sum_{\xi=0}^{9} \varphi(l_\xi)\cdot(F_{L_i}(l_{\xi+1}) - F_{L_i}(l_\xi)), \tag{11}$$

where F_{L_i} is the distribution function of the light intensities which we can express by the normal distribution function of the leaf area index with the parameters μ_{LAI_i} and σ_{LAI_i} (Eq. (8)) by $F_{L_i}(l) = F_{LAI_i}(-\ln(l)/\alpha)$. With (11) the system of ordinary differential equations (2) can be solved.

EMPIRICAL TREE DISPERSIONS

The evaluation of the tree dispersion data from Samedan (Fig. 2) indicates that the choice of a Poisson distribution (hypothesis $H_{0,1}$), and also of its normal approximation (hypothesis $H_{0,2}$) for the theoretical tree dispersion, is acceptable. For three of four height classes both hypotheses could not be rejected (tested levels of significance: $\alpha = 0.2$, 0.1, 0.05, 0.01); only for one height class they were rejected (at $\alpha = 0.1$ ($H_{0,1}$) and $\alpha = 0.05$ ($H_{0,2}$)).

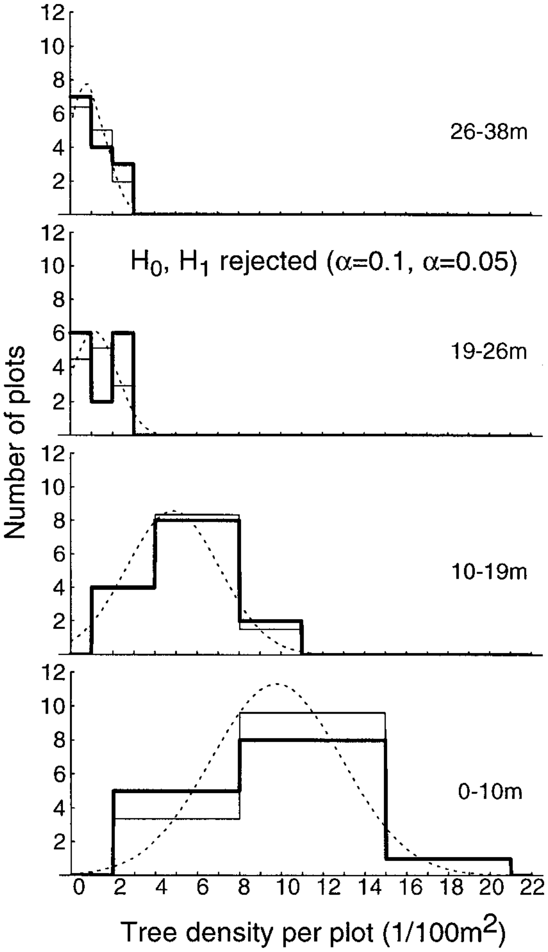

FIG. 2. Empirical and theoretical spatial tree density distribution (dispersion) of larch trees split into four height classes. Data from Baltensweiler and Rubli (1984) showing the frequencies (bold lines) over a profile of 14 plots of 100m^2 size each. Lines show the corresponding probability density functions of the Poisson distribution. For three of four height classes the hypothesis that the data can be described by a Poisson distribution ($H_{0,1}$) and its approximation ($H_{0,2}$) could not be rejected for the significance levels ($\alpha = 0.2, ..., 0.01$). The hypotheses were rejected only for height class 19–26m (at $\alpha = 0.1$ ($H_{0,1}$) and $\alpha = 0.05$ ($H_{0,2}$), respectively).

BEHAVIOR OF DISCFORM

To compare the results of DISCFORM to those of its predecessor FORCLIM-P, simulations were carried out for

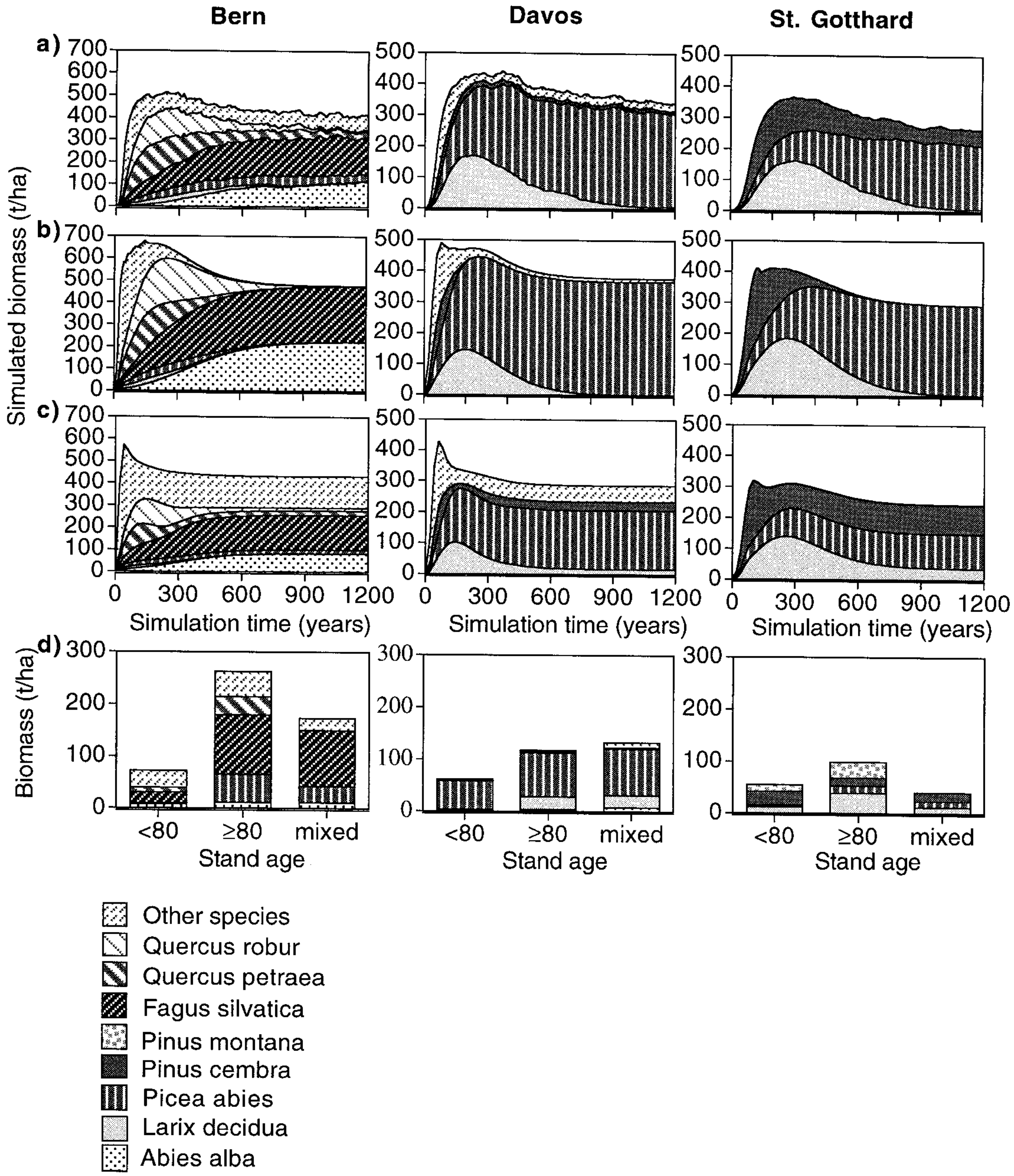

FIG. 3. Qualitative comparison of forest compositions at three selected sites in the Swiss Alps (see Table 1) representing the colline (Bern), upper montane (Davos) and subalpine (St. Gotthard) vegetation belt: (a) simulations with the patch model ForClim-P (Bugmann, 1994; Fischlin *et al.*, 1995); (b) simulations with the aggregated model DisCForM without variability; (c) simulations with DisCForM with variability; (d) data of the first Swiss National Forest Inventory (WSL, 1997). Please note the different scales of biomass. "Other species" are: *Pinus silverstris*, *Taxus baccata*, *Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *Alnus glutinosa*, *Alnus incana*, *Anus viridis*, *Betula pendula*, *Carpinus betulus*, *Castanea sativa*, *Corylus avellana*, *Fraxinus excelsior*, *Populus nigra*, *Populus tremula*, *Quercus pubescens*, *Salix alba*, *Sorbus aria*, *Sorbus aucuparia*, *Tilia cordata*, *Tilia platyphyllos*, *Ulmus glabra*. Simulated biomass comprises woody and leaf biomass of trees higher than 1.37m, biomass in data woody biomass from trees with DBH > 12cm. All biomass values are given in *t* dry weight/ha.

seven different sites in Switzerland (Table 1) with the same bioclimatic variables as inputs for both models. In all simulations the same 30 tree species (see legend Fig. 3) were used. The continuous time model DisCForM run with the explicit Euler method with a fixed yearly time step. The light distribution was discretized into 10 classes, the height into 15 classes.

Figure 3 shows the results of both models for three sites. In first simulations with DisCForM we assumed a uniform spatial tree distribution, i.e., set the variance of the tree distribution to 0. In these simulations (Fig. 3b) less species than in the data (Fig. 3d) and in the patch model simulations (Fig. 3a) could coexist in equilibrium (Table 2); e.g. at the subalpine site only one of three species present in the ForClim-P simulations and in the data survived.

Therefore, in the following simulations the tree distribution variance was set to the average population density in each height class, which corresponds to a random tree dispersion. This leads to results (Fig. 3c) which correspond to the ForClim-P simulation at all three sites in the overall pattern of the species composition, especially for the dominating species, and yields a slightly higher biodiversity than the ForClim-P simulations (table 2). Deviations occur mainly in the total biomass and particularly during early succession.

Both models differ from the data (Fig. 3d) of the less abundant species but reproduce to a same extent the main characteristics of the observed species compositions: the species-rich, *Fagus silvatica* dominated forest in the colline zone, the *Picea abies* dominated needle-leaf forest in the upper montane zone, and the *Larix decidua–Pinus cembra–Picea abies* forest in the subalpine zone. The transition of the simulated total biomass from low values in early succession over a maximum in intermediate succession to a lower level in the equilibrium is also indicated in the data of the colline and subalpine zone. The main deviations are in simulated biomass, which is considerably higher than in the data, and in the simulated portion of *Picea abies*, which is too low at Bern, and too high at St. Gotthard. Additionally, the number of equilibrium species in the data is slightly lower than in the simulations with ForClim-P and DisCForM, whereas higher than in the DisCForM simulations without variability.

A quantitative comparison of similarity and efficiency between the two models is shown in Fig. 4. At each site DisCForM was run with various height discretizations (2, 5, 10, 15, 20, 30, and 60 height classes). Each simulation of DisCForM was compared to the corresponding ForClim-P simulation by calculating the similarity index (Eq. (1)) and measuring the relative computing time. The shown values are averages over all six simulated sites.

The quality of the results, as well as the computing time, depended strongly on the height discretization. The

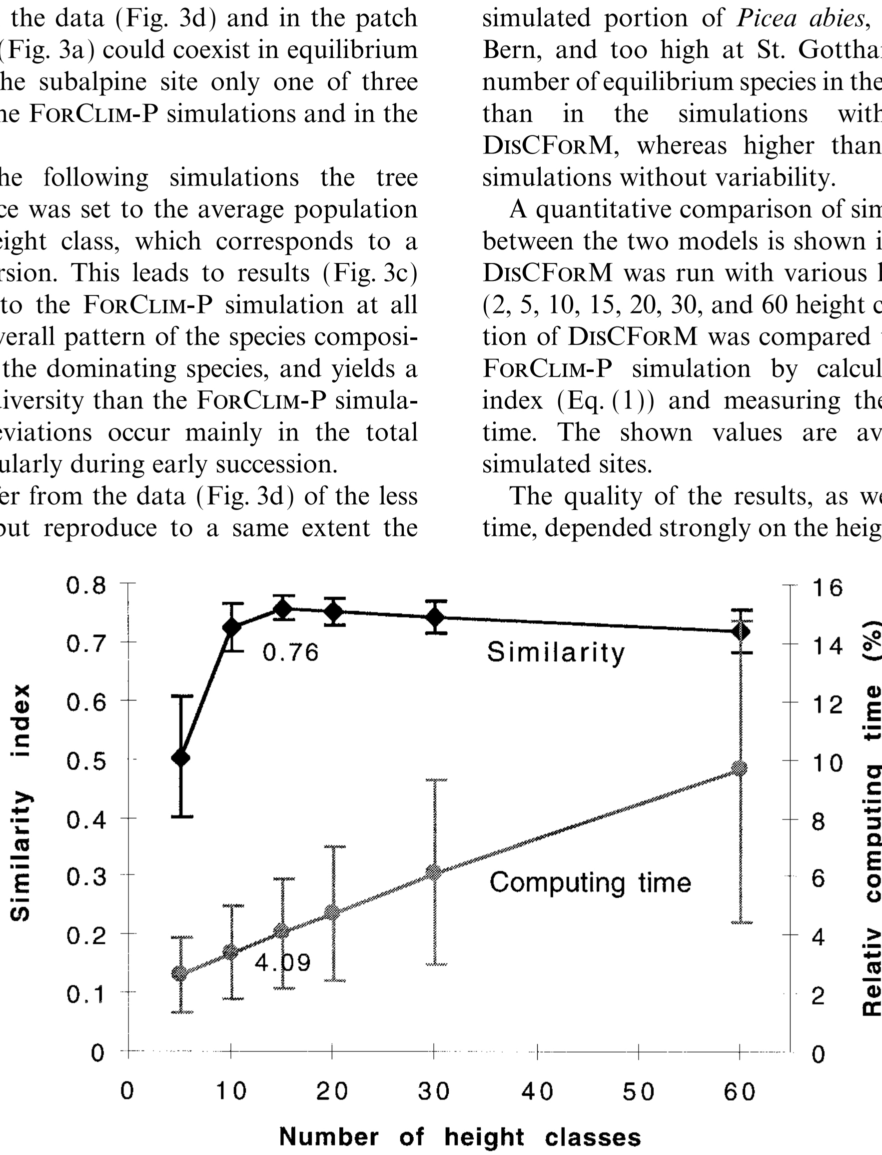

FIG. 4. Comparison between the overall behaviour of the new model DisCForM and that of the patch model ForClim-P (Bugmann, 1994; Fischlin *et al.*, 1995) in terms of computing time and degree of discretization of the tree heights; similarity indices (rhombi) and computing time (circles) were averaged over six sites in the Swiss Alps (Table 1) and are displayed vs. the number of height classes in DisCForM. Similarity indices (1) were computed from species abundances (t/ha) over the entire simulation period. The computing time DisCForM needed is shown as a fraction of the time needed by ForClim-P (~100%). Error bars: ±1 standard deviation.

optimum combination of similarity and efficiency could be reached with 15 height classes, with a computing time of about 4.1% (105 s on a SUNserver MP630) of the time needed by FORCLIM-P and a maximum similarity index of about 0.76. With respect to the model intrinsic uncertainties of FORCLIM-P the difference expressed by this similarity index might still be significant (Bugmann, 1994).

DISCUSSION

The presented derivation of a distribution-based, structured population model from an individual-based model is a stochastic, approximate aggregation, combining the concepts of Iwasa *et al.* (1987; 1989), Gard (1988), Murdoch *et al.* (1992), and Auger (1994).

The use of approximations was necessary, because a perfect stochastic aggregation (Gard, 1988), where the aggregated model contains exactly the same dynamic information about the aggregated variables as the individual based one, was not possible. Forests can be conceived as systems with only local interactions between sessile individuals and small population sizes in subunits, which is depicted, e.g., by the patch model approach. For such models, a direct aggregation of individuals to a population by simply letting their numbers go to infinity is difficult, if not impossible (Metz and de Roos, 1992).

The central assumption and approximation used in this model aggregation were the random spatial distribution of the trees in each height class and the approximation of the resulting Poisson distribution of the tree densities by a matching Normal distribution. The latter equivalent is rather crude for small means, but the evaluation of the empirical spatial tree distribution in the larch forest at Samedan suggests that this assumption might be acceptable in a majority of cases. Also in various studies of natural and near-natural forests (Abbott, 1984; Stoll *et al.*, 1994; Szwagrzyk and Czerwczak, 1993; Ward and Parker, 1989; Ward *et al.*, 1996; Williamson, 1975) the spatial tree distribution was close to random with a tendency to aggregated for young and to uniform for old trees.

The distribution-based approach produces similar results as the patch model approach. However, the results differ in details, particularly in the increase of biomass in early succession, accompanied with an overshooting. This is probably due to the height discretization, since in simulations with smaller height classes (not shown) the increase was much smoother. The increased biodiversity produced by DISCFORM simulations might indicate that the random distribution of the trees offers a too wide range of light regimes; reducing the variability will presumably improve the results.

The comparison of the simulations to the NFI-data was impeded by the fact that unmanaged and rarely managed forests are scarce in Switzerland. Thus, only few NFI-plots could be evaluated, the considered forests are probably not completely natural, and the samples had to be chosen from rather large regions.

Nevertheless, the results can give indications about the validity of FORCLIM-P and DISCFORM. Both models overestimate total biomass. This is probably due to the exponential allometric relationship $B_{\text{stem}} = 0.12 \cdot DBH^{2.4}$ used to calculate stem biomass B_{stem} from DBH. Since in the models biomass is only an output variable, i.e., does not feed back to the dynamics, correcting this formula (e.g., to the sigmoid one proposed and fitted to NFI-data by Perruchoud, 1996) will only affect total biomass, not the general results.

The major patterns of species composition, such as the forest types and the temporal development of biomass are reproduced by the models. The high portion of *Picea abies* in the data of the colline zone might be due to former management, whereas its high portion in the St. Gotthard simulations has probably to be attributed to the use of average instead of temporally varying climatic input (Bugmann, 1997). Simulations with the version FORCLIM-E/P of the patch-model which allows climate to fluctuate stochastically, e.g., lead to a strong suppression of *Picea abies* and a forest consisting of *Larix decidua* and *Pinus cembra*. Hence, besides spatial also temporal variability has the potential to influence forest dynamics. Such temporally variable input can presumably be incorporated into the aggregated model by a temporal aggregation of climate dependence functions (Lischke *et al.*, 1997a; Lischke *et al.*, 1997b).

The general form of the aggregated model resembles a height-discrete, time-continuous version of the continuity equation forest model of Kohyama (1992; 1993; 1995); i.e., it is an intermediate between this partial differential equation model and a discrete forward one-step transition matrix model (Lefkovitch, 1965; Takada and Hara, 1994).

However, there are differences. DISCFORM takes into account the spatial dispersion of the trees, which determines through the LAI and light distributions the distributions and means of the process rates.

Kohyama's first models (e.g., 1991) include variability by a diffusion term, where the diffusion constant, which corresponds to the variance of the growth rate, is derived from the mean growth rate. The mean growth rate in turn is a function of the mean cumulative basal area. Thus, there is no feedback from the spatial tree distribution to the dynamics. Since the diffusion term had no significant influence on the simulations, it was omitted in subsequent model versions (e.g., Kohyama, 1992). Yet, later Kohyama (1993; 1995) reintroduced spatial variability at a larger scale by the concept of ageing and dying patches (same as Karev, 1994) and by seed dispersal.

In DisCForM, in contrast, the tree and LAI distribution feeds back to the mean process rates. Since the connecting functions are nonlinear, these means can have significantly different values compared to those obtained by applying the functions to the mean LAI (which corresponds to the cumulative basal area). Consequently, in our simulations omitting variability produces considerably different results.

The aggregated model DisCForM has a number of advantages over the patch model and over another simplification of a patch model.

The difference in the outcome of DisCForM to the results of its predecessor is qualitatively minor, although quantitatively significant, and small with respect to the predictive uncertainties of both models. With an index of about 0.76 DisCForM's similarity to ForClim-P is in the same range as the similarity of the model FLAM (Fulton, 1991) to the patch model FORSKA (Leemans and Prentice, 1989), from which it had been derived, with an index of 0.8. FLAM also uses a discrete height structure, but still describes the dynamics of many patches by Monte Carlo simulations. Since the similarity indices of DisCForM and FLAM to their parent models do not differ much, we can conclude that the difference between DisCForM and ForClim-P has to be contributed mostly to the height structure which implies that the utilization of tree dispersions and of stochastic replicates of patches is almost equivalent. Such a predominant effect of height structure on forest dynamics has also been found by Kohyama (1993).

The efficiency gain of DisCForM vs. ForClim (4.1% relative computing time) is considerable. It is a little bit higher than that of FLAM vs. FORSKA (5% relative computing time). In addition to this similar relative performance, the absolute performance of the new approach can be judged as better. This is due to the use of theoretical distributions instead of Monte Carlo simulations. DisCForM simulates the theoretical distribution of the tree species, including its expected value, in one single simulation run. In contrast, patch models such as ForClim, FORSKA, and FLAM simulate many patches, and computing time increases linearly with the number of patches (cf. Appendix 2).

Another advantage of the new model type is its formulation in a closed form as a system of coupled ordinary differential equations. This formulation allows the numerical application of well established mathematical methods (e.g., equilibrium- and stability-analysis) to forest models which is difficult for models formulated as Monte Carlo algorithms such as FLAM or conventional patch models.

Not only does the model aggregation yield a technical improvement, but also new insights into forest dynamics.

In the model aggregation, the assumptions underlying the individual based model, together with the formulation and parametrization of the processes were retained; we only shifted the focus from single trees with height as the main characteristic to tree subpopulations in distinct height classes. The new model differs from its predecessor in only one central assumption: it assumes a random tree dispersion a priori, whereas in the individual based model the dispersion emerges from the individual processes and interactions. Since this assumption is the only deviation, comparing the results of the new model with those of its predecessor can be used to assess the assumption's validity.

We approximated the vertical–horizontal tree distributions by independent layers and random tree dispersions. That means we ignored the single tree histories and assumed the trees to be newly distributed over space in each single time step, whereas in a real forest trees live in rather stable groups which have been shaped by their present and past interactions. Despite this crude assumption, the overall tree population dynamics were still reproduced to a high degree. We conclude from this result that tree frequency distributions are sufficiently good population descriptors to capture stochastic spatial variability of a forest. This suggests that the changing frequency distributions of trees, and not primarily single tree history including its direct position, determine entire forest dynamics and it is a positive answer to the question (Pacala, 1989) "Can we adequately account for plant population dynamics without specifying the location of individuals?" and an extension of Fulton's (1991) conclusion, that "much of the information contained in individual tree descriptions is redundant if the main concern is with a dynamically sufficient representation of a forest patch" to the entire forest. Urban (1991) has also concluded that for the simulation of implicitly spatial phenomena space does not always have to be explicitly taken into account, same as Deutschman *et al.* (1997), whose study with the individual based forest model SORTIE revealed that it is not necessary to include intrapatch light variability to describe overall forest dynamics.

We hypothesise that frequency distributions are a minimum aggregation level, since other more aggregated population descriptors which do not take into account stochastic spatial variability, such as total species means or means of height classes failed to reproduce the forest diversity. Although in our model, same as in the patch model, seed supply is independent of parent trees, coexistence in this open system can be considered as a prerequisite for coexistence in the closed system, where seed supply is coupled to parent tree abundance. If coexistence is not possible in the open system, it is unlikely that it will occur in the closed system, since the positive feedback between parent abundance and recruitment will presumably further decrease the number of species which can coexist.

Our finding is supported by the comparison of a spatially explicit forest model with its mean field approximation, where light supply was averaged over space (Pacala and Deutschman, 1995). The simulation with the mean field model yielded half the biomass and enhanced the extinction of non dominant species. In a more general frame the hypothesis is consistent with the ecological evidence and theory of heterogeneity or disturbance-mediated coexistence of species (cf. e.g., Denslow, 1985; Hutchinson, 1978).

CONCLUSION

By the derivation of the distribution based, structured population model DisCForM from the individual based, stochastic patch model we reached three goals: The new model is faster and its results are similar to the patch model simulations, and new insights into forest dynamics were made possible by the changes.

The stochastic variability in a forest can be depicted by random tree distributions, which implies that tree frequency distributions determine forest dynamics and not primarily single tree histories or positions. However, distributions seem to be the minimal necessary aggregation level.

The approach of replacing the stochastic distributions obtained by Monte Carlo simulations with theoretical distributions can be applied to all patch models in which competition for light forms the only interaction between the individuals. The idea can also be extended to competition for other local resources, e.g., nutrients or water, if the supply of them is explicitly modelled. This approach is promising even for patch models with competition for several independent local resources.

With the good run-time behaviour of the model, many new applications of forest models are now possible, e.g., simulating tree species migration in past and future climate changes or forests in large areas on a fine grid. Moreover, this approach can be considered as a potential contribution to the development of larger scale dynamic vegetation models because it helps to "discover the rules that permit large-scale ecological models to be derived from fine-scale interactions" (Pacala and Deutschman, 1995).

APPENDIX 1: PROCESS RATES OF DisCForM

The following process functions of the aggregated model were derived from ForClim-P (Bugmann, 1994, 1996) (for explanation of parameters refer to Table 3):

- the growth rate $\gamma_{s,i}(l) = \gamma_{s,i,\max} \cdot C_s \cdot \omega_{s,i} \cdot g_s(l)$, with the light dependence function

$$g_s(l) = g_{1,s} - g_{2,s} \cdot e^{-1.84 \cdot l} - g_{3,s} \cdot e^{-4.84 \cdot l};$$

- the light dependent part of the mortality rate

$$\mu_{s,i}(l) = \begin{cases} 0.184, & C_s \cdot g_s(l) < \mathrm{Max}(0.1,\ 0.0003/\gamma_{s,i,\max}) \\ 0, & \mathit{else} \end{cases};$$

- and the establishment rate

$$\beta_s(l) = \begin{cases} 0, & l < l_{\beta crit,s}, \\ \beta_{\max,s}, & l \geqslant l_{\beta crit,s}. \end{cases}$$

APPENDIX 2: RUNTIME COMPARISON

On a SUNserver MP630 (40 MHz) FORSKA, e.g., would need approximately $\mathrm{TFk} = 0.42$ min. (Fulton, 1991) to simulate $\mathrm{np} = 1$ patch over 1200 years. We assume that applying our distribution based approach to FORSKA (run with $\mathrm{np} = 200$ patches) also reduces the computing time to about 4%. For a hypothetical distribution based FORSKA model this would lead to a run-time of $0.04 \times 200 \times 0.42\mathrm{min} = 3.44\mathrm{min}$, regardless the number of patches originally used in FORSKA. FLAM needs for np patches $0.05 \times \mathrm{np} \times \mathrm{TFk}$ min. Hence, for patch numbers $\mathrm{np} \geqslant 3.44/(0.05 \cdot \mathrm{TFk}) = 164$ the distribution based approach is faster than the Monte Carlo approach; it needs 18% less computing time for $\mathrm{np} = 200$, which is considered as the minimum necessary number of replicates in patch model simulations to warrant reliable estimates of the expected values of the species biomasses (Bugmann *et al.*, 1996).

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