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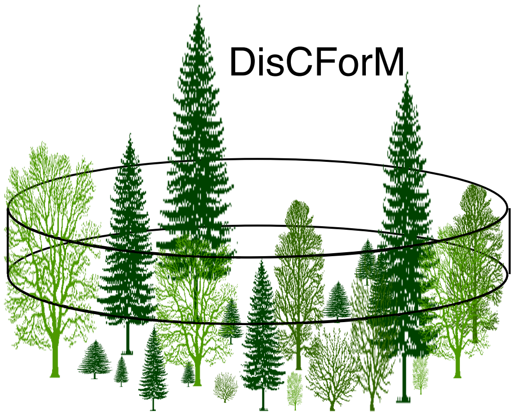

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Aggregation of Individual Trees and Patches in Forest Succession Models: Capturing Variability with Height Structured Random Dispersions

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Abstract

Individual based, stochastic forest patch models have the potential to realistically describe forest dynamics. However, they are inefficient and mathematically intransparent. 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 3.5% 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, dispersion, structured population, model simplification

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 individuals lead to a variability in the population which can strongly influence its overall dynamics (May, 1986; Koehl, 1989).

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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 (Murdoch *et al*., 1992; Grimm *et al*., 1996), i.e. close to what can be observed in nature, and to give insight into the mechanisms of community dynamics (Shugart, 1984; McCook, 1994).

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

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 size of the canopy area of one dominating tree (ca. 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 (Watt, 1947; Drury & Nisbet, 1973; Remmert, 1991). **(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 & 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 widely tested and successfully applied under various conditions (Solomon *et al*., 1981; Prentice, 1986; Kellomäki *et al*., 1992; Shugart & Prentice, 1992; Bugmann, 1994; Bugmann & Solomon, 1995; Fischlin *et al*., 1995b; Bugmann & Fischlin, 1996). Thus, they can be 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 similarly realistic 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 (Cale & Odell, 1979; Gardner *et al*., 1982; Gard, 1988; Iwasa *et al*., 1989; Murdoch *et al*., 1992; Auger & Roussarie, 1994).

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, which also uses an explicit height structure, i.e. assumes the forest consists of several discrete height layers (discs). The new concept is to take into account the stochastic variability in a forest by distributions of tree densities and light intensities, which replace the distinct patches and the random variates of the Monte Carlo simulation used in patch models. One example of the new model type is the distribution based climate driven forest model DISCFORM, which we aggregated from the forest patch model FORCLIM (Bugmann, 1994; Fischlin *et al.*, 1995a), 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) of different species usually on 200 patches which are assumed to be independent of each other. These patches represent different realizations of the stochastic process running at a specific site. We interprete these realizations 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, 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 simulation server of RAMSES.

SITES AND FOREST TYPES

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 6 climatically different sites in Switzerland (tab. 1).

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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 1: Characteristics of sites used to test the forest model DISCFORM.

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

For Bern and Davos we compared qualitatively the simulated equilibrium species compositions to the observed natural forests (tab. 2). The latter were compiled from phytosociological descriptions by Ellenberg & Klötzli (1972) taking into account all recorded points within a distance of 20 km from the study site and a similar altitude.

SIMILARITY INDEX AND RUN-TIME MEASUREMENT

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

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

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 (fig. 39, Baltensweiler & Rubli, 1984). These data are given as stem diameter at breast height (DBH) and position of each tree on a profile consisting of 14 quadratic plots, each with a size of about 100 m^2. The tree density n (1/100 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 (0-17.9 cm, 17.9-35.7 cm, 35.7-53.6 cm, and 53.6-89.3 cm). The DBH was transformed into height by using the empirical allometric relationship (Ker & 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 52 m and 1.85 m, respectively (Bugmann, 1994). This leads to the height classes 0-10 m, 10-19 m, 19-26 m, and 26-38 m.

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 modeled 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 modeled 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, 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.

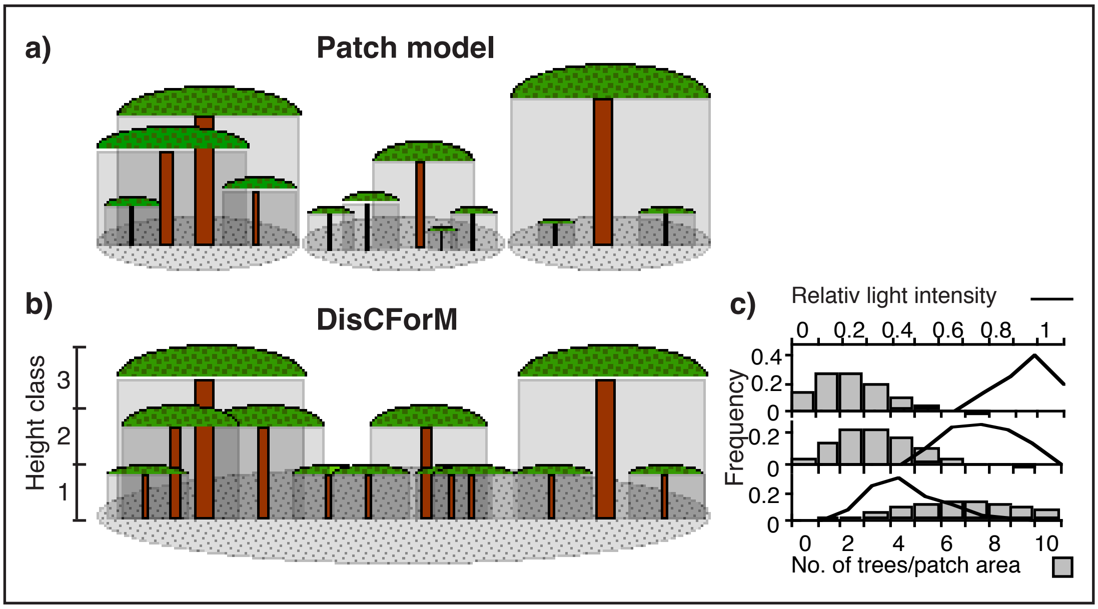

Figure 1: Distribution of trees and light in a forest, as simulated by a conventional forest patch model and the new model DISCFORM. In both cases the leaves are assumed to be concentrated at the tree top. The grey areas portray the shading by the canopy. **a)** In a conventional forest patch model individual 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 forest discs as modeled by DISCFORM. Within these discs the tree dispersion is assumed to be random and is modeled with a Poisson distribution.

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 modeled 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 summarization of the symbols is contained in table 3 in the annex):

$N_{s,i}$ 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 is determined by death $D_{s,i}$ (3), growth $G_{s,i}$ (4) and birth $B_{s,i}$ (5). Trees grow into height class i from height class $i\text{-}1$ ($G_{s,i-1}$) and leave height class i by outgrowing ($G_{s,i}$). Birth (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.

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

$$D_{s,i} = \overline{\mu}_{s,i} \cdot N_{s,i} \tag{3}$$

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

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

The species specific death, growth, and birth rates $\overline{\mu}_{s,i}, \overline{\gamma}_{s,i}$, and $\overline{\beta}_s$ are the expected values of the light dependent rates $\mu_{s,i}(l), \gamma_{s,i}(l)$, and $\beta_s(l)$ (Bugmann, 1994). Since light 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

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

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

$$\mu_{LAI_i} = \frac{1}{\zeta}\sum_{j>i}\sum_{s} N_{s,j} \cdot a_{s,j}$$

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

With the full light intensity (= 1) above the topmost height class and α 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} (8).

If $f_Y(y)$ is the density function of a random variable Y at a specific realization 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 $f_Y(y) = f_X(h(y)) \cdot \left|\frac{d\,h(y)}{d\,y}\right|$ (equation 2.4.1.9 in 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

$$\overline{\varphi} = \sum_{\xi=0}^{9} \varphi(l_\xi) \cdot \left(F_{L_i}(l_{\xi+1}) - F_{L_i}(l_\xi) \right), \qquad (11)$$

where F_{L_i} is the distribution function of the light intensities which we can express with the normal distribution function of the leaf area index with the parameters μ_{LAI_i} and σ_{LAI_i} (8) by $F_{L_i}(l) = F_{LAI_i}\left(-\frac{\ln(l)}{\alpha}\right)$. 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: α = 0.2, 0.1, 0.05, 0.01); only for one height class they were rejected (at $\alpha = 0.1$ ($H_{0,1}$) and $\alpha = 0.05$ ($H_{0,2}$)).

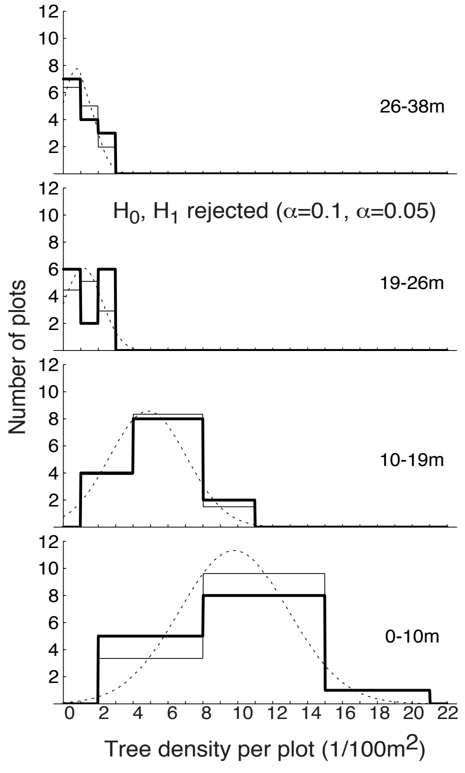

Figure 2: Empirical and theoretical spatial tree density distribution (dispersion) of larch trees split into four height classes. Data from Baltensweiler and Rubli (1984) showing the frequencies (bold lines) over a profile of 14 plots of 100 m^2 size each. Lines show the corresponding probability density functions of the Poisson distribution (thin), the dotted curves those of the truncated, normal approximation 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 (α = 0.2,...,0.01). The hypotheses were rejected only for height class 19-26 m (at $\alpha = 0.1$ ($H_{0,1}$) and α = 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 six different sites in Switzerland (tab. 1) with the same bioclimatic variables as inputs for both models. 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 two sites. The model results correspond well at all sites in the overall pattern of the species composition, especially for the dominating species. Bigger deviations occur only in the total biomass and during early succession.

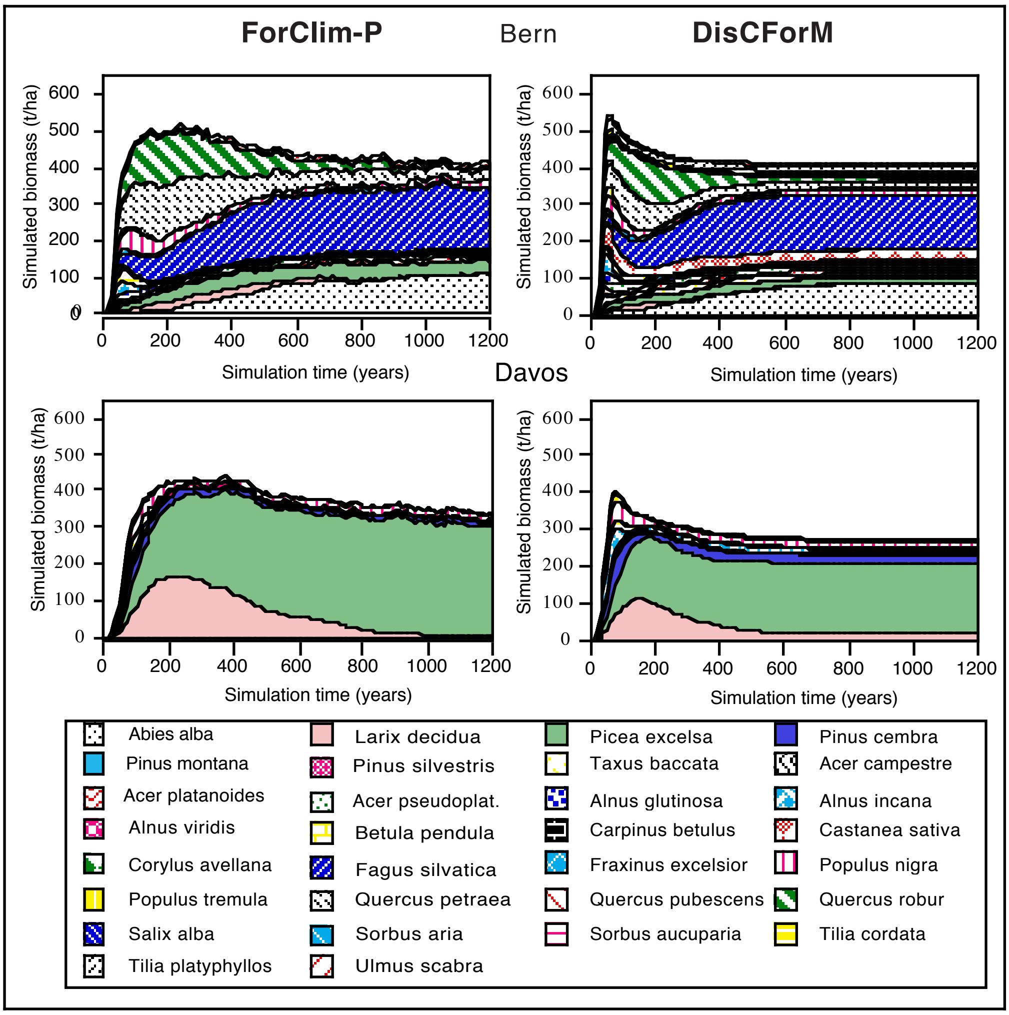

Figure 3: Comparison between forest compositions as simulated (left) by the patch model FORCLIM-P (Bugmann, 1994; Fischlin *et al.*, 1995a) and (right) the new model DISCFORM at two selected sites (Bern and Davos, tab. 1) in the Swiss Alps. (For overall performance see fig. 4.)

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 (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 optimum combination of similarity and efficiency could be reached with 15 height classes, with a computing time of about 3.5% (90 s on a SUNserver MP630) of the time needed by FORCLIM-P and a maximum similarity index of about 0.75. With respect to the model intrinsic uncertainties of FORCLIM-P the difference expressed by this similarity index might still be significant (Bugmann, 1994).

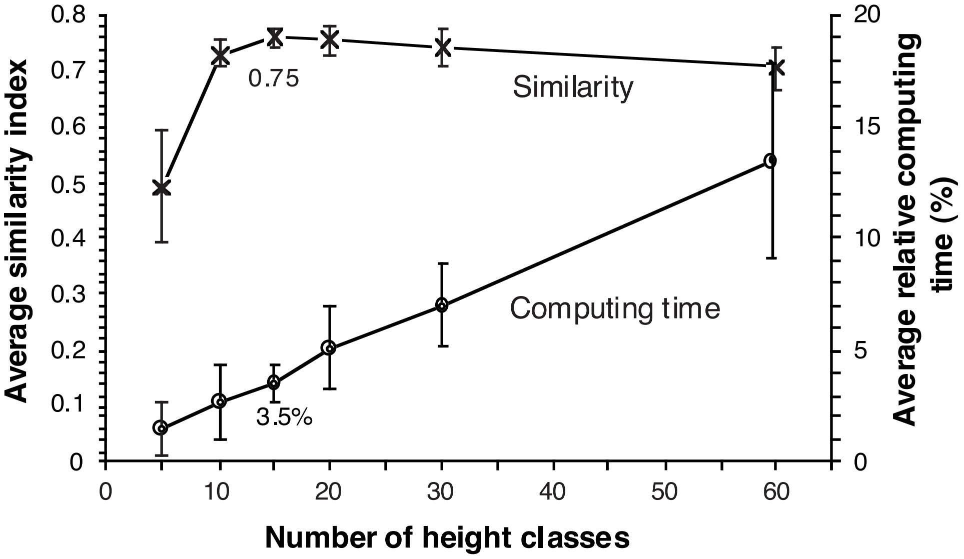

Figure 4: Comparison between the overall behavior of the new model DISCFORM and that of the patch model FORCLIM-P (Bugmann, 1994; Fischlin *et al.*, 1995a) in terms of computing time and degree of discretization of tree heights: Similarity indices (crosses) and computing time (circles) were averaged over six sites in the Swiss Alps (tab. 1) and are displayed vs. the number of height classes in DISCFORM. Similarity indices (1) were computed from species abundancies (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.

To test whether the discrepancies between the two models are in the range of the predictive uncertainty of the parent model, we qualitatively compared for two selected sites the equilibrium species compositions simulated by both models to that of the natural vegetation (tab. 2), which had been compiled from phytosociological data (Ellenberg & Klötzli, 1972). Both models differed from the data for the less abundant species but reproduced to a similar extent the main characteristics of the observed forest compositions. Thus, the differences between the models can be interpreted to be smaller than their predictive uncertainties.

Table 2: Observed natural (Ellenberg & Klötzli, 1972) and simulated forest types at two selected sites (Bern and Davos, tab. 1). Simulated equilibrium forests were generated by FORCLIM-P and the new model DISCFORM.

Data source	Bern	Davos
Potential forest types compiled from Ellenberg (1972)	Mixed beech forest with ash, maple, oaks, and lime plus few silver fir and Norway spruce.	Softwood forest dominated by Norway spruce and with silver fir, few larch, and mountain pine.
FORCLIM-P simulation	Mixed-deciduous forest with beech, silver fir, and few Norway spruce.	Forest dominated by Norway spruce with very few black poplar, larch and even less Arolla pine.
DISCFORM simulation	Mixed-deciduous forest with beech, oak, lime, sweet chestnut, maple, some silver fir, and Norway spruce.	Softwood forest dominated by Norway spruce with few larch and Arolla pine.

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 (e.g.Metz & de Roos, 1992).

The central assumption and approximation used in this model aggregation were the random dispersion 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.

The new distribution based approach produces similar results as the patch model approach. Moreover, the new model DISCFORM has a number of advantages over the current 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 0.75 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 & 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 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.

The efficiency gain of DISCFORM vs. FORCLIM (3.5% 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 better 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.

On a SUNserver MP630 (40 MHz) FORSKA e.g. would need approximately T_{Fk} = 0.42 minutes (Fulton, 1991) to simulate n_p = 1 patch over 1200 years. We assume that applying our distribution based approach to FORSKA (run with n_p = 200 patches) also reduces the computing time to about 3.5%. For a hypothetical distribution based FORSKA model this would lead to a run-time of 0.035·200·0.42 min. = 2.94 min., regardless the number of patches originally used in FORSKA. FLAM needs for n_p patches $0.05 \cdot n_p \cdot T_{Fk}$ min. Hence, for patch numbers $n_p \geq 2.94 / (0.05 \cdot T_{Fk}) = 140$ the distribution based approach is faster than the Monte Carlo approach; it needs 30% less computing time for n_p = 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).

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.

Because we approximated the vertical-horizontal tree distributions by independent layers and random tree dispersions we ignored the single tree histories. Nonetheless, the 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. This is a positive answer to the question (Pacala, 1989) "Can we adequately account for plant population dynamics without specifying the location of individuals?" and is 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.

We hypothesise that frequency distributions are a minimum aggregation level. 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 dynamics, i.e. led to the extinction of most species. This hypothesis is consistent with the ecological evidence and theory of heterogeneity or disturbance-mediated coexistence of species (Hutchinson, 1978; Denslow, 1985).

Conclusions

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 modeled. 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 dynamic global vegetation models.

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Annex

Table 3: Used symbols

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	m^{-2} $year^{-1}$
$G_{s,i}$	Trees of species s growing from height class i to height class $i+1$	m^{-2} $year^{-1}$
$B_{s,0}$	New saplings of tree species s	m^{-2} $year^{-1}$
$\mu_{s,i}(l)$	Per tree 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	m $year^{-1}$
$\beta_s(l)$	Birth (establishment) rate of species s at light intensity l	m^{-2} $year^{-1}$
$\overline{\mu}_{s,i}, \overline{\gamma}_{s,i}, \overline{\beta}_s$	Expected values of mortality, growth, and birth rates with respect to light intensity	$year^{-1}$, m $year^{-1}$, m^{-2} $year^{-1}$
$f_Y(y)$	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, $833m^2 = 1/12$ 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	–

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