An efficient method for estimating the steady-state species composition of forest gap models

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Abstract: Forest gap models are used widely in forest ecology, but their complexity and stochasticity makes simulation studies rather demanding even on modern computers, thus often precluding extensive simulation studies. In this paper, a new method is proposed to efficiently estimate the steady-state species composition of gap models. It is based on the assumption that the stochastic process underlying gap models is weakly stationary. Hence the average of one realization of the process over time (i.e., model behaviour on one forest patch of 0.083 ha) is the same as the average of the process across many patches in the steady state. The new method is described in detail. Extensive simulation studies conducted with the FORCLIM model suggest that the new method is much more efficient for estimating the steady-state species composition, requiring only 12.9% of the simulation time for the conventional experiment of simulating the dynamics of many patches reliably.

Résumé : Des «gap models» sont largement utilisés en écologie forestière, mais leur complexité et leur caractère stochastique rendent les études de simulation plutôt exigeantes, même avec les ordinateurs modernes, faisant ainsi souvent obstacle aux études exhaustives de simulation. Dans le présent article, une nouvelle méthode est proposée pour estimer efficacement la composition en espèces de l'état stable des «gap models». La méthode est basée sur l'hypothèse que le processus stochastique sous-jacent aux modèles de trouées est faiblement stationnaire. En conséquence, la période de temps moyenne pour que le processus s'accomplisse une fois, c'est-à-dire le comportement du modèle sur une placette de forêt de 0.083 ha, est la même que la durée moyenne du processus dans un grand nombre de placettes à l'état stable. La nouvelle méthode est décrite en détail. De vastes études de simulation menées avec le modèle FORCLIM indiquent que la nouvelle méthode est beaucoup plus efficace pour estimer la composition en espèces de l'état stable, nécessitant seulement 12,9 % du temps qu'exigent les expériences conventionnelles pour simuler, de façon fiable, la dynamique d'un grand nombre de placettes.
[Traduit par la Rédaction]

Introduction

A large number of models based on the hypothesis of gap-phase dynamics (Watt 1947) have been developed and applied for a wide variety of research questions (Shugart 1984). These "gap models" simulate the establishment, growth, and death of trees on small patches of land (typically 0.083 ha) as a mixture of deterministic and stochastic processes. The dynamics at the level of the forest are then obtained by averaging the simulated dynamics across a large number of patches. Bugmann et al. (1996a) suggested that 200 independent patches should be simulated if one wants to reliably estimate the average species composition. This is much larger than the sample size used in most published studies (Bugmann et al. 1996a), and it makes simulation studies rather demanding, even on modern computers.

The first gap model, JABOWA (Botkin et al. 1972), was fairly simple with respect to the number and formulation of the processes incorporated in the model. Subsequently, more eco-

logical factors were introduced in gap models, and the level of detail used for their formulation was increased (cf. review in Bugmann 1996). The increasing complexity imposes severe limits on the feasibility of extensive simulation studies, and it makes the analysis, testing, and application of the models rather tedious (Bugmann and Martin 1995).

In recent years, several gap models were derived that are more efficient to run and, thus, more easily amenable to a detailed analysis than their predecessors. There are various ways to achieve this:

(1) Simplification of the model structure from a technical point of view. For example, Fulton (1991) derived the FLAM model by considering only a small number of tree height classes instead of the several hundred classes that are used in other gap models.

(2) Simplification of the model structure from an ecological point of view. For example, Bugmann (1994, 1996) used the FORECE model (Kienast 1987) as a template to derive a simplified model, FORCLIM, incorporating only those ecological factors of FORECE that contribute significantly to the simulated dynamics.

(3) Fitting simplified models to the output of forest gap models. For example, Acevedo et al. (1995) fitted a deterministic, analytically tractable Markov model to the forest-level output of the ZELIG model (Urban 1990), i.e., they replaced the continuous behaviour of ZELIG by a small number of discrete system states, plus the associated transition probabilities.

Fig. 1. Empirical test of the stationarity of the stochastic process underlying forest gap models. The graph shows the average ± 1 SD of the total aboveground biomass obtained from 400 patches in the FORCLIM-E/P model V2.4 (Bugmann 1994; Fischlin et al. 1995) over 5000 years at the low-elevation Bern site (Switzerland), starting from bare ground. The transient behaviour ends after some 1000 years; afterwards, the average and the standard deviation have reached constant values. The derivation of the input data was described by Bugmann (1994).
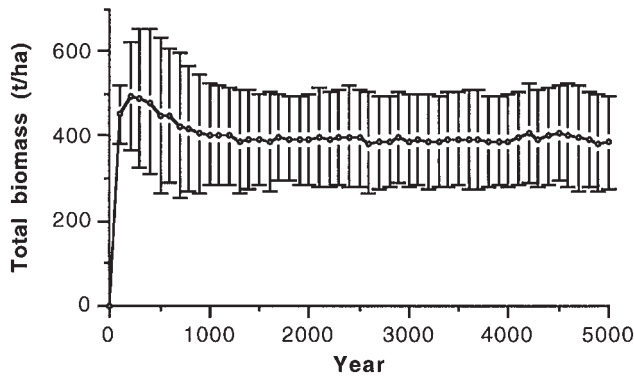
In the present paper, I follow a fourth route to derive an efficient method designed for estimating the steady state of forest gap models. This method does not involve any changes to the model structure, but it still reduces the required simulation time by 87%. It is based uniquely on statistical considerations of the stochastic process underlying forest gap models. As a case study, the derivation of the method is based on version 2.4 of the gap model FORCLIM, which has been described elsewhere (Bugmann 1994, 1996; Fischlin et al. 1995).

Material and methods

Forest gap models as a stochastic process

Traditionally, simulation experiments with gap models are set up so that p independent realizations of the stochastic process (i.e., p patches) are simulated for 600–1200 years (e.g., Solomon 1986; Kienast 1991; Bugmann 1994). The steady state is then estimated as the average across the p patches at the end of the simulation period. In this approach the transient behaviour of the model is simulated repeatedly, although it often is not of prime interest. Since many model applications focus on the interpretation of the steady states, it would be desirable to have an estimation method that avoids repeated simulation of the transient behaviour.

The present study is based on the assumption that the stochastic process underlying forest gap models is weakly stationary, implying that its average and variance do not change with time in the steady state (Box and Jenkins 1976). The stationarity of gap models probably cannot be proven formally because of the complexity of the process, but stationarity is empirically evident from the simulation results that have been obtained from gap models so far (cf. Fig. 1 for an arbitrary example). Assuming that gap models are weakly stationary, it is possible to estimate their steady state by sampling the process from just one patch (i.e., one realization) over a sufficently long time. Discarding the first centuries of transient behaviour, the average species composition over time will be the same as the average species composition across many patches.

The species composition of two points in time of one patch is autocorrelated (Bugmann et al. 1996a); hence the time interval between any two samples (Δt) should be chosen so that autocorrelation becomes negligible. On the other hand, the number of samples (n) should be sufficiently large. Following Bugmann et al. (1996a), the recommended sample size for the conventional estimation procedure (i.e., when simulating p patches) is $p = 200$, and the recommended simulation period is larger than $t_{end} = 700$ years (Bugmann and Fischlin 1994); often, 1200 years are simulated (e.g., Kienast 1987; Bugmann 1994). If Δt and n fulfil the inequality

[1] $\Delta t n < p t_{end}$

then the new method is more efficient than the conventional one. In this context, there are two basic questions to be answered:

(1) How close to the "true" steady state are the estimates as a function of n and Δt? In addition to theoretical reasoning, simulation experiments can yield quantitative information on the precision of such estimates.

(2) How similar to each other are two estimates of the same steady state, using a given n and Δt? This question is especially important if two model variants are to be compared, e.g., for assessing the effect of climatic change on species composition. Moreover, is it possible to develop a threshold of significant differences between steady states for a given n and Δt?

Simulation experiments and data processing

To answer the above two questions, two sets of simulation experiments were conducted with the FORCLIM-E/P model V2.4 (Bugmann 1994, 1996; Fischlin et al. 1995). Bugmann et al. (1996a) found that temporal autocorrelation in gap models is important at lags up to more than $\Delta t = 100$ years, and they suggested that the sample size (p) should be larger than 100. If $\Delta t = \infty$ (infinity), then the required n would equal p because autocorrelation would become zero. Thus, to answer question 1, an experimental design was used with $n = 50, 100, 200, 400, 1000$, and $\Delta t = 100, 150$ years. This yielded a total of 10 experimental setups. For each setup, 20 simulation runs were performed, and a steady state was estimated from each run. The first 1000 years of each run were discarded (transient behaviour, Bugmann 1994). The "true" steady state was assumed to be the average of the 20 steady states estimated with $n = 1000$ and $\Delta t = 150$, thus corresponding to 20 000 points in time. Simulations were conducted for the low-elevation site Bern, Switzerland (Table 1; for the input data, see Bugmann 1994).

To compare the different estimates of the steady states, a percentage similarity coefficient (eq. 2) was used; it relates any two data sets $X = \{x_1, x_2, ..., x_n\}$ and $Y = \{y_1, y_2, ..., y_n\}$ as follows:

[2] $$PS = 1 - \frac{\sum\limits_{i=1}^{n} |x_i - y_i|}{\sum\limits_{i=1}^{n} (x_i + y_i)}$$

where $0 \leq PS \leq 1$ (Bugmann and Fischlin 1994). This coefficient can be interpreted as the fraction of values common to both sets of data.

Table 1. Characteristics of the test sites used in the present study.

Site	Lat. (°N)	Long. (°E)	Elev. (m)	Annual mean temp. (°C)	Annual precip. sum (mm)	Vegetation zone and major species
Davos	46.8	9.8	1590	3.0	1007	Subalpine (*Picea excelsa*)
Airolo	46.5	8.6	1149	6.1	1616	Montane (*P. excelsa*, *Abies alba*, *Fagus silvatica*)
Bern	46.9	7.4	570	8.4	1006	Colline (*Fagus silvatica*, *Quercus* spp.)

Note: Data were adopted from Bugmann (1994).

Fig. 2. Convergence of the percentage similarity coefficient (PS) between estimated steady states and a conjectured "true" steady state at the Bern site as a function of the sample size (n) and the sampling interval (Δt).
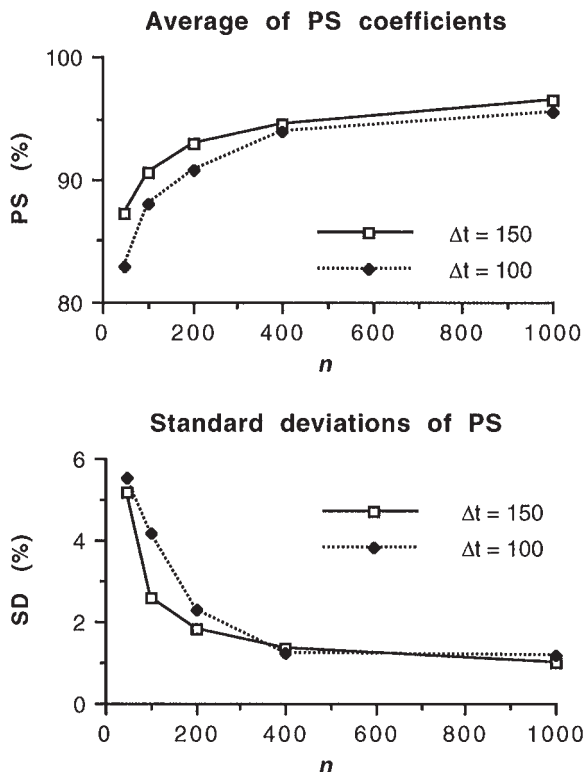
From the results of the first set of simulations, the combination of $n = 200$ and $\Delta t = 150$ years was chosen to answer question 2. It may be hypothesized that it is easier (both in a forest gap model and in reality) to quantitatively estimate the composition of a forest that has only a few tree species than that of a diverse forest. In addition, the abundance of a species that is always present on a patch but has low biomass is easier to estimate than that of a species with episodic occurrence, but that attains large biomass when it is present. Thus, the PS between independent estimates of the same steady state at a given site should depend on the number of species and their ecological roles (cf. Shugart 1984). To test this hypothesis, 400 steady states were estimated at three test sites along a gradient of altitude and species diversity in the Swiss part of the European Alps, i.e., Bern, Airolo, and Davos (Table 1, Fig. 4). The distributions of the PS coefficients calculated from 200 pairs of independent steady states at each site were analysed statistically.

Finally, for illustrative purposes the results from the conventional experiment of simulating the dynamics on $p = 200$ patches with $t_{end} = 1200$ years are compared with the results from the new method using $n = 200$ and $\Delta t = 150$ years at the three test sites Bern, Airolo, and Davos (Table 1).

Plant nomenclature throughout the paper is according to Hess et al. (1980).

Results and discussion

Similarity of estimates to the "true" steady-state species composition

As the sample size (n) increases, the averages and standard deviations of the PS coefficients converge towards the values of the "true" steady state (Fig. 2). There is a strong increase in the average PS and a corresponding decrease in its standard deviation up to $n \approx 200$ (Fig. 2); with larger values of n, the increase in precision becomes comparably small. Even with $n = 1000$ the average similarity between two independent estimates is roughly only 95%, thus underlining the stochastic nature of gap models (Bugmann 1994).

Note that about the same increase in the average PS coefficient is achieved when the sampling interval (Δt) is increased by 50% (from 100 to 150 years) as when the sample size (n) is doubled. Hence, increasing Δt is more efficient, but this would not be true for much larger Δt where autocorrelation is negligible (Bugmann et al. 1996a).

The choice of any given sample size (n) and sampling interval (Δt) for a simulation experiment always represents a compromise between the required simulation time (constrained by the available computer resources) and the desired accuracy of the estimate. From the above results, I conclude that the choice of $n = 200$ and $\Delta t = 150$ years provides a good compromise (Fig. 4). This choice is further corroborated by the findings of Bugmann et al. (1996a) concerning the sample size p required for the conventional experiment as well as the autocorrelation function of the major variables.

### Similarity of independent estimates of the same steady state

The frequency distribution of the 200 PS coefficients obtained from 400 simulation runs at the three test sites conform to the hypothesis that in species-poor forests the PS coefficient between two independent estimates of the same steady state should be higher than in species-rich forests (Fig. 3, Table 2): For the *Larici–Piceetum* community at Davos with its few tree species (Ellenberg and Klötzli 1972; Fig. 4), the PS coefficients are highest; in the more diverse forests of Airolo and Bern (Fig. 4), they are considerably lower.

Table 2. Statistics of the distribution of the percentage similarity coefficients (PS) at the three test sites ($n = 200$, $\Delta t = 150$).

	Bern		Airolo		Davos	
	Un-transformed	Arcsine transformed	Un-transformed	Arcsine transformed	Un-transformed	Arcsine transformed
CI $_{upper}$	0.955	0.950	0.963	0.957	0.989	0.983
μ (PS)	0.902	0.903	0.907	0.909	0.954	0.956
CI $_{lower}$	0.849	0.844	0.850	0.844	0.920	0.916

Note: CI denotes the lower and upper 95% confidence interval of PS; μ denotes the mean. The arcsine transformation is according to Zar (1984).

Fig. 3. Frequency distribution of the percentage similarity coefficients (PS) from 200 pairs of steady states estimated at the sites Bern, Airolo, and Davos, using $n = 200$ and $\Delta t = 150$ years. The distributions at the sites Bern and Airolo are not significantly different from each other ($p = 0.12$, Kolmogorov–Smirnov test, Zar 1984).
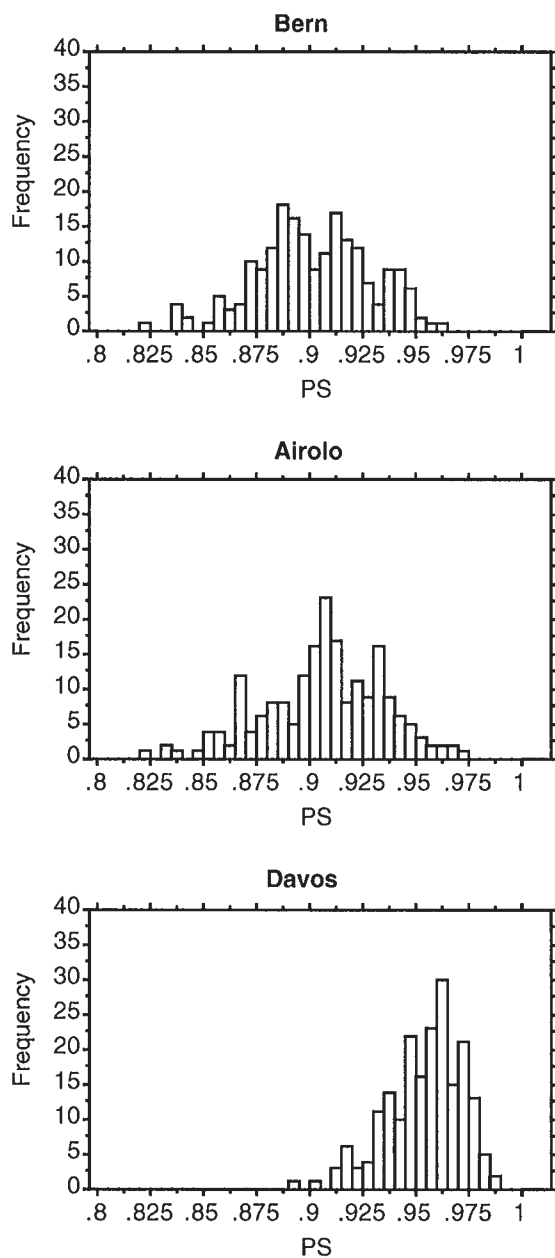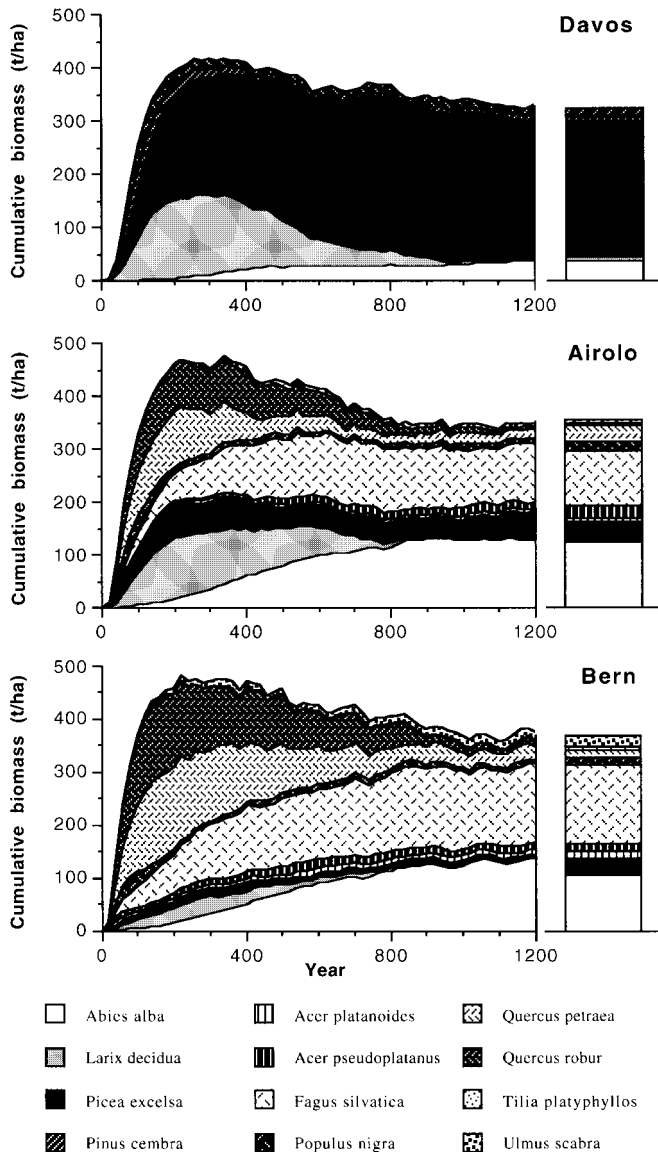

Table 3. Averages (μ) and coefficients of variation (CV) of 400 species-specific steady-state biomass estimates at the Davos site ($n = 200$, $\Delta t = 150$).

Variable	μ (t/ha)	CV (%)
Total biomass	340.8	2.4
Picea excelsa	269.7	3.8
Abies alba	34.5	16.2
Populus nigra	13.8	16.6
Larix decidua	8.9	61.3
Pinus cembra	6.5	36.3
Total of other species	7.4	—

The reason for the inverse relationship between the PS coefficients and species richness can be explained by considering the averages of the estimated species-specific biomasses and their coefficients of variation (Zar 1984) from the 400 steady states at each site. Results are shown here for the Davos site (Table 3). Evidently, the coefficient of variation tends to increase with decreasing species-specific biomass (e.g., *Picea excelsa* vs. *Larix decidua* at Davos, Table 3). The ecological role of the species (Shugart 1984) is important as well: for example, *L. decidua* and *Pinus cembra* have similar biomass at Davos; since *P. cembra* is moderately shade tolerant and usually present with low biomass, its coefficient of variation is considerably smaller than that of *L. decidua*, which is not shade tolerant and thus usually absent except after gap formation, when it can establish and grow to a large size. Similar reasoning applies to the results from the other sites (not shown here).

Thus Table 2 and Fig. 3 suggest that the statistical properties of the PS coefficient between two independent estimates of the same steady state cannot be stated generally: they depend on both the number of species participating in the succession and their autecological properties (Shugart 1984). Since the forest simulated by FORCLIM-E/P at the Bern site is among those with the highest tree species richness under European conditions (Bugmann 1994; Fig. 4), this site may be considered as a "worst case" for the statistical properties of the PS coefficients. Thus we can assume that two steady states of species-rich forests that are estimated using $n = 200$ and $\Delta t = 150$ years are significantly ($\alpha = 95\%$) different from each other if PS < 0.85 (cf. Table 2). The fewer species are present, the higher the lower confidence limit; for forests with few tree species (in Europe typically to be found at higher elevations or latitudes, e.g., Davos), the lower boundary of the confidence interval ($\alpha = 95\%$) increases to ≈ 0.92 (Table 2).

Fig. 4. Comparison of the conventional setup of simulation experiments (left, average of $p = 200$ patches, $t_{end} = 1200$ years) with the new method for estimating the steady-state species composition developed in this paper (right, $n = 200$, $\Delta t = 150$ years) at three test sites in the European Alps.

of 31 000 years, which is only 12.9% of the 240 000 simulation years for the conventional experiment involving $p = 200$ patches and $t_{end} = 1200$ years (eq. 1; Bugmann et al. 1996*a*).

If one desires to apply the present method to estimate the steady-state species compositions under varying environmental regimes (e.g., climatic change), or to study the parameter sensitivity of a gap model, we may conclude that two steady states are significantly different from each other if their PS coefficient (eq. 2) is smaller than 0.85. However, for a more accurate estimate of this threshold under the specific conditions of a model application using species and environmental settings that differ from the ones used in this paper, the present analysis would have to be repeated.

In this paper, the FORCLIM model was used as a case study to derive the new method, and it may be argued that the results thus apply uniquely to this model. However, most forest gap models share a common structure, and the formulations for many of the ecological factors incorporated in the models are similar or even identical across many models (cf. Bugmann et al. 1996*b*). Therefore I surmise that the results obtained in the present study are representative of a wide range of forest gap models, not only FORCLIM. Yet, further studies involving other models, other sets of species, and other environmental settings are certainly required to address this issue in detail.

Acknowledgements

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Conclusions

In the present study, statistical considerations were used to derive a method for efficiently estimating the steady-state species composition of the forest gap model FORCLIM (Bugmann 1994, 1996; Fischlin et al. 1995). This method complements other approaches aimed at obtaining more efficient gap models by simplifying their structure.

In the case of FORCLIM, it is possible to obtain a reliable estimate of the steady-state species composition by sampling the stochastic process on just one forest patch, using a sample size of $n = 200$ samples in time and a sampling interval of $\Delta t = 150$ years, while discarding the transient behaviour of the first 1000 years. This experiment requires simulation of a total

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