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A computationally efficient forest succession model: Design and initial tests

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ABSTRACT

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A computationally efficient forest-stand simulation model, using a concise set of state variables, is described. The model (called FLAM: Forest LAyer Model) simulates the interaction of height-class-structured tree populations on a small patch, in contrast to gap models of the JABOWA/FORET type, which model individuals. FLAM has been derived from a generalized gap model, FORSKA, by two approximations: (1) all trees of a species in a given height class have the same stem volume, leaf area, and growth increment; and (2) the distribution of tree heights within a class is uniform. Promotion from one height class to another is simulated as a binomially distributed random variable; the probability of promotion is the ratio of the predicted height growth to the depth of the height class. Height-class distributions and leaf-area-density profiles generated by FLAM were 80% and 93% similar (respectively) to profiles generated by FORSKA, but FLAM ran in 5% of the c.p.u. time. The effect of variations in spatial resolution (number of height classes) and temporal resolution (number of years per time step) were tested by comparing leaf-area-density profiles from FORSKA and FLAM. The performance of FLAM was insensitive to temporal and spatial resolution over a wide range of resolutions (1–5-year time-step, 4–20 height classes). Performance deteriorated if the temporal or spatial resolution was coarser.

INTRODUCTION

The initial stage in modeling a system is to select the relevant components and the variables to be used to describe their state. For example, population ecology concerns itself with numbers of individuals. The classical equations of population growth use only the total number of individuals as a description of the state of the population. The fact that this state description is inadequate in many situations, e.g. where age or size structure matters, is well known, and has led to frequent criticisms of theory developed from these equations. Recently, Huston et al. (1988) have advocated the use of models in which each individual is modeled as a separate entity. This computationally demanding solution may not be necessary in all cases. If relevant differences between individuals can be identified, it may be sufficient to model classes of

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individuals whose behavior is expected to be similar. For example, Werner and Caswell (1977) compared age-class and stage-class descriptions of teasel populations, and found the predictions of the latter to be consistently superior.

'Gap models' based on JABOWA (Botkin et al., 1972) and its descendant FORET (Shugart and West, 1977) are well-known examples of individual-based ecological models, and have effectively mimicked structural and compositional features of forests under a wide variety of conditions. The two key features of these models are as follows:

(1) The scale of interaction of individuals is identified. Many simple models of population interactions have assumed that conditions can be averaged over large areas. Gap models assume horizontally uniform conditions over a small (0.01–0.1-ha) patch.

(2) Specific mechanisms of interaction between individuals are modeled – a reduction of growth due to the depletion of a soil resource, and a vertically structured competition for light. The choice of a specific patch size corresponds to an assumption that competition occurs over such areas.

Light competition is asymmetric. This asymmetry is brought about by differences in canopy height, which implies that it may be possible to use the equations of individual growth and interaction to model the growth and interaction of size-structured populations of trees on a patch. The term 'population', in this case, means the set of trees of a given species occupying a modeled patch, not the (usually larger) populations considered by geneticists. The model described in this paper (called FLAM, for Forest LAyer Model) simulates tree populations of each species in a small number of height classes. The vertical spatial resolution (number of height classes) can be varied. The effects of variation in this parameter, and in the model time-step, were explored.

MODEL STRUCTURE

FLAM was designed to parallel an existing model as closely as possible. The purpose was to isolate the effects of the differences in state description from other possible differences between gap models, and examine their effect on the predictions of the model. The central problem in this development was the application of individual-tree growth equations to a model of interacting structured populations. A few simple assumptions allowed this to be carried out with a minimum of violence to the basic assumptions underlying gap models. This discussion will begin with a short description of the model used as a basis for FLAM, followed by a description of mechanisms peculiar to FLAM.

Brief description of FORSKA

The model used as a basis for FLAM is FORSKA, developed for Scandinavian forests by Leemans and Prentice (1989) and tested by predictions of the structure and composition of a spruce/pine forest in central Sweden (Prentice and Leemans, 1990). This model differs from standard gap models based on JABOWA (Botkin et al., 1972) and FORET (Shugart and West, 1977) in several ways, which will be outlined below. A description of an earlier version of FORSKA, including some of the features described below, can be found in Leemans and Prentice (1987).

The most basic differences between FORSKA and conventional gap models are in the state variables and model structure. In conventional gap models, species and D_{bh} (diameter at breast height) alone suffice to indicate the state of a tree. FORSKA models the D_{bh}, leaf area, and bole height (height of leafless stem) separately for each tree in the patch.

Establishment is similar to other gap models, in that a small number of saplings are 'planted' in a year if conditions allow, but the only condition used is light intensity. If light on the forest floor exceeds the compensation point of the species then establishment can occur. The initial size of saplings (D_{bh}) varies over a small range so that the size and growth of all trees established in a given year is not identical. Initial leaf area is a linear function of the square of D_{bh}, in accordance with the pipe-model theory of plant form (Shinozaki et al., 1964), and the fact that saplings have little or no heartwood.

As in other gap models, height and diameter are functionally related, but FORSKA uses an asymptotic relationship that does not require the specification of a maximum diameter:

$$H = 1.3 + (H_{max} - 1.3)(1.0 - \exp(-AD)) \qquad (1)$$

where: H is height (m) and $D = D_{bh}$. H_{max} (maximum height (m)) and A are species-specific constants which can be estimated from height and D_{bh} data by non-linear regression (Leemans and Prentice, 1989).

Growth depends on net assimilation integrated with respect to height. Several factors enter into the equation for growth: the vertical distribution of leaf area; light extinction; the curve for the response of net assimilation to light; below-ground competition; and a cost for the maintenance of leaf area at a given height. The vertical distribution of leaf area is calculated by assuming that each tree has its leaf area distributed uniformly from the top of the tree to the bole height, instead of being all at the top of the tree, as is assumed in conventional gap models. Light extinction is calculated according to the Beer-Lambert Law (Monsi and Saeki, 1953):

$$l_z = l_0 \exp(-kF_z) \qquad (2)$$

where: l_z is available light; l_0, light at the top of the canopy; k, light-extinction coefficient; and F_z is cumulative leaf area at depth z in canopy. Assimulation is based on a maximum net assimilation rate per leaf area, multiplied by a rectangular hyperbolic function of available light:

$$P_z=(kl_z-c)/(kl_z+\alpha-c) \tag{3}$$

where: P_z is proportion of maximum photosynthesis carried out by leaves at depth z in the canopy; α, half saturation point; and c, compensation point of photosynthesis/light response curve. The growth equation is:

$$(\mathrm{d}(D^2H))/\mathrm{d}t=((W_{\max}-W_{\mathrm{tot}})/W_{\max})\int_B^H S_L(\gamma P_z-\delta_z)\mathrm{d}z \tag{4}$$

where: W_{tot} is total biomass on patch (proportional to stem volume: D^2H); $W_{\max}$, the maximum biomass; S, vertical leaf-area density; γ, species-specific growth-scaling constant; δ, species-specific maintenance cost; and B, bole height. W_{tot} and $W_{\max}$ model below-ground competition in a crude manner similar to many conventional gap models. The rationale for the cost factor scaled to height comes from the 'pipe model' theory of plant form (Shinozaki et al., 1964), and reflects the maintenance cost of the sapwood required to support a given leaf area at a given height. The integral is solved by evaluating the function over small discrete intervals and taking the sum. The stem-volume growth increment is converted to a D_{bh} increment by use of Eqn. (1) and its first derivative.

Leaf area is not just a function of D_{bh}. New leaf area is added proportional to the basal area increment, then two mechanisms independently reduce leaf area: (1) a certain minimum percentage of leaf area is considered to be lost each year to 'sapwood turnover'; and (2) leaf area that is shaded below the compensation point for that species is 'pruned', and the bole height is raised accordingly.

The probability of mortality of trees in a time-step is calculated as a function of the ratio of growth efficiency (volume-increment/leaf-area; Waring, 1983) to the maximum growth efficiency for the species. When the ratio is less than a specified threshold the probability of mortality is greatly enhanced.

Structure of FLAM

FLAM simulates the number of stems, stem volume (more precisely, the product of diameter squared and height), leaf area and top bole layer (highest layer without leaves) for each tree species in a small number of height classes. The leaf area of the trees in a height class is assumed to be evenly distributed from the top of the height class to the top of the top bole layer. In this discussion, the term 'layer' refers to a volume of space in the simulated patch corresponding to the height class of the trees whose tops are found in that layer.

The state for each height class and species is updated using the following equations:

$$N(t+1)_{ij}=N(t)_{ij}-M_{Nij}-P_{Noutij}+P_{Ninij} \tag{5}$$

$$V(t+1)_{ij}=V(t)_{ij}+D_{Vij}-M_{Vij}-P_{Voutij}+P_{Vinij} \tag{6}$$

$$L(t+1)_{ij}=L(t)_{ij}+D_{Lij}-M_{Lij}-P_{Loutij}+P_{Linij}-L_{\mathrm{prune}} \tag{7}$$

where: $N(t)_{ij}$, $V(t)_{ij}$, and $L(t)_{ij}$ are number of stems, total stem volume and leaf area, respectively, for the species i and height class j at time t; D_V, D_L, growth increments of stem volume and leaf area, respectively; M_N, M_V and M_L, mortality of individuals, stem volume and leaf area respectively; P_{Nout}, P_{Vout} and P_{Lout}, promotion of individuals, stem volume and leaf area, respectively, into the height class(es) above; P_{Nin}, P_{Vin} and P_{Lin}, promotion of individuals, stem volume and leaf area, respectively, from below; and L_{prune}, leaf area pruned. The calculation of each of these terms is described below under the headings of establishment, growth, promotion, pruning and mortality.

Establishment (promotion into layer 1)

Promotion into the lowest height class is similar to 'establishment' in FORSKA, with small modifications. As in FORSKA, if the light below the bottom layer is above the compensation point for the species, a number (Poisson variate) of 'saplings' is introduced. These have a stem volume based on the product of height (1.3 m) and diameter at the base of the trunk (calculated from a linear extrapolation of the height/D_{bh} relationship to a height of 0.0 m):

$$v=1.3(1.3/s)^2 \tag{8}$$

where: s is the initial slope of height D_{bh} function: $A*(H_{\max}-1.3)$ (Eqn. 1)), to which is added 50% of the expected growth increment of a tree of this size during the time-step. Because the growth of trees in FLAM has a stochastic element (movement between height classes), it is not necessary to introduce random size variations at this step.

Growth (D_V and D_L)

Growth in stem volume is calculated using the same equations as FORSKA for a basis, but the evaluation of the integral is made more efficient by the assumption of homogeneously distributed leaf area of each species within each layer. Equation (3) becomes:

$$\mathrm{d}(D^zH)/\mathrm{d}t=((W_{\max}-W_{\mathrm{tot}})/W_{\max})\sum_{L=L_{\mathrm{b}}+1}^{L_{\mathrm{h}}}\int_{L_{\mathrm{t}}(\mathrm{L}-1)}^{L_{\mathrm{t}}(\mathrm{L})}S_L(\gamma P_z-\delta z)\mathrm{d}z \tag{9}$$

where: L_{b} is top bole layer; L_{h}, height class of trees; and $L_{\mathrm{t}}(L)$, height of top of layer L. Because F_z is a linear function of canopy depth within a layer, the integral in this equation has an analytical solution. The equation returns the total volume increment for all the trees of a species in a height class.

The growth equation returns a volume increment, but growth in leaf area requires a notional basal area (or diameter squared) increment, and promotion into higher height classes requires a notional height increment. The evaluation of these increments is the first problem encountered in translating individual growth equations into structured population terms. The problem is solved by assuming that trees in a given height class allocate volume growth to diameter and height growth as a 'representative tree' would. A representative tree is one with height halfway between the upper and lower limits of the height class. Given the representative height, the relationship between height and diameter for trees of that species (Eqn. 1), and the model's definition of stem volume, the relationship between the time differentials of stem volume, diameter and height can be derived and calculated. These are calculated as constants specific to each combination of species/layer. The relationship between the total volume (D^2H) increment and total diameter squared increment for all the trees of a species in a layer is:

$$\mathrm{d}(D^2)/\mathrm{d}t=(2/(D_\mathrm{r}C_{HD}+2H_\mathrm{r}))(\mathrm{d}V/\mathrm{d}t) \tag{10}$$

where: H_r and D_r are height and D_bh of the 'representative tree' for the layer; and $C_{HD}=\mathrm{d}H/\mathrm{d}D$ evaluated at $D=D_\mathrm{r}$ (see Eqn. 1). The relationship between the volume increment and height increment for a representative tree is:

$$\mathrm{d}H/\mathrm{d}t=(1/N(t))((1/D_\mathrm{r}^2)(1-(2H_\mathrm{r}/(D_\mathrm{r}C_{HD}+2H_\mathrm{r})))(\mathrm{d}V/\mathrm{d}t) \tag{11}$$

This representative height increment can be used to calculate the probability of promotion to the next height class (see below).

Promotion (P_{Nout}, P_{Vout}, and P_{Lout})

The promotion of trees from one height class to the class(es) above is the other salient problem that must be solved in the application of individual growth equations to a stage-structured population model. As noted in the discussion of growth, the idea of a representative tree allows the calculation of diameter and height growth, given a volume growth increment. The problem is how to translate this continuous height growth into the discontinuous promotion required by the model. Two assumptions are made: (1) the distribution of tree heights within the height class is uniform; and (2) all trees in the height class (of a given species) have the same increment of height growth. The number of trees promoted out of the layer can then be simulated as a binomially distributed random variable, with:

$$\text{Number of trials} = N(t)_{ij} - M_{N_{ij}} \tag{12}$$

$$\text{Probability of promotion} = \text{minimum } (D_H/\text{THICKNESS}, 1.0) \tag{13}$$

where: D_H is height growth increment; and THICKNESS, difference between the upper and lower limits of the height class. Stem volume and leaf area are assumed equal for all trees of a species within a height class, so these variables are updated accordingly. Promotion out of one height class becomes promotion into the height (class(es) above, so the model state is updated beginning with the lowest height class. If D_H is greater than the thickness of one or more of the layers above, the program can allow trees to 'skip' one or more layers, allocating trees to each layer with a binomial variate calculated in a fashion analogous to the above.

Pruning (L_{prune} and top bole layer)

Pruning of leaf area works on the same principle as FORSKA, but it is applied on a layer-by-layer basis instead of continuously. If the light falling on the top of a layer falls below the compensation point for a species, the leaf area within that layer is pruned and the top bole layer is raised to that layer. However, trees may not prune away all of their leaf area; the top bole layer is always below the height class of the trees. The top bole layer is initialized to layer zero (below the first layer), and is reset to zero whenever there are no trees in that height class.

Mortality (M_N, M_V and M_L)

The probability of mortality in a time-step is a step function of the relative growth efficiency. Probability of mortality is the same for all trees of a species in a height class, so the number killed is simulated as a binomially distributed random variable. It is assumed that all trees in a height class have the same stem volume and leaf area, so these variables are updated accordingly.

MODEL PERFORMANCE

The purposes of this modeling exercise were: (1) to show how a gap model can be converted from an individual-based model to a model of interacting size-structured populations; and (2) to investigate the differences in model predictions caused by this conversion. The performance of FLAM, therefore, was evaluated by comparison with output from its parent model, FORSKA. Strictly speaking, the results presented here are model verifications rather than validations (sensu Shugart, 1984) by comparison with actual forest data. FORSKA has, however, predicted detailed structural features of a forest in central Sweden with high accuracy (Prentice and Leemans, 1990).

The two models were compared using height-class distributions (in 5-m

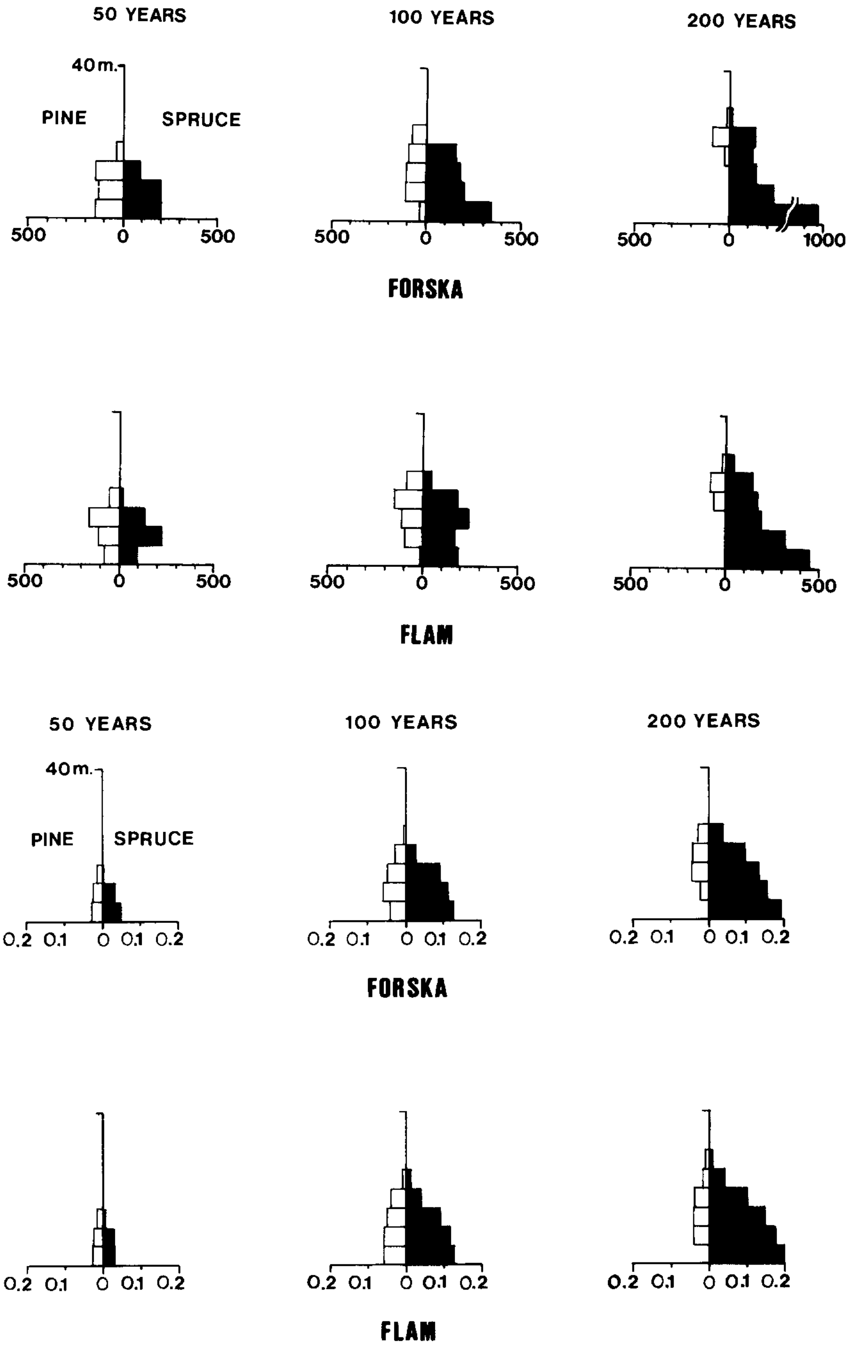

Fig. 1. Comparisons of runs of FLAM and FORSKA for simulated spruce/pine forest in central Sweden for 50, 100, and 200 years after stand initiation. (a) Number of stems ha^{-1} in 5-m height classes. (b) Leaf-area density (m^2/m^3) profiles.

classes) and leaf-area density profiles. The latter comparison was made because the distribution of foliage in the canopy is one of the strongest predictors of primary productivity in terrestrial ecosystems (Monsi et al., 1973). Both FORSKA and FLAM have a detailed description of leaf area distribution compared to standard gap models, and both can be used to predict leaf area density profiles.

Height-class distributions and leaf-area density profiles from model runs of 50, 100 and 200 years are shown in Fig. 1 for FORSKA and FLAM. The profiles from each model represent the average of 30 replicate patches, using parameter values appropriate for a spruce/pine forest in central Sweden (Leemans and Prentice, 1989). FLAM was run with eight layers (each 5 m thick), and a 2-year time-step. FORSKA was run with a 0.1-m vertical integration step and a 2-year time-step.

Both set of profiles (Fig. 1) show typical features of Scandinavian spruce/pine forest dynamics, such as the increasing dominance of shade-tolerant Norway spruce (*Picea abies*) with time and the shading-out of shade-intolerant Scots pine (*Pinus sylvestris*) in the understory. The qualitative differences between the two sets of profiles are small. FLAM has a tendency to promote trees more rapidly to higher layers and to miss the tapering of the leaf-area density of pine in the lower layers. The two sets of profiles were compared quantitatively using the Bray and Curtis (1957) index and treating each combination of layer/species/duration as a separate 'species'. The height-class distributions were 80% similar and the leaf area density profiles were 93% similar.

It took the program FORSKA 35 min of C.P.U. time to simulate 200 years of growth for 30 replicate patches on a Microvax II VMS computer. The corresponding run took FLAM 90 s.

EFFECT OF TEMPORAL AND SPATIAL RESOLUTION

The patch size prescribed for gap models is often approximately equal to the canopy area of a fully grown dominant tree. Models run with this patch size will show typical gap-phase dynamics, in which the death of a dominant canopy tree will allow regeneration of shade-intolerant as well as shade-tolerant species (Shugart, 1984). In Boreal forests, however, only multiple-tree gaps, such as those created by storms of fires, allow regeneration and growth of shade-intolerant species (Prentice and Leemans, 1990). These dynamics can be effectively modeled by simply using a patch size of ca 0.1 ha, which is much larger than the canopy area of a single dominant spruce (Leemans and Prentice, 1987). This patch size was used for the runs of FLAM reported here, as well as the runs of FORSKA used for comparison.

After the patch size is set, the spatial resolution of a standard gap model is fixed by the fact that individual trees are presented. The model FLAM allows the manipulation of vertical spatial resolution or grain (sensu Allen and Starr, 1982) by variation in the number of height classes simulated. It is of interest from both practical (computation time) and theoretical points of view to know what is the minimum number of height classes needed for an accurate simulation. The question being asked is: "How much (or how little) does one have to know about the height and growth of each individual to accurately simulate the structure and dynamics of a forest?". The effect of variations in the time step is a related issue; here, the concern is with how long current trends of growth can be extrapolated before an updated state description is required.

The effects of variation in spatial and temporal resolution on the model FLAM were investigated as follows. Leaf-area-density profiles from 50, 100, and 200 simulated years for the two-species system described above were generated by FLAM and FORSKA. The profiles were averages of 30 replicate patches. FORSKA was run with a 2-year time-step. FLAM was run with all combinations of 2, 4, 8, and 20 layers and time-steps of 1, 2, 5, 10, and 25 years. The performance of FLAM was measured by the Bray-Curtis (1957) similarity between its leaf-area-density profiles and those generated by FORSKA. As above, the similarity was calculated for all model durations together: each combination of layer, duration, and species was taken as a 'species' in the index, giving an overall measure of model performance. The results are shown in Fig. 2. FLAM is insensitive to changes of spatial and temporal resolution over a fairly wide range (≥4 layers, ≤10-year time-step). If the resolution is too coarse, either in space or time, the performance drops off

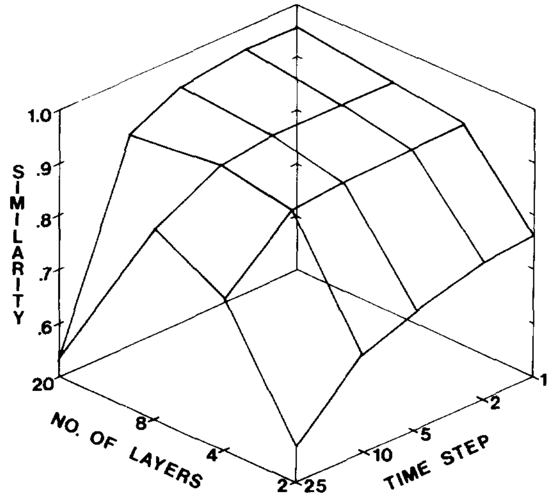

Fig. 2. Performance of FLAM at various spatial and temporal resolutions, as measured by Bray-Curtis similarity of leaf-area-density profiles to those generated from FORSKA.

sharply. The shape of the response surface indicates that there is no appreciable interaction between the number of layers and the time-step.

DISCUSSION

The results from the test of the effect of spatial resolution underscore an aspect of light competition as simulated by gap models: it is a positive-feedback mechanism that magnifies initial differences in height. A state description too coarse to capture the differences will not model the system accurately. Standard gap models are based on an explicit theory about the horizontal scale of tree/tree interactions (Shugart, 1984). This test indicates that a certain minimum vertical resolution is needed as well. The surprise is in how little resolution is needed.

There is no fundamental conceptual change implied in the transition from an individual-based model to a model based on interactions of size-structured populations. Populations consist of individuals by definition. Both FLAM and FORSKA model populations of interacting individuals, and the scale of interaction of individuals (the patch size) is the same for both models. Confusion arises only if the 'population' considered here is mistaken for the (typically larger) populations of individuals connected by reproduction and propagule exchange that are considered by geneticists. Gap models do not directly address processes occurring on the level of reproductive/genetic populations. This is apparent from the fact that establishment in most gap models is solely a function of the environment; the trees actually present on the patch do not affect establishment rates.

The construction of this model is, therefore, largely a technical accomplishment; the ecological logic is the same as that of gap models. However, its success in mimicking FORSKA implies that much of the information contained in individual tree descriptions is redundant if the main concern is with a dynamically sufficient (sensu Van Hulst, 1980) representation of a forest patch. For this purpose, a minimal model does not seem to have trees as unique individuals.

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