



TreeMig core model

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This is a documentation of the core TreeMig model, it follows in parts the ODD (Overview, Design concepts, and Details) protocol (Grimm et al. 2020), but with a stronger focus on explaining the equations and processes and the FORTRAN routines and their sequence.

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References to the subroutines in the source code are given in red.

1.1 Introduction

1.1.1 *Spatially dynamic models for landscapes*

Ecosystems and landscapes exhibit complex patterns that are driven by a variety of processes. The patterns may be apparent in space (landscape pattern) and/or in time (landscape dynamics) and result from various processes acting at different scales. The driving processes can either be exogenous, including disturbance (e.g., fire), or endogenous (e.g., inter-species competition). Exogenous processes drive patterns via interactions of the system with externally imposed environmental factors.

The environmental factors are usually of abiotic nature and involve climate, soil, topography disturbance (e.g., fire, wind). Endogenous processes shape landscapes via the changes resulting from internal interactions between the individual system components. Spatio-temporal ecological pattern as a function of driving processes can be analyzed and predicted using landscape modelling approaches. A broad variety of landscape models are currently available, starting from many different viewpoints and concepts (Shifley et al. 2017 2001, new developments, Petter et al. 2020). Among them, spatially dynamic models allow individual biotic units at different locations, usually in a spatial grid to undergo spatially linked demographic dynamics. One such model, TreeMig, has been developed from the temporal, distribution based, structured population model DisCForM (Lischke et al. 1998a, Löffler and Lischke 2001). TreeMig responds to the most recent requirements in landscape modelling for a variety of reasons: (a) the model is a spatially dynamic model, i.e. simulates local demographic processes and spatial interactions, with (b) special focus on reproduction including seed production and empirically based, mechanistic species-specific seed dispersal, (c) and it includes within-stand variability with a simplified algorithm.

1.1.2 General TreeMig concept

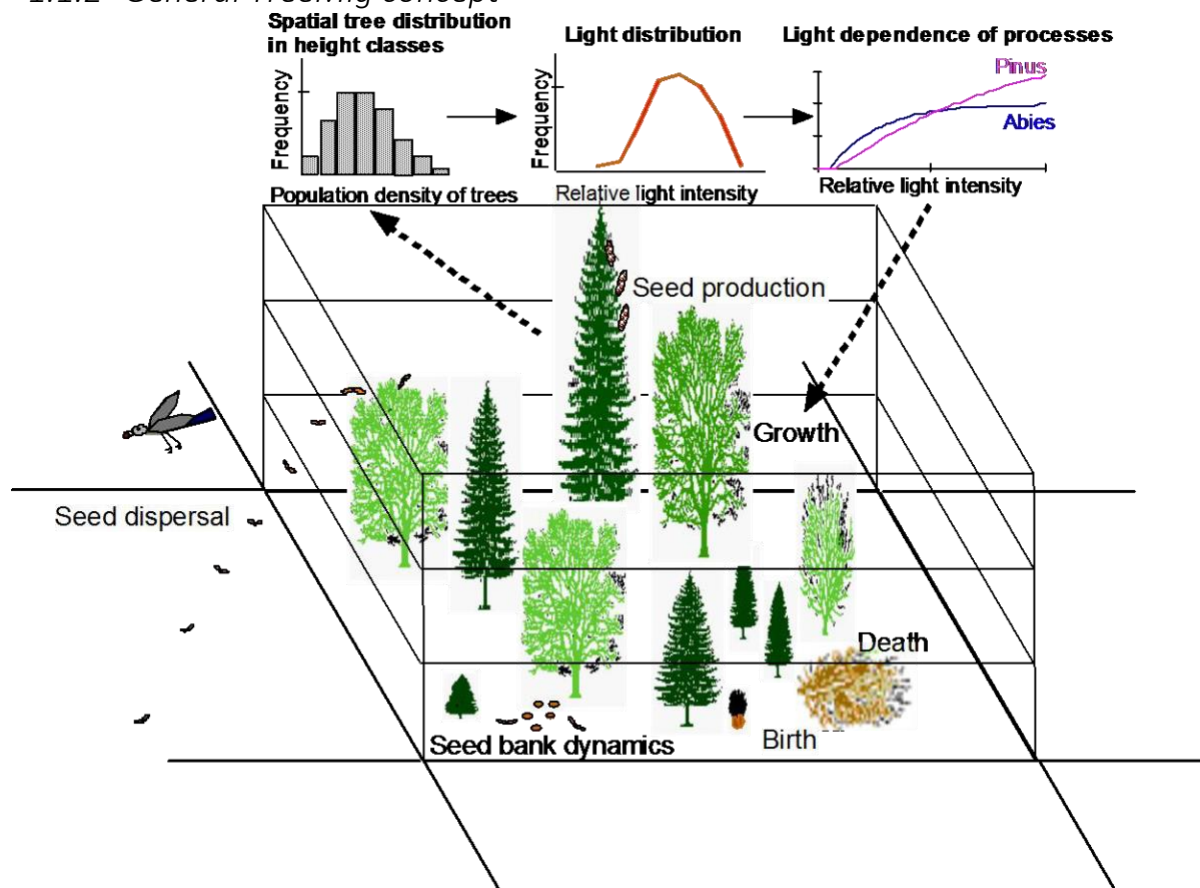


Figure 1: Concept of the model TreeMig. The model is implemented on a rectangular grid. In each grid cell, trees in different height classes germinate, grow, die and produce seeds. In each height class a theoretical distribution of tree densities across the entire stand is calculated based on the average population density per height class. The resulting light distribution determines the process rates and the dynamics of all trees within this height class. The seeds are dispersed to the same or other grid cells, where they enter the seed bank. Seed bank dynamics includes a species-specific density

TreeMig (Lischke et al. 2006, Lischke 2020) is a quantitative, spatially and temporally explicit model designed to simulate forest landscape change over large spatial and temporal scales. It is based on the distribution based, height structured forest population model DisCForM (Lischke et al. 1998a, Löffler and Lischke 2001). The model describes local stand dynamics in each cell of a spatial grid by the demographic processes birth, growth, death, seed production (fecundity), seed-bank dynamics, germination and sapling development (Figure 1). The spatial interactions between the cells are realized by species-specific seed dispersal which accounts for short- and rare long-distance seed transport. With this design it goes beyond traditional stand simulators such as gap models which ignore seed production and seed dispersal. By introducing height classes and theoretical distributions of tree densities in space (Figure 1) it accounts for within-stand variability in each cell. The model concept and a general description of the major processes accounted for are shown in Figure 1 and Figure 2. The model is set up to simulate the *spatial* and the *local dynamics*. The spatial dynamics in TreeMig is mirrored using species-specific seed dispersal that connects the individual cells with each other. The local dynamics describes the forest development in each cell. The juvenile dynamics is simulated using processes that encompass seed bank dynamics, germination, seed survival and establishment rates, which are followed by sapling development. Finally, adult tree dynamics determines seed production. The seeds are subsequently fed into the spatial dynamics module. The model consists of a set of coupled

difference equations for the state variables mean population densities of the seeds in the seed bank (Sb , 2) and the trees in the different height classes (N , 1).

The coordinates of the cell are (x, y) , s is the species, i the height class and t the time. The tree densities are assumed to be Poisson distributed (Lischke et al. 1998b). N is the average tree population density and Sb the seed bank, i.e. the seed density per patch area in the entire forest soil. The tree population density at time $t+1$ is a function of the population density, growth G (4), death D (5) and birth B (3) at time t . The seed bank changes through death D_{sb} , germination (birth) B and seed inflow I . The seed input I is determined by dispersal and thus a function of the conspecifics N_s in all cells and their seed production (6

1.2 Processes and dynamics

This section explains how the main model processes are simulated, and gives the link to the corresponding subroutines.

1.2.1 Governing model equations

LocalForestDynamics

The rate of change of the state variable number of trees per species, height class and grid cell ($N_{s,i,x,y,t}$) is given by mortality, growth and germination from the seed bank.

Temporal change of tree numbers $N_{s,i,x,y}$ per species s , height class i and grid cell x,y at time t

$$N_{s,i,x,y,t+1} = N_{s,i,x,y,t} - \bar{\mu}_{tot,s,i,x,y,t} N_{s,i,x,y,t} \quad (1)$$

$$- \frac{\bar{\gamma}_{s,i,x,y,t}}{h_{i+1} - h_i} N_{s,i,x,y,t} + \begin{cases} \frac{\bar{\gamma}_{s,i-1,x,y,t}}{h_i - h_{i-1}} N_{s,i-1,x,y,t} & i = 1, \dots, 15 \\ \text{birth}(Sb_{s,x,y,t+1}) & i = 0 \end{cases}$$

s : species

x,y : grid cell

t : time

h_i : height of height class i

μ_{tot} : mortality rate (37) (here averaged over light classes, , in code calculated by light class)

γ : growth (49) (here here averaged over light classes, in code calculated by light class)

Birth: seedlings germinating from seed bank and surviving first year

Temporal change of seed bank: **Regen, SeedsDispFromThisCellAndSpec**

$$Sb_{s,x,y,t+1} = Sb_{s,x,y,t} (1 - \mu_{Sb,s} - germ_s) + \sum_{\check{x},\check{y},i} S_{s,i,\check{x},\check{y},t} k_s(z), \quad (2)$$

$$z = \sqrt{(\check{y} - y)^2 + (\check{x} - x)^2}$$

Sb : number of seeds in seed bank

S : number of seeds produced (14)

k : seed dispersal kernel

μ_{sb} : seed mortality

$germ$: germination rate

x,y (\check{x},\check{y}): coordinates of sink (source) cell

1.2.2 Process overview and scheduling

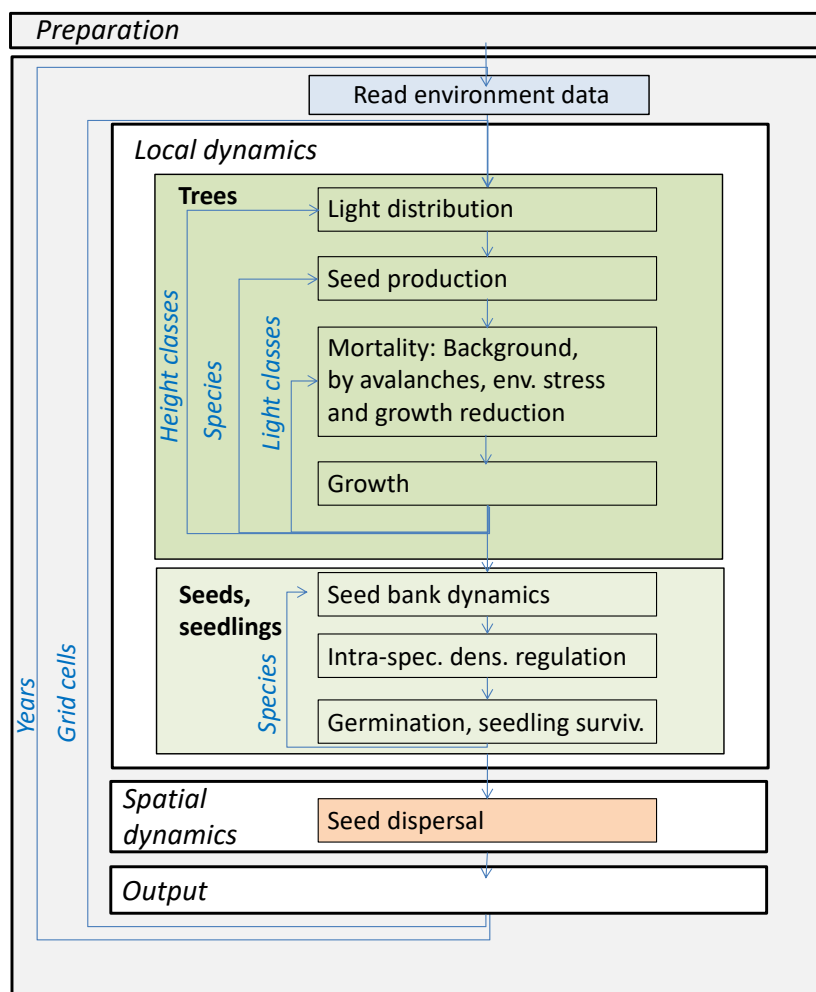


Figure 2: Sequence of processes in TreeMig

1.2.3 Simulation of environmental conditions in landscape

1.2.3.1 Organization of the landscape

The landscape is divided into a rectangular grid consisting of square grid cells of size to be chosen. Grid cell side lengths make sense between 25m and 10km. Fine discretizations come with large computing times and large discretizations involve discretization errors related to missing the within cell heterogeneity and to the dispersal kernel. A Boolean mask (stockability) defines which grid cells are active. non-active cells, e.g. by land-use or water-bodies, are ignored during the simulation, no seeds are allowed there. The cells are characterized by both constant (location, elevation, slope, aspect, water holding capacity) and time-variable (temperature, precipitation) state variables. Constant drivers are initialized once at the beginning of each simulation run, time-variable drivers updated each year based on the input data. **GetStand**

1.2.3.2 Calculation of environmental conditions

There are additional environmental attributes, that drive the demographic processes and that are derived from basic input data for each cell.

- **Bioclimate:** The bioclimatic variables are calculated outside the TreeMig core model in the R routine `getBioClimate.R`. They are read in in `ReadNewBioClim`. The simulation is only performed in cells for which bioclimate is available. The bioclimatic variables

are

- WiT: the annual minimum monthly temperature means (MinWT) based on monthly temperature means,
- DD: Annual sum of growing degree-days (GDD, based on monthly temperatures and a correction function (Bugmann, 1994).
- Annual drought index (DrStr) based on soil WHC, slope, aspect, monthly temperature means and precipitation sums, slope, aspect) (cf. Bugmann and Cramer, 1998). See SoilMoisture.R in the wrapper.
- Stockability
 - stock: indicates whether in a cell forest growth is prevented due to land use, or physical reasons other than bioclimate, i.e. rocks, water bodies, or glaciers (then set to 0, otherwise 1). This stockability is used to mask out cells in the bioclimate input file.
- Optionally, further inputs changing in space and time can be used, but must be added as columns with fixed names in the bioclimate file. If not provided they are set to constant values, which can be changed by the user.
 - germDrought: drought stress for germination
 - brwpr: browsing pressure
 - distu: deterministic disturbance, normally large scale
 - avNit: available nitrogen

1.2.3.2.1 Temporally varying light distribution

Lfcalc

A central characteristic of TreeMig are frequency distribution of light conditions (between 0-1) in each height class, based on the (assumed) random distribution of the trees in this height class and their LAI (assumed to be at the top of the trees Lischke et al. 1998a). The mean process rates are calculated using the frequencies of light conditions in the height class over the simulated stand (Lischke et al. 1998a, Löffler and Lischke 2001). The light frequencies are determined by the frequencies of the tree densities per unit area. Thus, the variability within a stand is implicitly included in the horizontal frequency distributions and the vertical height classes of the trees. Since light intensity is a random variable, these mean values are calculated with the probability density function f_{L_i} of light intensity L_i in height class i ,

$$\bar{\varphi} = \int_{-\infty}^{\infty} \varphi(l) \cdot f_{L_i}(l) dl = \int_0^1 \varphi(l) \cdot f_{L_i}(l) dl, \text{ with } \varphi = \mu_{s,i}, \gamma_{s,i}, \beta_s \quad (3)$$

To determine the light density function f_{L_i} , all trees of each species s in each height class j are assumed to be randomly distributed over the cell, which for tree population densities $X_{s,j}$ leads to a Poisson distribution with mean $N_{s,j}$, itself approximated by a Normal distribution with mean $N_{s,j}$ and standard deviation $\sqrt{N_{s,j}}$.

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, 833m²) 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

$$LAI_i = \frac{\sum_{j>i} \sum_{s,j} a_{s,j}}{\zeta} \quad (4)$$

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 i , it is also normally-distributed with the parameters

$$\mu_{LAI} = \frac{1}{\zeta} \sqrt{\sum_{j>i} \sum_S N_{s,j} a_{s,j}} \quad \text{and} \quad \sigma_{LAI} = \frac{1}{\zeta} \sqrt{\sum_{j>i} \sum_S N_{s,j} a_{s,j}^2} \quad (5)$$

With full light intensity 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 the Beer-Lambert law: $l_i = e^{-\alpha \cdot LAI_i}$. Thus, a certain light intensity l_i in height h_i is achieved through the leaf area index LAI_i , which fulfils

$$LAI_i = -\frac{\ln(l_i)}{\alpha} \quad (6)$$

Using transformation (6), 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} (5). Hence,

$$f(l) = -\frac{\ln(l)}{\alpha} \frac{1}{l \alpha} \quad (7)$$

The density function f_{L_i} is scaled to 1 by $\int_0^1 \cdot f_{L_i}(l) dl = 1$, to partly compensate for the errors introduced by replacing Poisson distributions by non-truncated Normal ones.

In the implementation, light intensity was discretized into 10 light classes ξ , so that light-dependent rates could be calculated once in advance, thus accelerating the computation. In this discrete formulation, (3) becomes

$$\bar{\varphi} = \sum_{\xi=0}^9 \varphi(l_\xi) \left(F_{L,i}(l_{\xi+1}) - F_{L,i}(l_\xi) \right) \quad (8)$$

where F_{L_i} is the distribution function of the light intensities, which can be expressed by the Normal distribution function of the leaf area index with the parameters μ_{LAI} and σ_{LAI} by

$$F_{L,i}(l) = F_{LAI,i} \left(-\frac{\ln(l)}{\alpha} \right). \quad (9)$$

1.2.3.3 Feedbacks between forest structure and environmental conditions

A feedback between the forest structure (i.e., the number of trees per cell, species, and height class, and the assumed random distribution of the trees) and environmental conditions is only simulated regarding the light conditions, calculated with the Lambert-Beer law. Further developments of TreeMig allow simulating feedbacks between the forest structure and a dynamic hydrology model (Speich et al. 2020), rockfall (Moos and Lischke 2022), or with avalanche release (Zurbriggen et al. 2014), but the standard version of TreeMig described here does not contain such feedbacks.

1.2.4 Tree processes

1.2.4.1 Allometries

InitAndSetConstHeightClProps Only the number of trees by height class is determined, i.e. height is the basic tree attribute. All additional tree attributes are estimated based on

allometric relationships, all depending on height h_i in height class i or on each other. The used coefficients $c1$, $c2$ and $a1$, $a2$ are discrete, species specific values depending on the species type with respect to broad/needleleaf (tb) and on the species type stn (set in **GetSpc**).

- Diameter at breast height (DBH, $d_{i,s}$): **DBHFromHeight**

$$d_{i,s} = d_{max,s} \left(1 - \sqrt{\min \left(\max \left(1 - \frac{h_i - h_{min}}{h_{max,s} - h_{min}}, 0 \right), 1 \right)} \right) + d_{min} \quad (10)$$

where $d_{min} = 0.0127 \text{ cm}$, $h_{min} = 1.37 \text{ m}$

- Biomass: based on DBH: **BiomassFromDBH**

$$folwgt = c1(tb_s) a1(stn_s) e^{\ln(d_{i,s} 100.0) a2(stn_s)} \quad (11)$$

$$stmwgt = 0.5 \cdot 0.12 e^{\ln(d_{i,s} 100.0) 2.4}$$

$$biom_{i,s} = folwgt + stmwgt$$

Biomass consists of the weight of the foliage ($folwgt$) and the weight of the stem ($stmwgt$) (half of the stem volume), which both depend on the DBH.

- Leaf area: based on DBH, i.e. eventually on height **LAFromDBH**

$$la_{s,i} = c2(tb_s) * a1(stn_s) * e^{\ln(d_{i,s} 100.0) a2(stn_s)} \quad (12)$$

- Seed production dependence: based on leaf area **GetSpc**

$$sp_{s,i} = \begin{cases} 0 & \text{if } i < i_{s, \min} \\ \frac{la_{s,i}}{la_{s, \max}} & \text{else} \end{cases} \quad (13)$$

The seed production height dependence is proportional to the leaf area. $i_{s, \min}$ is the height class in which a tree starts producing seeds (class of maturity height), $la_{s, \max}$ the leaf area in the highest class for this species.

1.2.4.2 Regeneration

Species' reproduction depends on the availability of seeds in the seed bank and therefore on the presence of seed-producing trees and the dispersal of the seeds produced annually.

Reproduction is split into the processes of seed production, seed dispersal, seed bank dynamics, germination and sapling development (Lischke and Löffler 2006).

1.2.4.2.1 Seed production

SeedProd

The seed production is calculated depending on height. Only from a critical height on ("maturity height"), trees are assumed to be mature and to produce seeds. The seed amount is scaled according to the leaf area and a maximum seed production parameter.

The number of seeds $S_{s,i,t}$ (14) produced by the trees of species s in height class i at time t is defined as the product of the number of trees $N_{s,i,t}$, by the maximum fecundity $S_{max,s}$ per tree and year, a height dependence function $sp_{s,i} \in [0,1]$ (13), and a sine function for mast seeding with period p_s .

$$S_{s,i,t+1} = N_{s,i,t} S_{max,s} sp_{s,i} 0.5 \left(1 + \sin \left(\frac{2\pi t}{p_s} \right) \right) \quad (14)$$

All seeds produced per species and cell are summed up. The seeds are then dispersed to the same or other cells (15) and thus close the feedback loop between the generations.

1.2.4.2.2 Seed dispersal

Interact

Each species is characterized by a specific circular seed dispersal kernel, which consists of a weighted mean of two negative exponential functions for short-distance and long-distance transport. The steepness of these functions is described by a parameter for the mean distance. The kernel is normalized to 1 and cut at predefined small value.

The seeds produced in each source cell with >0 seeds per species are distributed to all sink cells according to the dispersal kernel. The model allows deterministic and stochastic seed dispersal by a binomial distribution.

Optionally, in each year a small number of seeds of all species enters the cell additionally to the standard dispersal.

The seed inflow $I_{s,x,y,t}$ into a cell (x,y) is defined as the seeds produced in all cells and heights $S_{s,i,\check{x},\check{y},t}$ (14), multiplied by the dispersal kernel $k_s(z)$, which is a distance dependent probability density function.

$$I_{s,x,y,t} = \sum_{\check{x},\check{y},i} S_{s,i,\check{x},\check{y},t} k_s(z), \quad z = \sqrt{(\check{y} - y)^2 + (\check{x} - x)^2} \quad (15)$$

$$k_s(z) = (1 - \kappa_s) \cdot \frac{1}{\alpha_{s,1}^2} e^{-\frac{z}{\alpha_{s,1}}} + \kappa_s \cdot \frac{1}{\alpha_{s,2}^2} e^{-\frac{z}{\alpha_{s,2}}}, \quad \kappa_s \in [0,1] \quad (16)$$

$k_s(z)$ is a circular continuous function of distance z between the parent tree and the site where a seed finally reaches the seed bank. It is normalized so that its sum over all sink cells is one. The asymptotic behaviour of the dispersal function at large distances, i.e. the shape of its tail, is crucial for the spread (Clark 1998). If the function decreases faster than an exponential (“the tail is too thin”), the long distance transport is underestimated compared to empirical seed distributions. If the function is flatter than an exponential (“the tail is too fat”), the spread of the simulated populations accelerates continuously (Clark et al. 2001). Various formulations of dispersal kernels have been tested against empirical data (unfortunately rarely of European tree species) and different functions were shown to yield the best fit: the negative exponential (Willson 1993), the lognormal distribution (Greene et al. 2004), the general 2DT function (Clark et al. 1999), or a combination of a negative exponential and an inverse power function (Bullock and Clarke 2000, Greene et al. 2004). We defined the dispersal kernel as a linear combination of two negative exponentials for short- and long-distance transport. The value κ_s of the kernel defines the relative proportion of long-distance transport. The values $\alpha_{s,1}$ and $\alpha_{s,2}$ define how fast the short- and long-distance terms decline. $k_s(z)$ is set to zero at a predefined value, e.g. 10^{-4} . Seeds are assumed to be transported from each point of the source cell to each point of the sink cell. This is approximated by calculating the kernel values between the centres of 50m x 50m sub-cells, then adding them up for each cell. The number of seeds from one source cell arriving in a sink cell can be simulated deterministically by interpreting the corresponding kernel value as a proportion or stochastically by sampling from a binomial distribution. The parameters $\alpha_{s,1}$ and $\alpha_{s,2}$ refer to distances in metres. The kernel is therefore independent of the cell size. Cell size, however, introduces a discretization effect during the simulation, because the distribution of the forests within a cell is not known, and thus has to be assumed to be uniform.

Seed dispersal is a convolution between the produced seeds per grid cell and the seed dispersal kernel. This convolution can be evaluated directly, by applying the kernel to each grid cell. This can be very computing intense, depending on the number of grid cells in the area and covered by the kernel.

1.2.4.2.2.1 Seed dispersal by FFT

In certain conditions (many grid cells in the simulation area and covered by the kernel) the convolution by Fast Fourier Transform (FFT) can strongly speed up the simulation. The main approach here is to transform both the seed production and the dispersal kernel (per species) which are in the spatial domain by 2D FFT to the complex frequency domain, then to multiply the two transform and to backtransform the product to the spatial domain. This is simple in principle but tricky in the details. We use the GFT code in Fortran95 of Jalel Chergui [`;/Users/lischke/Documents/TM/FFTWsources/gft-1.0.1.tar/gft-1.0.1/GFT-1.0.1`]. There are several requirements to be fulfilled: 1) the seed production area and the kernel need to be extended to even grid cell number dimensions 2) the kernel that is first centered needs to be mirrored at the center of its area, i.e. the value in the center will then be in the four corners and the lowest values will be in the center. 3) the extended area and the mirrored kernel need to be zero-padded, i.e. they are stored at the 0,0 corner of a larger area full of zeros, with dimensions of the next power of 2 as compared to the original dimensions. 4) the result then has to be shifted back to the original coordinates. For an overview of the different steps and the subroutines involved see Figure 3 and **Error! Reference source not found.**, respectively.

The dimensions of the small extended and large extended areas are set in `SetDimsForFFT`, where the small extended area has dimensions of the next power of 2, and the large one of the overnext power of 2.

`CalculateKernelTransformation` calculates the transformed kernel by first shifting it to the next even dimensions, then reordering, i.e. mirroring it, putting it to the large extended area and then fast fourier transforming it. This FFT is only performed once per simulation and species, the transformed kernel is stored in the `spc-object`.

The convolution of the kernel with the seed production is done in each time step in `GFTConvolution2D`. Here first the seed production area is buffered at the top and right by stripes of the kernel-radius and extended to dimensions of the next power of two (intermediate area), so that the original simulation area is in the 0,0, corner. Then this intermediate area is put to the corner of the large extended area that has dimensions double to those of the intermediate area. This large area is then FF transformed, however indicating the dimensions of the intermediate area. The resulting FF transformed seed production area is multiplied with the FF transformed kernel and then the product is back-transformed. Very low values are interpreted as noise and are set to zero. Finally, the original area is cut out of the result that is on the size of the intermediate area.

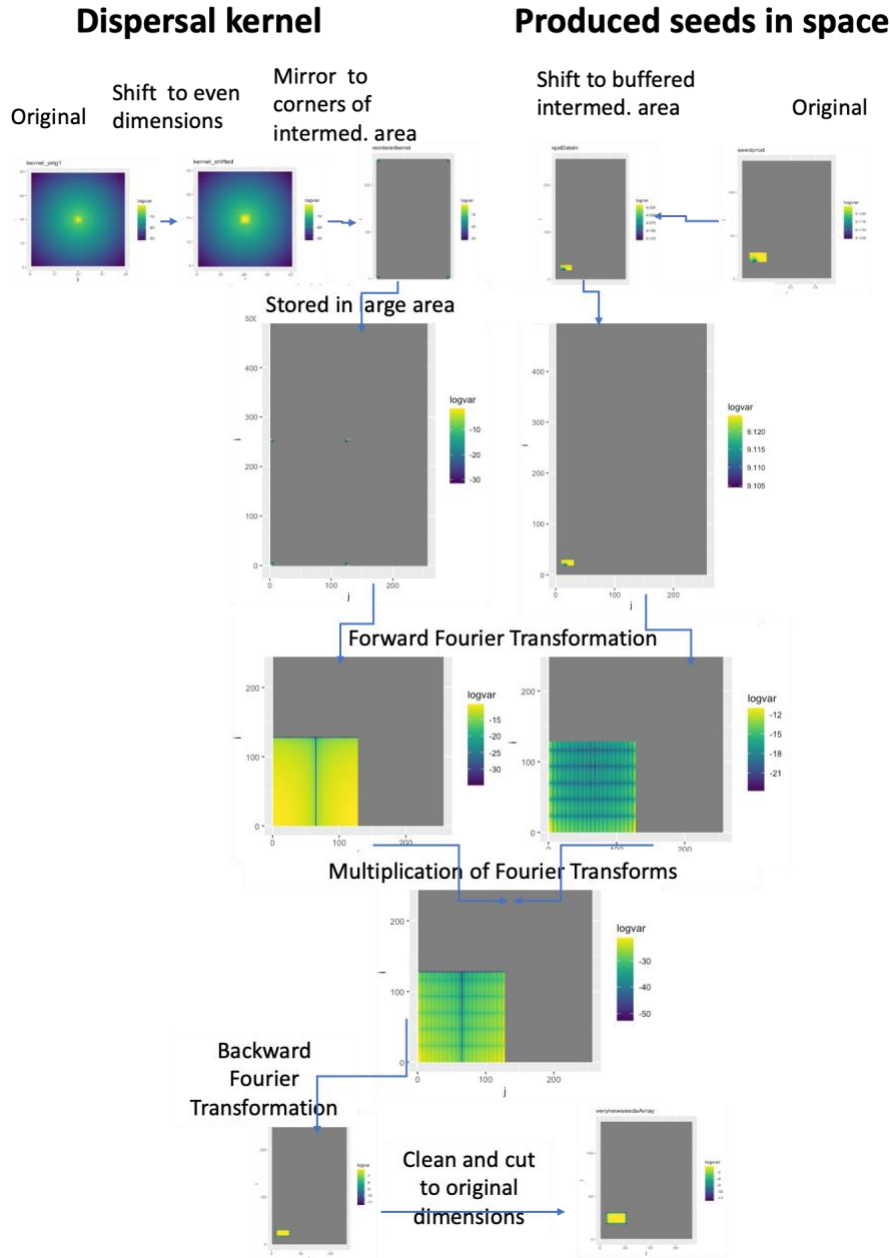


Figure 3: Example of seed dispersal by FFT convolution.

1.2.4.2.3 Seed bank dynamics

The seeds enter the seed bank by dispersal, a certain fraction (set to 0.1333 for all species) dies, and another fraction germinates. In each year, optionally a small amount of seeds of all species enters some predefined cells (immigration), or to all cells, additionally to the local dispersal.

The seed bank $Sb_{s,t+1}$, i.e. all seeds which are available for germination, is increased by seed inflow $I_{s,t+1}$ (15, contained in $Sb_{s,t+1}$), and reduced by four processes: intra-specific density regulation germination $\bar{\beta}_{s,t+1}$, loss of germinability ϕ_s and loss of seeds ($\mu_{s,S}$).

$$Sb_{s,t+1} = \bar{S}b_{s,t+1}(1 - \bar{\beta}_{s,t+1})(1 - \phi_s)(1 - \mu_{s,S}) \quad \text{Regen} \quad (17)$$

1.2.4.2.4 Loss of germinable seeds

Seeds can germinate only for a limited time, $T_{germ,s}$. The yearly rate of loss of germinability ϕ_s , was derived by assuming that after $T_{germ,s}$ years only 5% of the seeds can still germinate, i.e.

$$\phi_s = 1 - 0.05^{\frac{1}{T_{germ,s}}} \quad (18)$$

Furthermore, a high proportion ($\mu_{s,s}$) of the seeds is lost, e.g. through grazing by non-specific predators.

1.2.4.2.5 Self-Regulation:

Self-Regulation

Intra-specific density regulation can be simulated in two different ways.

One type of intra-specific density regulation is modelled with generic antagonists (e.g. insects or pathogens) that regulate the seed densities available in each cell (21). These antagonists are assumed to be species-specific and have their own population dynamics. They are thus not formulated as constant proportions.

$$Sb_{s,t+1} = Sb_{s,t} + I_{s,t+1} - graz \quad (19)$$

$$A_{s,t+1} = A_{s,t} + \nu graz - \mu_A A_{s,t} \quad (20)$$

$$graz = (Sb_{s,t} + I_{s,t+1}) A_{s,t} \Psi(A_{s,t}) \quad (21)$$

$$\Psi(A_{s,t}) = \frac{1}{A_{s,t} + \frac{1}{g}} \quad (22)$$

Their dynamics follows the Lotka-Volterra predator prey model, where $A_{s,t}$ are the species-specific antagonists of species s , e.g. a seed pathogen or seed predator. The antagonists consume seeds through the grazing function $graz$.

The share Ψ , that each antagonist obtains, decreases from the maximal grazing rate g to nearly 0 with increasing density of antagonists. The efficiency ν describes the conversion, i.e. the number of new antagonists produced per seed eaten. The mortality of seed antagonists is given by μ_A .

An alternative type of regulation is a simplified formulation of the species-specific antagonist dynamics, ignoring fluctuations. It is a function for surviving new seeds derived from a logistic model for seed dynamics (23) with a carrying capacity K .

$$\frac{dSb_c(\tau)}{d\tau} = I(\tau) \left(1 - \frac{Sb_c(\tau)}{K}\right) \quad (23)$$

$$\text{with } I(\tau) = const = I_{s,t}, \quad t \leq \tau < t+1, \quad Sb_c(\tau = t) = Sb_{s,t} \quad (24)$$

$$\Rightarrow Sb_c(\tau) = K - (K - Sb_{s,t}) \exp\left(-\frac{I_{s,t}(\tau - t)}{K}\right)$$

$$\text{With } \bar{Sb}_{s,t+1} = Sb_c(\tau = t+1) \quad (25)$$

$$\Rightarrow \bar{Sb}_{s,t+1} = K - (K - Sb_{s,t}) \exp\left(-\frac{I_{s,t}(t+1-t)}{K}\right)$$

$$= K - (K - Sb_{s,t}) \exp\left(-\frac{I_{s,t}}{K}\right)$$

The logistic model (23) was formulated assuming a continuous, constant input by dispersal during the year and a seed bank dynamics $Sb_c(\tau)$. The solution of this logistic model gives the seed bank value $\bar{Sb}_{s,t+1}$ at the beginning of the next year. Because $Sb_{s,t}$ always remains below K , if its initial value is below K , increased seed input results in a higher $\bar{Sb}_{s,t+1}$.

Both biotic interactions, the antagonists and the density regulation, impose an upper limit of seeds per cell on each species. Therefore, both define a species-specific carrying capacity for seeds in a forest. As a default, the density regulation should be used in the code.

1.2.4.2.6 Establishment:

Regen

A certain fraction of seeds in the seedbank germinate and subsequently survive the seedling stage each year, depending on light at the forest floor, minimum winter temperature and degree-day sum. The seedlings of all species are limited to a predefined number, i.e. the newly germinated seedling numbers are restricted according to their numbers.

$$G_{s,t+1} = \overline{Sb}_{s,t+1} \overline{\beta}_{s,t+1} \quad (26)$$

$$B_{tot} = \frac{G_{tot} G_{crit}}{G_{tot} + G_{crit}}, G_{tot} = \sum_{\sigma} G_{\sigma,t+1} \quad (27)$$

$$B_{s,t+1} = \frac{G_{s,t+1}}{G_{tot}} B_{tot} \quad (28)$$

$$N_{s,0,t+1} = N_{s,0,t+1}$$

The number of germinating seedlings $G_{s,t+1}$ depends on the density-regulated seed bank $\overline{Sb}_{s,t+1}$ (25) and the establishment rate $\overline{\beta}_{s,t+1}$, which is influenced by browsing, winter temperature, degree-day sum, and light, and averaged over all light conditions in the stand. Additionally, we introduced an optional formulation for the competition for space between the new seedlings (27). This function limits asymptotically the total number G_{tot} of new seedlings $G_{\sigma,t+1}$ of all species σ by the maximum number of seedlings G_{crit} that is determined by dividing the available space, i.e. the patch size, through a fixed average seedling crown area. The number $B_{s,t+1}$ of surviving seedlings of species s is then the proportion of B_{tot} corresponding to the proportion of the species' germinated seedlings to all germinated seedlings (28). Together with the environmental constraints this general density regulation limits the number of surviving seedlings $B_{s,t+1}$, which enter the 0th height class (1).

1.2.4.2.7 Environmental dependence of establishment

Regen

Establishment, here defined as germination and survival of first year, depends on a maximum germination rate $germ$, light l , minimum winter temperature WiT , degree days (above 5.5°C) DD , germination drought stress, and on browsing pressure with the species specific functions $f_{L,germ,s}$, $f_{WiT,s}$, $f_{DD,s}$, and $f_{GermDr,s}$, $f_{Brows,s}$, respectively.

$$\beta_s = germ_s f_{L,germ,s}(l) f_{WiT,s}(WiT) f_{DD,s}(DD) f_{GermDr,s}(germDrStr) f_{Brows,s}(BrPr) \quad (29)$$

$$l_{thresh_{sap,s}} = \begin{cases} 0.1 shadesens_{sap,s} - 0.4 & shadesens_{sap,s} \geq 5 \\ \max(0, 0.025 (shadesens_{sap,s} - 1)) & shadesens_{sap,s} < 5 \end{cases} \quad \text{GetSpc}$$

$$gl1 = 1 - e^{-4.64(l-0.05)}$$

$$gl9 = 2.24(1 - e^{-1.136(l-0.08)})$$

$$f_{L,germ,s}(l) = gl1 + \frac{l_{thresh_{sap,s}}^{-1}}{8} (gl9 - gl1) \quad \text{CalcContLightDep} \quad (30)$$

$$f_{WiT,s}(WiT) = \begin{cases} 1 & WiT \geq WiT_{crit,s} \\ 0 & \text{else} \end{cases} \quad \text{CalcCurrentDepFuncsInCell} \quad (31)$$

$$f_{DD,s}(GDD) = \begin{cases} 1 & WiT \geq DD_{min,s} \\ 0 & \text{else} \end{cases} \quad \text{CalcCurrentDepFuncsInCell} \quad (32)$$

$$f_{GermDr,s}(germDrStr) = \sqrt{\max\left(1 - \frac{germDrStr}{germDrTol_s}, 0\right)} \quad (33)$$

CalcCurrentDepFuncsInCell

$$f_{Brows,s}(BrPr) = 1 - \frac{BrPr}{30}(brsens_s - 1) \quad \text{CalcCurrentDepFuncsInCell} \quad (34)$$

1.2.4.3 Sapling development

Growth, Mort

$$N_{s,0,t+1} = N_{s,0,t} \left(1 - \bar{\mu}_{tot,s,0,t} - \frac{\bar{\gamma}_{s,0,t}}{h_1}\right) + Seedl_{s,t+1} \quad (35)$$

The germinated seedlings (28) add to the saplings $N_{s,0,t+1}$, which grow and die similarly to the adult trees (35). The only difference lies in the parameter of the light dependence function, for which the threshold value of light dependence for establishment is used.

The saplings growing out of this 0th height class enter the first height class in the adult model.

1.2.4.4 Adult dynamics

LocalForestDynamics

$$N_{s,i,t+1}(l_\xi) = N_{s,i,t}(l_\xi) \left(1 - \mu_{tot,s,i,t}(l_\xi) - \frac{\gamma_{s,i,t}(l_\xi)}{h_{i+1} - h_i}\right) + N_{s,i-1,t} \frac{\gamma_{s,i-1,t}(l_\xi)}{h_i - h_{i-1}}, \quad (36)$$

$i = 1, \dots, 15; \xi = 0 \dots 9$

In each time step the dynamics of the tree numbers per height class i and light class ξ with light intensity l_ξ are calculated.

The growth rate $\gamma_{s,i,t}$ (49) and the mortality $\mu_{tot,s,i,t}$ (37) are environment, particularly light, dependent.

1.2.4.5 Mortality

Mort

Annual mortality probability is estimated separately for each height and light class based on a) a species-specific intrinsic background mortality rate $\mu_{c,s}$, b) a growth- and stress-dependent mortality rate $\mu_{s,i,t}(l)$, and c) a generic disturbance-induced mortality $\mu_{dist,t}$

$$\mu_{tot,s,i,t}(l) = \mu_{c,s} + \mu_{s,i,t}(l) + \mu_{dist,t} \quad (37)$$

The background mortality rate ($\mu_{c,s}$), which is constant over the entire lifespan of a tree, is estimated based on the species-specific maximum age under the assumption that 1% of the individuals would reach the maximum age A_{max} when applying this mortality rate.

$$e^{-\mu_{c,s}A_{max}} = \frac{1}{100} \Rightarrow \mu_{c,s} = \frac{\ln(100)}{A_{max}} \quad (38)$$

The stress-dependent mortality rate assumes an increased mortality due to environmental stress by drought, low degree-day sums, and insufficient light (l), and acts if vitality (42) is reduced below 10% by these factors.

The growth dependent mortality considers if growth is below another threshold. The more severe of both is chosen.

The position of a species specific light threshold $l_{thresh,s}$ (which is calculated from the shade sensitivity $shadesens_s$ (klighs_s)) with respect to the light values at the upper and lower bounds of the current light class, l_{low} and l_{up} , is used to determine the mortality:

$$\tilde{\mu}_{s,i,t}(l) = \begin{cases} 0 & \text{if } l_{low} > l_{thresh,s} \\ 1 & \text{if } l_{up} < l_{thresh,s} \\ \frac{l_{thresh} - l_{low}}{l_{up} - l_{low}} & \text{if } l_{low} < l_{thresh,s} \leq l_{up} \end{cases} \quad (39)$$

$\tilde{\mu}_{s,i,t}(l)$ is then multiplied with 0.184 which is half of the mortality used in the predecessor patch model ForClim (Shugart 1984, Kienast 1987, Bugmann 1994), because in ForClim, the trees died only if the environmental conditions are unsuitable for two consecutive years, whereas in TreeMig, they die in each year if the conditions are bad.

$$\mu_{s,i,t}(l) = 0.184 \tilde{\mu}_{s,i,t}(l) \quad (40)$$

The disturbance-induced mortality $\mu_{dist,t}$ is the sum of a small scale disturbance $\mu_{dist,t,small}$ that is calculated stochastically and an optionally provided deterministic large scale disturbance $\mu_{dist,t,large}$. The disturbance frequency ($freq_{dist}$) defines the probability of the small scale disturbance in each time step and cell. If a small scale disturbance occurs, a random number between 0 and the disturbance intensity $int_{dist} \in [0,1]$ yields the additional mortality $\mu_{dist,t,small}$. The disturbance-related mortality is

$$\mu_{dist,t,small} = \begin{cases} r_2 \cdot int_{dist} & \text{if } r_1 < freq_{dist} \\ 0 & \text{else} \end{cases}$$

$$\mu_{dist,t} = \max(1, \mu_{dist,t,small} + \mu_{dist,t,large}) \quad \text{LocalForestDynamics} \quad (41)$$

where r_1 , r_2 are random numbers, uniformly distributed in $[0,1]$, and int_{dist} and $freq_{dist}$ are the intensity (proportion of trees dying) and frequency of the small scale disturbances. The latter occur in single cells independently from other cells.

All mortalities are summed up and limited to 1. Then, mortality is applied deterministically, i.e. the tree numbers in this height and light class are reduced by the mortality fraction.

Trees have a small chance to get older than their defined maximum age, i.e. they are not killed when they reach this threshold. Mortality is applied according to the growth and environmental conditions of each single year. No carry-over effects from one year to the next are taken into account.

1.2.4.5.1 Environmental dependence of mortality

The vitality function $f_s(E)$ (also used for the growth) depends on the light conditions, the average annual drought index (DrStr), the annual sums of growing degree-days (DD), and the available nutrients (avNit). This means, for each of these environmental conditions the relative reduction factor is calculated (which also depends on species-specific parameters such as the drought or shade tolerance), and the realized vitality is calculated by considering the geometric mean of the latter three reduction factors. Photosynthesis respiration, CO₂ fertilization, and competition for space are not explicitly included in the model. Nutrients enter via a general nutrient availability (avNit).

$$f_s(E) = f_{L,s}(l) \sqrt[3]{f_{DD,s}(DD) f_{Dr,s}(DrStr) f_{N,s}(avNit)} \quad (42)$$

CalcCurrentDepFuncsInCell

$$f_{L,s}(l) = gl1 + \frac{shadesens_s - 1}{8} (gl9 - gl1) \quad \text{GetSpC, CalcContLightDep} \quad (43)$$

$$gl1 = 1 - e^{-4.64(l-0.05)}$$

$$gl9 = 2.24(1 - e^{-1.136(l-0.08)})$$

with the species parameter $shadesens_s = klighs_s$ and $shadesens_s = kligha_s$ for saplings (height class 0) and taller trees (height class ≥ 1), respectively.

$$f_{Dr,s}(DrStr) = \sqrt{\max\left(1 - \frac{DrStr}{kDrTol_s}, 0\right)} \quad \text{CalcCurrentDepFuncsInCell} \quad (44)$$

$kDrTol_s$ is the drought tolerance $kDrt$ species parameter.

$$f_{N,s}(avNit) = \max\left(0, 1 - e^{kN1_s(avNit - kN2_s)}\right) \quad \text{CalcCurrentDepFuncsInCell} \quad (45)$$

$kN1_s$ and $kN2_s$ are determined from lookup tables (set in **GetSpC**), via the species parameter $kNtol_s$

1.2.4.6 Growth

Growth

Annual growth (γ) of each tree height and light class is simulated using an empirical growth model based on the species-specific maximum growth rate and limited by the maximum diameter and height. It is further reduced by non-optimal environmental conditions, including light (l), i.e. by the vitality function $f_s(E)$ (42).

The growth rate $\gamma_{s,i,t}(l)$ has been derived from the growth function for individual tree diameter at breast height (d) (Moore 1989)

$$\frac{\delta}{\delta t} d = f_s(E) \gamma_{max} \frac{d \left(1 - \frac{h}{h_{max}}\right)}{2h_{min} + (h_{max} - h_{min}) \left(\frac{6d}{d_{max}} - \frac{4d^2}{d_{max}^2}\right)} \quad (46)$$

Using the allometric relationship between height (h) and dbh (d) by (Ker and Smith 1955) and deriving it with respect to d

$$h = h_{min} + (h_{max} - h_{min}) \left(\frac{2d}{d_{max}} - \frac{d^2}{d_{max}^2}\right) \quad (47)$$

$$\Rightarrow \frac{\delta h}{\delta d} = (h_{max} - h_{min}) \left(\frac{2d}{d_{max}} - \frac{d^2}{d_{max}^2}\right)$$

results, after some calculation, in the continuous height growth

$$\frac{\delta h}{\delta t} = \frac{\delta d}{\delta t} \frac{\delta h}{\delta d} = f_s(E) \gamma_{max} \frac{d \left(1 - \frac{h}{h_{max}}\right) \left(1 - \frac{d}{d_{max}}\right)}{\frac{h_{min} d_{max}}{(h_{max} - h_{min})} + d \left(3 - 2 \frac{d}{d_{max}}\right)} \quad (48)$$

h_{min} , h_{max} and d_{max} are maximum and minimum values of height and diameter, γ_{max} is the maximum growth rate. $f_s(E)$ is the vitality function, a modifier which depends on light intensity l , degree-day sum, drought stress, and nutrient availability (42). All these parameters and functions are species-specific. The growth rate $\gamma_{s,i,x,y,t}$ of species S in height class i at time t is then defined as

$$\gamma_{s,i,t}(l) = \frac{\delta h_{i,s,t}}{\delta t} = f_s(E) \gamma_{s,i,max} \quad (49)$$

$$= \gamma_{s,i,max} f_{L,s}(l) \sqrt[3]{f_{DD,s}(DD) f_{Dr,s}(DrStr) f_{N,s}(avNit)}$$

$$\gamma_{s,i,max} = \gamma_{max} \frac{d \left(1 - \frac{h_{i,s}}{h_{max,s}}\right) \left(1 - \frac{d_{i,s}}{d_{max,s}}\right)}{\frac{h_{min,s} d_{max,s}}{(h_{max,s} - h_{min,s})} + d_{i,s} \left(3 - 2 \frac{d_{i,s}}{d_{max,s}}\right)} \quad (50)$$

$$\bar{\gamma}_{s,i,t} = \sum_{\xi=0}^9 \gamma_{s,i,t}(l_{\xi}) \left(F_{L,i}(l_{\xi+1}) - F_{L,i}(l_{\xi})\right) \quad (51)$$

Adding $\gamma_{s,i,t}(l)$ to the current lower and upper boundaries of height class i determines the new upper and lower boundaries of the new height interval for trees currently in height class i and light class l_{ξ} . The trees are then shifted to the new height classes, proportionally to the fraction of the calculated height interval which falls into each of the new classes. This shift is based on the assumption that all trees within a height class are uniformly distributed. It has to be noted that with small to medium growth rates, only a fraction of the population in the current height class grows into the next one, while the rest remains in the same class. The mean growth rate is $\bar{\gamma}_{s,i,t}$ (50), according to (8).

1.2.4.6.1 Environmental dependence of growth:

Growth is reduced under non-optimal environmental conditions by the vitality function $f_s(E)$ (42, also used for the stress dependent mortality) of the light conditions, the average annual drought index (DrStr), the annual sums of growing degree-days (DD), and the available nutrients (avNit).

1.3 Species parameters

For the parameter values, see the TreePars files in the P folder of the TreeMig framework.

Table 1. Species parameters in TreeMig.

Short Par. name	Parameter	Unit	Explanation
Name	Species name	-	-
Abbrv	Abbreviation of species name		
kAMax	Maximum age	Year	-
minmat	Height at maturity	Year	-
klighs	Shade tolerance young	-	Class [1,9], for establishment
kligha	Shade tolerance adults	-	Class [1,9], for growth and survival
alfa1	Mean dispersal distance short range d.	m	Short distance dispersal
alfa2	Mean dispersal distance long range d.	m	Long distance dispersal
dispFac	Fraction of long-distance dispersal	-	Either 0 or 0.001
repFac	Relative pollen productivity per seed	-	0-4, only for output if wished (rel. to <i>Picea abies</i>)
kG	Gmax	kg/year	Maximum growth rate
kDMax	Max DBH	cm	Maximum tree diameter
kHMax	Max height	m	Maximum tree height
sType/B	Leaf habit	-	Evergreen or deciduous; influences allometries
sType/N	Foliage type	-	Class [1,5]; affecting LAI calculations and other allometries
kDDMin	Min degree-days	°C	Minimum growing degree-days required for establishment, growth and survival
Delta75	Delta 75% degree-days	°C	How many ddegs are needed to reach 0.75 of maximum DD sum
kWiT	Min temperature	°C	Minimum temperature required for establishment
kDrT	Drought tolerance	-	Relative tolerance [0,1], for growth, survival and establishment
kbrow	Browsing tolerance	-	Class [1,3]; does usually not apply, no browsing assumed
kNTol	Nutrient requirements		Usually Not simulated, assumed optimal [0-3]
seedLoss	Seed mortality. E.g. by predators	1/year	For seed bank dynamics
seedMaxAge	Max age of seeds in seed bank	year	For seed bank dynamics
seedGerm	Germination rate	1/year	For seed bank dynamics and regeneration
period	Period of seed masting	year	For seed production
maxseed	Max seed number per tree	-	For seed production

1.4 (Additional) Topics following ODD protocol

The above documentation covers in part the ODD (Overview, Design concepts, and Details) protocol of (Grimm et al. 2020). Here, missing topics for this protocol are listed.

1.4.1 Model Purpose

TreeMig is designed to simulate forest dynamics and tree species migration at the landscape to continental scale over decades to millennia. It has originally been developed for Central Europe, but parameterizations are also available for some North American and Chinese species.

1.4.2 Model entities and state variables

A complete list of all attributes characterizing the model entities is provided in Table 2.

Table 2. Fixed property (FP), state variables (sensu systems dynamics; SV), derived variables (DV), parameters (P), constant drivers (CD), and variable driver (VD) in TreeMig.

Attribute	Type	Entity	Temporally variable	Unit	Explanation
Species identity	FP	Tree number	No	-	Linked with species parameters (Table 1)
Height class	FP	Tree number	No	Decade	-
Cell	FP	Tree number	No		
Number in height class	SV	Tree number	Yes	-	Number of trees in height class
Number of seeds in seed bank	SV	Seed number	Yes		
Diameter at breast height	Derived variable	Height class	Yes	cm	Derived from height
LAI	Derived variable	Height class	Yes	-	Derived from height
Biomass	Derived variable	Height class	Yes	kg	Derived from height
Seed production	Derived variable	Height class	Yes	-	Derived from height
Distribution of Light conditions	Derived variable	Height class	Yes	-	Relative light intensity based on LAI of larger trees
Location	FP	Grid cell	No	x, y position	-
Slope	CD	Grid cell	No	°	-
Stockability	CD	Grid cell	Yes	-	For different land uses; here mostly constant
Aspect	CD	Grid cell	No	°	-
Monthly mean temperature	VD	Grid cell	Yes	°C	Provided as input data
Monthly precipitation sums	VD	Grid cell	Yes	mm	Provided as input data
Maximum soil water holding capacity	CD	Grid cell	No	cm	Height of water column
Browsing intensity	VD	Grid cell	No	-	Relative intensity [0,1] (here used as constant)
Annual growing degree-days	Derived variable	Grid cell	Yes	-	based on monthly temperatures
Minimum winter temperature	Derived variable	Grid cell	Yes		
Annual drought index	Derived variable	Grid cell	Yes	-	Relative index [0,1]

The state variables are the numbers of trees (per 833 m², which corresponds to the size of a patch in a traditional gap model). They are the basic entities simulated. These tree numbers are always associated with species s , height classes i (about 4m wide) and grid cells x, y (spatial units with a specific location) which contain the biophysical conditions driving the demographic processes of the cohorts.

1.4.3 Scales

- Spatial scales
 - Spatial extent of simulated landscape: stand to continent, depending on simulation time, resolution, and available computing resources.
 - Resolution, size of single grid cell: from 25m x 25m to 10km x 10km. Default: 1 km x 1km.
 - Forcing factors (climate, topology) are transformed to the same resolution
 - Trees do not have an explicit spatial location within a grid cell, but it is implicitly assumed that they are randomly distributed in the grid cell.
- Temporal scales
 - The model proceeds in **annual time steps**
 - Climate factors are considered in **monthly time steps** and aggregated to annual bioclimatic indicators

1.4.4 Basic principles

The model is mainly based on the succession theory and on the niche concept. Each species is characterized by a set of parameters defining its potential niche. The interactions between the environment and the trees, as well as interactions among the trees, determine the main demographic processes germination, survival, and growth, resulting in the local forest succession.

1.4.5 Structure

Each grid cell consists of one stand, influenced by the environmental drivers in the grid cell. The structure of the stand is taken into account by vertical layers and by assuming a random spatial distribution of the trees within each layer, which results in a theoretical frequency distribution of the light conditions. The stand is assumed to be spread over the entire grid cell.

1.4.6 Local interaction

Trees within stands interact indirectly by altering the light distribution in the height classes, which affects the demographic processes. Trees' demography is driven by the environmental conditions in the grid cells, but apart from their effect on the light conditions, the trees do not influence the environmental conditions. It is possible to include a feedback effect of trees on the soil water content, but in the used model version, such an effect was not considered. The available space is distributed to seedlings of the species according to their numbers. On top of this interspecific competition, also an intraspecific, logistic competition of the seeds in the seedbank with a generic carrying capacity is included.

1.4.7 Spatial interaction

is included by seed dispersal with a seed dispersal kernel.

1.4.8 Emergence

The forest dynamics at the landscape level, i.e. the spatio-temporal development of forest structure and composition, is the key result emerging from the lower level processes (i.e., dispersal, regeneration, mortality and growth of trees; influenced by external forcing factors and intra-specific competition for light, which in turn depends on growth).

1.4.9 Adaptation, Objectives, Learning, Prediction

Not included.

1.4.10 Stochasticity

Stochasticity is involved in disturbance mortality processes, optionally in seed dispersal, and in climate inputs, if not measured data are used.

1.4.11 Collectives

Not individual trees, but tree numbers of species in height classes are simulated.

1.4.12 Observation

Model states i.e. the numbers of the seeds in the seed bank and of the trees in all height classes and of all species and cells are saved in text state-files at the end of each year. Different output variables can be derived and output at selected time steps (biomass, LAI, numbers, light conditions).

1.5 References

- Bugmann, H. 1994. On the ecology of mountainous forests in a changing climate: A simulation study. Dissertation. Swiss Federal Institute of Technology, Zurich.
- Bullock, J. M., and R. T. Clarke. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* **124**:506-521.
- Clark, J. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* **152**:204-224.
- Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. *American Naturalist* **157**:537-554.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* **80**:1475-1494.
- Greene, D. F., C. D. Canham, K. D. Coates, and P. T. Lepage. 2004. An evaluation of alternative dispersal functions for trees. *Journal of Ecology* **92**:758-766.
- Grimm, V., S. F. Railsback, C. E. Vincenot, U. Berger, C. Gallagher, D. L. DeAngelis, B. Edmonds, J. Q. Ge, J. Giske, J. Groeneveld, A. S. A. Johnston, A. Milles, J. Nabe-Nielsen, J. G. Polhill, V. Radchuk, M. S. Rohwäder, R. A. Stillman, J. C. Thiele, and D. Ayllón. 2020. The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. *Jasss-the Journal of Artificial Societies and Social Simulation* **23**.
- Ker, J. W., and J. H. G. Smith. 1955. Advantages of the parabolic expression of height-diameter relationships. *For. Chron.* **31**:235-246.
- Kienast, F. 1987. FORECE - A forest succession model for southern Central Europe. ORNL-TM / 10575, Oakridge National Laboratories. Environmental Division, Oak Ridge, TN.
- Lischke, H. 2020. Simulation der Baumartenmigration im Klimawandel. *Schweiz. Z. Forstwes.* **171**:151-157.
- Lischke, H., and T. J. Löffler. 2006. Intra-specific density dependence is required to maintain diversity in spatio-temporal forest simulations with reproduction. *Ecological Modelling* **198**:341-361.
- Lischke, H., T. J. Löffler, and A. Fischlin. 1998a. Aggregation of individual trees and patches in forest succession models: Capturing variability with height structured, random, spatial distributions. *Theor Popul Biol* **54**:213-226.
- Lischke, H., T. J. Löffler, and A. Fischlin. 1998b. Aggregation of individual trees and patches in forest succession models - Capturing variability with height structured random dispersions. *Theor Popul Biol* **54**:213-226.
- Lischke, H., N. E. Zimmermann, J. Bolliger, S. Rickebusch, and T. J. Löffler. 2006. TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling* **199**:409-420.
- Löffler, T. J., and H. Lischke. 2001. Incorporation and influence of variability in an aggregated forest model. *Natural Resource Modeling* **14**:103-137.
- Moore, A. D. 1989. On the maximum growth equation used in forest gap simulation models. *Ecological Modelling* **45**:63-67.
- Moos, C., and H. Lischke. 2022. Modelling the effect of rockfall on forest development in a dynamic forest model. *Ecosphere* **13**:e3909.
- Petter, G., P. Mairota, A. Katharina, P. Bebi, J. Bruna, H. Bugmann, A. Haffenden, R. Scheller, D. R. Schmatz, R. Seidl, M. J. R. Speich, G. Vacchiano, and H. Lischke. 2020. How robust are future projections of forest landscape dynamics? Insights from a systematic

- comparison of four forest landscape models. *Environmental Modelling & Software* **134**.
- Shifley, S. R., H. S. He, H. Lischke, W. Wang, W. Jin, E. J. Gustafson, J. R. Thompson, F. R. Thompson III, W. D. Dijak, and J. Yang. 2017. The past and future of modeling forest dynamics: From growth and yield curves to forest landscape models. *Landscape Ecology* **32**:1307-1325.
- Shugart, H. H. 1984. *A theory of forest dynamics: The ecological implications of forest succession models*. Springer, New York a.o.
- Speich, M., M. Zappa, and H. Lischke. 2020. FORests and HYdrology under Climate Change in Switzerland v1.0: a spatially distributed model combining hydrology and forest dynamics. *Geoscientific Model Development* **13**:537-564.
- Willson, M. F. 1993. Dispersal mode, seed shadows and colonization patterns. *Vegetatio* **107/108**:261-280.
- Zurbriggen, N., J. E. M. S. Nabel, M. Teich, P. Bebi, and H. Lischke. 2014. Explicit avalanche-forest feedback simulations improve the performance of a coupled avalanche-forest model. *Ecological Complexity* **17**:56-66.