

Appendix A: Demographic processes modelled in Samsara2 and initialization

1. Generalities

The spatially explicit, individual based model Samsara2 is designed to simulate in detail the relations between stand structure and dynamics in uneven-aged forest stands and the impact of alternative management strategies. It provides the possibility to analyse the development of trees within a stand and the resulting collective dynamics and to vary the types of trees harvested (species, size, additional individual characteristics) and their spatial distribution.

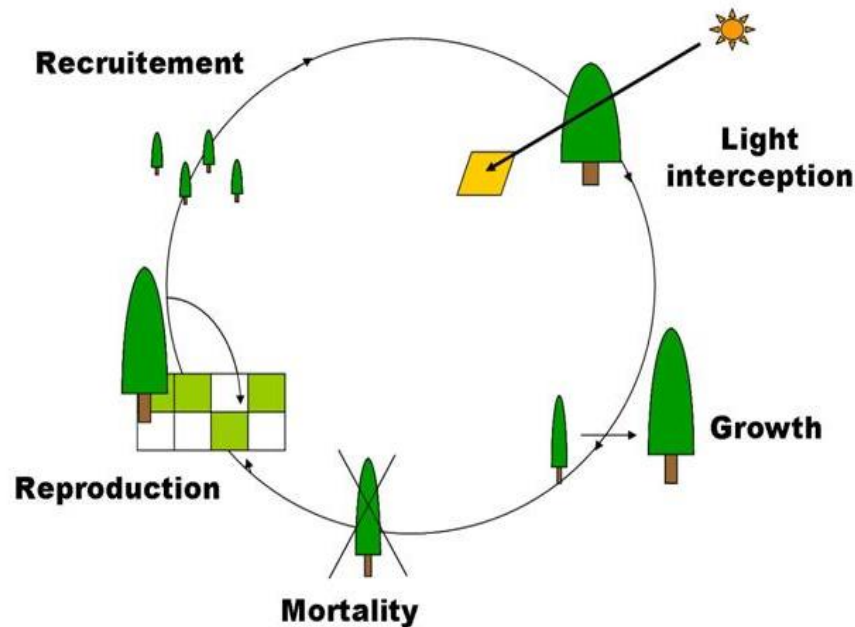


Figure A1: the succession of processes in the model Samsara2

A forest stand simulated in Samsara2 relies on a list of trees and saplings, which have explicit 3D coordinates on a plot. This plot is attributed a slope and an exposition, and is sub-divided in ground cells. Light conditions drive stand dynamics. Allometries are used to calculate tree crown dimensions (total height, radius and base height) based on diameter at breast height (dbh). Irradiance under canopy on each ground cell and the amount of radiation intercepted by each adult tree throughout a vegetation season are calculated together in an integrated approach based on light ray interception by crowns (Courbaud *et al.*, 2003). Individual tree annual increments are calculated based on the radiation they intercept. Tree mortality is the result of a Bernouilli test with a probability that depends on tree size and competition environment. Seeds are dispersed in the surrounding of adult trees. Seeds germinate and seedlings survive and grow depending on ground cell irradiance. When saplings overpass a critical height, they are recruited as adult trees.

Harvests can also be simulated using specific algorithms (Dufour-Kowalski *et al.*, 2012; Lafond *et al.*, 2012; Lafond *et al.*, 2013)

Typically, plot area is one hectare (100m x 100m) and ground cell area is 25m² (5m x 5m). As real stands generally have areas larger than one hectare, historical management data have to be scaled prior to their use with Samsara2.

Belowground competition is not represented in the model, limiting its application to locations where water is not an essential limiting factor. The fertility of the site is taken into account indirectly through the value of the different demographic parameters. The model should then be recalibrated for different site conditions.

2. Allometries

Allometries used in Samsara2 have been presented in (Vieilledent *et al.*, 2010).

They were calibrated on trees coming from 9 plots in the Alps of size ranging from 0.25 to 1ha. Six plots were located in the French Alps, two in the Italian Alps and one in the Swiss Alps. Stands were uneven-aged with *Abies alba* and *Picea abies* as dominant species.

Allometries were calibrated using a hierarchical Bayesian approach. Plot effects were used in the model. We report here parameter values for the plot Queige. This plot represents conditions of the montane level in the French Northern Alps.

2.1. Height-DBH allometry

H_{it} (height of tree i at time t in m), follows a Gompertz function of D_{it} (in cm) with a multiplicative residual $\exp(\varepsilon_{it})$. This model ensures that H_{it} is strictly positive.

$$H_{it} = k_i \exp\left[-\ln(k_i / 1.3) \exp(-r \cdot D_{it})\right] \cdot \exp(\varepsilon_{it})$$

Linearised as:

$$\ln(H_{it}) = \ln(k_i) - [\ln(k_i) - \ln(1.3)] \exp(-r \cdot D_{it}) + \varepsilon_{it}$$

$$\ln(k_i) \sim N(mk, sk^2)$$

$$\varepsilon_{it} \sim N(0, \sigma^2)$$

k_i is the maximum potential height of tree i . Individual effects are represented by drawing $\ln(k_i)$ in a Normal distribution when new trees are recruited.

Parameter	Definition	Fir		Spruce	
		Mean	SE	Mean	SE
mk	Mean of the logarithms of max individual heights	3.28E+00	3.59E-02	3.53E+00	2.84E-02
sk^2	Variance of the logarithms of max individual heights	3.12E-02	7.42E-03	1.08E-02	2.33E-03
r	Shape parameter	8.46E-02	1.55E-03	7.67E-02	1.45E-03
σ^2	Residual variance	2.94E-02	3.61E-03	4.03E-02	2.45E-03
Transformation	SD of the logarithms of max individual heights	1.77E-01	2.10E-02	1.04E-01	1.12E-02

2.2. Crown Base Height – Height allometry

Crown base height of tree i at time t CBH_{it} (in m), follows a linear function of height H_{it} (in m) with a multiplicative residual $\exp(\varepsilon_{it})$. This model ensures that CBH_{it} is strictly positive.

$$CBH_{it} = \left[\frac{1}{1+k_i} \right] H_{it} \cdot \exp(\varepsilon_{it})$$

Linearised as:

$$\ln(CBH_{it}) = -\ln(1+k_i) + \ln(H_{it}) + \varepsilon_{it}$$

$$\ln(k_i) \sim N(mk, sk^2)$$

$$\varepsilon_{it} \sim N(0, \sigma^2)$$

k_i is a slope parameter for tree i . Individual effects are represented by drawing $\ln(k_i)$ in a Normal distribution when new trees are recruited.

Parameter	def	Fir		Spruce	
		Mean	SE	Mean	SE
mk	mean of the logarithm of individual effect	7.14E-01	6.16E-02	4.88E-01	8.45E-02
sk^2	Variance of the logarithms of individual effects	2.13E-01	3.44E-02	3.80E-01	5.10E-02
σ^2	Variance of log-residuals	1.78E-02	5.36E-03	4.48E-02	1.16E-02
Transformation	SD of the logarithms of individual effects	4.62E-01	3.73E-02	6.16E-01	4.14E-02

2.3. Crown Radius – DBH allometry

Crown radius of tree i at time t R_{it} (in m), follows a power function of dbh D_{it} (in cm) with a multiplicative residual $\exp(\varepsilon_{it})$. This model ensures that R_{it} is strictly positive.

$$R_{it} = k_i (D_{it})^b \cdot \exp(\varepsilon_{it})$$

Linearised as:

$$\ln(R_{it}) = \ln(k_i) + b \cdot \ln(D_{it}) + \varepsilon_{it}$$

$$\ln(k_i) \sim N(mk, sk^2)$$

$$\varepsilon_{it} \sim N(0, \sigma^2)$$

k_i is a scale parameter for tree i . Individual effects are represented by drawing $\ln(k_i)$ in a Normal distribution when new trees are recruited.

Parameter	def	Fir		Spruce	
		Mean	SE	Mean	SE
mk	mean of the logarithm of individual effect	-3.54E-01	4.30E-02	-7.74E-01	4.48E-02
sk^2	Variance of the logarithms of individual effects	1.48E-02	2.78E-03	2.49E-02	4.23E-03
b	Shape parameter	4.54E-01	1.33E-02	5.25E-01	1.20E-02
σ^2	Variance of log-residuals	1.34E-02	2.70E-03	1.48E-02	3.35E-03
Transformation					
sk	SD of the logarithms of individual effects	1.22E-01	1.14E-02	1.58E-01	1.34E-02

3. Growth

The growth model and its calibration are presented in (Vieilledent, 2009).

The model was calibrated on of the observation plot of Queige, located in the French Northern Alps (45°41'57''N – 6°27'30''E) at 1358 m of elevation. The plot surface is 0.5ha, with a slope of 27° oriented to 23° (North).

The stand was constituted of 77 *Abies alba* and 85 *Picea abies* trees of dbh > 10 cm that were measured and mapped.

Increment cores were made to obtain 25 measures of radial increment from 1977 to 2001 for each tree.

The model Samsara2 was used to calculate the radiation intercepted by each tree during each growing season.

We use a Random Individual and Temporal Effects model (RITES) that relates individual basal area increment to individual light interception.

ΔG_{it} , the basal area increment of tree i at time t (in cm^2/year), follows a power function of the radiation intercepted by tree i during vegetation season t E_{it} (in GJ/year) with a multiplicative residual $\exp(\varepsilon_{it})$. This model ensures that ΔG_{it} is strictly positive.

$$\Delta G_{it} = a_{it} E_{it}^b \cdot \exp(\varepsilon_{it})$$

Linearised as:

$$\text{Ln}(\Delta G_{it}) = \text{Ln}(a_{it}) + b \cdot \text{Ln}(E_{it}) + \varepsilon_{it}$$

$$\text{Ln}(a_{it}) = \alpha + \beta_i + \lambda_t$$

$$\beta_i \sim N(0, sb^2)$$

$$\lambda_t \sim N(0, sl^2)$$

$$\varepsilon_{it} \sim N(0, \sigma^2)$$

ΔG_{it} : basal area increment of tree i during year t ($\text{cm}^2 / \text{year}$)

E_{it} : radiation intercepted by tree i during vegetation season t (GJ / year)

a_{it} : scale parameter, that depends on a constant α an individual effect β_i and a temporal effect λ_t

b : shape parameter of growth response to light interception

ε_{it} : residual

Individual effects are represented by drawing β_i in a Normal distribution when new trees are recruited, and temporal effects are represented by drawing λ_t in a Normal distribution each year.

Diameter at breast height annual increment ΔD is related to basal area increment ΔG by:

$$\Delta D = \frac{2 \cdot \Delta G}{\pi \cdot D}$$

Parameter	def	Fir		Spruce	
		Mean	SE	Mean	SE
α	growth potential	-2.02E+00	2.02E-01	-3.97E+00	4.25E-01
b	light effect	4.16E-01	1.90E-02	5.88E-01	3.80E-02
sb^2	Variance of individual effects	3.63E-01	6.50E-02	3.60E-01	5.90E-02
sl^2	Variance of temporal effects	3.40E-02	1.10E-02	1.10E-02	4.00E-03
σ^2	Variance of log-residuals	1.70E-01	6.00E-03	1.62E-01	5.00E-03
Transformation					
sb	SD of individual effects	6.02E-01	5.39E-02	6.00E-01	4.92E-02
sl	SD of temporal effects	1.84E-01	2.98E-02	1.05E-01	1.91E-02

4. Mortality

4.1 Basic Mortality

We model the probability of dying within a 5 year period with a logistic model using to covariables: DBH (in cm) and BAL (in cm²/ha), the basal area of all trees larger than the subject in the 15 m radius IFN plot. The past growth of dead trees is not available in the French IFN, making it impossible to use past increment as a covariable.

The sub-model can be written as:

$$y_i \sim \text{Bernouilli}(Pm_i)$$

$$Pm_i = \frac{1}{1 + e^{-z_i}}$$

$$z_i = p_1 + p_2 D_i + p_3 BAL_i$$

With

$y_i = 1$ if the tree is dead and 0 if the tree is alive

Pm_i : Probability for tree i to dye within a 5year period

D_i : Dbh of tree i

BAL_i : Basal area of trees larger than tree I on the 15m radius surrounding plot

Coefficient estimates

Species	Coefficient	Estimate	SE	Pvalue
Fir	p_1	-3.207913	2.54E-01	<2e-16
	p_2	-0.030081	7.76E-03	0.000106
	p_3	2.28E-02	5.36E-03	2.01E-05
Spruce	p_1	-3.597711	1.35E-01	<2e-16
	p_2	-1.25E-02	4.02E-03	0.00182
	p_3	2.20E-02	2.73E-03	7.39E-16

Variance-Covariance matrixes

Fir	beta_1	beta_2	beta_3	Spruce	beta_1	beta_2	beta_3
p_1	6.46E-02			p_1	1.82E-02		
p_2	-1.47E-03	6.02E-05		p_2	-4.17E-04	1.62E-05	
p_3	-1.15E-03	1.58E-05	2.87E-05	p_3	-2.93E-04	3.86E-06	7.46E-06

4.2. Mortality of very big trees

As nearly all French forests are managed, these trees are very rare in the data set. We then added an empirical probability of mortality law to force the death of trees when they approach the maximum size encountered in the literature.

The empirical rule is:

$$z_i' = p_4 + p_5 D_i^2$$

$$P'm_i = \frac{1}{1 + e^{-z_i'}}$$

Species	Nb ref	Dmax min	Dmax moy	Dmax max
Fir	7	150	183	250
Spruce	6	100	166	250

Parameters were chosen empirically that the probability of dying was close to 0.1 for Dmax_min, close to 0.6 for Dmax_moy and close to 1 for Dmax_max

Species	Coefficient	Value
Fir	p_4	-9
	p_5	0.0004
Spruce	p_4	-6
	p_5	0.0004

The two mortality processes are combined by using the highest of the two probabilities:

$$\max(Pm_i, P'm_i)$$

Converting 5 year mortality in annual mortality

The probability of surviving 5 years can be written as a function of the annual probability of mortality p or as a function of the probability of dying during a 5-year period P through:

$$1 - P = (1 - p)^5$$

$$p = 1 - (1 - P)^{1/5}$$

5. Regeneration

Natural regeneration is composed of several sub-processes described below: seed production, seedling installation and survival, sapling growth and tree recruitment (= end of sapling stage).

Our permanent plots in uneven-aged stands of the Alps were not diversified enough to provide good data for regeneration modelling because the number of plots was too low and the conditions of light and conspecific adult densities were not diversified enough. Correlation between conspecific density and total canopy tree density was high, and we could not separate correctly the process of seed production from the process of survival.

We used data from an experiment in Bavaria with very contrasting situations, from clear cuts to dense canopies (Burschel *et al.*, 1992) at the stand scale (0.5 ha). Seeds were trapped during 10 years and seedling survival was recorded during ten years after the exceptional masting years of 1977 and 1978.

These data are very interesting because

- They come from very contrasting competition situations
- They allow analyse separately seed production and survival

Unfortunately, the data available are aggregated at the stand scales for only 5 stands.

We estimated radiation under canopy in Bavarian stands (in % of above canopy light) using the relation:

$$L_j = 100e^{-0.028 * Cover_j}$$

In this part, index j refers to a stand in the Bavarian data and small ground patches in Samsara.

5.1. Seed production

We modelled the number of viable seeds N_j on a plot for an average year as a Quasi Poisson distribution, with mean parameter λ depending on conspecific basal area around the plot G_j (in m²/ha), and dispersion parameter ϕ allowing an overdispersion compared to a Poisson distribution.

$$N_j \sim QuasiPoisson(\lambda_j, \phi)$$

$$\lambda_j = \alpha_1 \cdot G_j$$

Species	Coefficient	Estimate	SE	Pvalue
Spruce	α_1	7726	2043	0.0324
	phi	26664.29	Not Available	
Fir	α_1	2548	1004	0.0848
	phi	53244	Not Available	

5.2. Seedling survival

The Bavarian data allow estimate a seedling survival during the 10 first years.
The sub-model can be written with a logistic model as:

$$N'_j \sim \text{Binomial}(N_j, p_j)$$

$$p_j = \frac{1}{1 + e^{-z_j}}$$

$$z_j = b_1 + b_2 L_j + b_3 L_j^2$$

With:

N'_j : Number of seedlings after 10 years on plot j

N_j : Number of seeds on plot j

p_j : Probability of seedling survival during the 10 first years

L_j : Irradiance under canopy on plot j (in % of above canopy light)

The coordinates of each sapling within the ground cell are drawn in uniform distributions.

Coefficient estimates

Species	Coefficient	Estimate	SE	Pvalue
Spruce	b_1	-9.276	3.15E-02	<2e-16
	b_2	0.24	1.41E-03	<2e-16
	b_3	-1.89E-03	1.23E-05	<2e-16
Fir	b_1	-6.109	2.67E-02	<2e-16
	b_2	1.87E-01	1.26E-03	<2e-16
	b_3	-1.50E-03	1.15E-05	<2e-16

Variance-Covariance matrixes

Spruce	beta_1	beta_2	beta_3	Fir	beta_1	beta_2	beta_3
b_1	9.94E-04			b_1	7.10E-04		
b_2	-4.30E-05	1.98E-06		b_2	-3.22E-05	1.58E-06	
b_3	3.44E-07	-1.66E-08	1.52E-10	b_3	2.64E-07	1.37E-08	1.33E-10

5.3. Adaptation to the Alps

The model calibrated on the Bavarian data must be adapted to make predictions of recruits in the observation plot of the Alps for two reasons

- We need to predict the number of recruits reaching a DBH of 7.5 cm instead of 10 year-old seedlings
- The ecological context is different and both the number of seedlings and the relative fitness of the species may be different.

We calculated for 8 plots in the Alps with both species and no recent harvest the irradiance using the basal area- irradiance relation, the seed production using the linear model calibrated in Bavaria, the seedling survival using the survival model calibrated in Bavaria.

We then analysed the relation between observed recruits in the 8 plots and predicted seedlings. The linear regression coefficient is the coefficient factor to apply to predict recruits in the Alps.

$$N_j'' = \alpha_2 \cdot N_j' + \varepsilon_j$$

$$\varepsilon_j \sim N(0, \sigma^2)$$

Species	Coefficient	Estimate	SE	Pvalue	ResidualSE	AdjustedR2
Spruce	Alpha_2	0.009942	0.002073	0.00197	0.9671	0.7334
Fir	Alpha_2	0.0034971	0.0004536	0.000115	0.8946	0.8796

The three processes are combined as $\alpha = \alpha_1 \alpha_2$

$$N_j \sim \text{QuasiPoisson}(\alpha G_j p_j, \varphi)$$

5.4. Sapling growth

To estimate the time span between seed production and tree recruitment we need to model sapling growth. As growth data on Burschel plot are only for very small seedlings, we use another published data set obtained from (Stancioiu and O'Hara, 2006).

We model annual relative height growth $\frac{\Delta H_i}{H_i}$ using a model depending on L_j , the irradiance under canopy on plot j (in % above canopy light) with horizontal asymptote at 100.

$$\frac{\Delta H_i}{H_i} = 100 - \exp\left[p_1 + p_2 \text{Ln}(L_j)\right] \exp(\varepsilon_i)$$

This model can be linearised as

$$\text{Ln}\left(100 - \frac{\Delta H_i}{H_i}\right) \sim N(\mu_j, \sigma^2)$$

$$\mu_j = p_1 + p_2 \text{Ln}(L_j)$$

Coefficient estimates

Species	Coefficient	Estimate	SE	Pvalue	AdjustedR2
Spruce	p1	4.654416	0.015114	<2e-16	0.7562
	p2	-0.049239	0.004459	2.02E-13	
Fir	p1	4.545857	0.013231	<2e-16	0.5141
	p2	-0.026963	0.003709	2.84E-09	

Variance-Covariance matrixes

Spruce	alpha	beta	Fir	alpha	beta
alpha	2.28E-04		alpha	1.75E-04	
beta	-6.37E-05	1.99E-05	beta	-4.58E-05	1.38E-05

5.5. Tree recruitment

When saplings reach a recruitment height of 3.8m for *Picea abies* and of 4.6m for *Abies alba*, they are recruited as trees in the stand. These recruitment heights correspond to a dbh of 7.5cm (which is the minimal dbh recorded in adult tree data).

6. Initialization of tree spatial positions

Trees are first assigned random coordinates within the stand. Then, an algorithm adapted from (Goreaud *et al.*, 2004) is used to modify tree positions within the simulated stand until they fit the spatial organisation of a reference plot. A tree is randomly selected in the stand and is assigned new random coordinates each algorithm iteration. Then, Ripley functions (Ripley, 1977) are used to quantify several spatial patterns of the simulated stand and of the reference plot, namely, the attraction/repulsion between all trees without species or dbh distinctions, within species (fir vs fir and spruce vs spruce) and within dbh categories (medium vs medium (<42.5cm), large vs large (>42.5cm) and medium vs large). A cost function is defined to summarize the difference between the simulated stand and the reference plot (Goreaud *et al.*, 2004). The new tree position is accepted if the cost function decreases in the new configuration compared to the previous one. Typically, 10,000 iterations are performed, which is largely sufficient to reach the minimum cost function value.

7. Initialization of the sapling layer

Initial sapling composition, abundance and locations were simulated using Samsara2 regeneration process: a 100-year long demographical dynamics was simulated, applying only the sapling installation and sapling growth processes with no change in the adult stand. Saplings reaching the recruitment height threshold during that phase were not recruited as adult trees but simply removed. Adult trees (dbh > 17,5cm) were thus not impacted by this initialization step. We found that 100 years were sufficient to obtain quasi-equilibrium between sapling installation and removal and thus a sapling population in balance with the adult stand.

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