Diversity as a management tool for forest ecosystem services

A theoretical exploration using control theory and viability analyses

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1 Summary

Defining optimal forest management strategies in a changing world is a challenge in the field of forest ecology. The complexity of forest ecosystems, coupled with the uncertainty of future climate conditions, makes it difficult to determine the best course of action. The concept of forest diversity is a key consideration in this debate, as it is believed to be a significant factor in the resilience of forest ecosystems. This study aims to explore whether diversity can be used as a management tool to maintain ecosystem services. To this end, we will use a theoretical model of a mixed-species, multi-layered forest, and apply control theory and viability analyses to assess the relationship between diversity and management trajectories, considering both species and vertical diversity at the stand level.

Keywords: forest management, diversity, control theory, viability theory

2 Intro

Defining optimal forest management strategies in a changing world is a challenge in the field of forest ecology. The complexity of forest ecosystems, coupled with the uncertainty of future climate conditions, makes it difficult to determine the best course of action. But forest health is already decreasing in France (REF) and to cope with the collapse of ecosystem new management practices have already been studied : replacing monospecific forets stand by mixted species stand or uneven forest management by replacing clear-cutting by retention forestry and selection cutting.
Knowledge on this two practices is still limited and the results are not always consensual but they are already implemented and rely on the idea that diversification is a way to increase multiple ecosystem services.

Work on composition diversification and its effects is mainly driven by the first work on biodiversity ecosystem functioning (BEF) from grassland studies in the 70's (Tilman 1996).They showed that there was a positive link between biodiversity and ecosystem functioning. But the mechanisms behind this link are still not well understood. Numerous hypothesis were made to explain this link: competitive exclusion, niche complementary, sampling effect, etc. (Ali 2023). This uncertainty makes it difficult to predict the impact of biodiversity loss, and even more in other ecosystems than grasslands. While the hypothesis of BEF relationship, and its relevance is still debated, it fuels an entire segment of research. The study of BEF in forest is more recent and mainly focused on the link between species diversity and productivity. A positive relattionship has been demonstrated at a global scale (Liang et al. 2016), but also in specific forest (X. Morin et al. 2011; Paquette and Messier 2011; Jourdan et al. 2021). But as for grassland the mechanisms are not understood and the interaction is not positive in every forest type. (Forrester and Bauhus 2016). However one of the way to explain the contrasting results could be that the biodiversity-productivity interaction is context dependant. The relationship seems to be mostly positive in harsh climate and low tree density but negative in suitable environment (Jucker et al. 2016). It is also reductive to consider productivity as the only characteristic of forest ecosystems, and many other should be accounted for : support of habitat and biodiversity, regulation of flood, carbon storage and also cultural and aesthetic values. All of them might not be impacted in the same way. For example there doesn't seem to be an effect of mixture on other soil biodiversity (Korboulewsky, Perez, and Chauvat 2016). To have a better understanding of the impact of biodiversity on forest functioning it seems necessary to study multiple functions at the same time. It has been shown that diversity can increase multi-functionality by the jack-of-all-trades mechanism (Van Der Plas et al. 2016) while not optimizing any of them. This compromise can be seen in the balance between young and old grown forests, if the firsts are more productive, they store less carbon than the last (Caspersen and Pacala 2001). It is thus important to define the functions that we want to preserve as well as threshold for each of them.

Vertical diversity brought back in forest by uneven forest management have also been advocated to be a possible solution to the increasing fralgility of this ecosystem (Guldin 1996). Today only 25% of managed forest in europe is composed of uneven aged stand (foresteurope.org), but the actual effect of such management is hardly consensual. In his review in 2017 Nolet (Nolet et al. 2018) concludes that "overall, the complexity of comparing even- and uneven- aged silviculture may explain the surprisingly limited number of studies that compare ecological effects of even- and uneven- aged silviculture".

All of this aims at increasing the diversity in forest, both in term of species and vertical

structure. But the reults are not unanimous and it is impossible to extract an optimal management trajectory with our knowledge and the added complexity of maximizing multiple functions at the same time.

2.1 Control theory and viability and utility for the subject

There doesn't seem to be any optimal solution to manage such complicated ecosystems, while taking into account their multi-functionality. Viability theory could be an appropriate tool to define management trajectories that could keep the system in a desirable state. These desirable states have to be defined beforehand, but a lot less hypothesis and knowledge are needed for control, this allows to try different and new trajectories. This analyses define the set of desirable states that can be kept inside our constraints : the "viability kernel" (Rougé, Mathias, and Deffuant 2013) :

$$Viab(K) = \{x_0 \in K \mid \forall t \geq 0, \exists u(\cdot), \forall t \geq 0, x(t) \in K\} \tag{1}$$

The viability kernel is the set of initial states x_0 in our constraints K for which there exists a set of control $u(\cdot)$ that can keep the system in K for all time. This type of analyses has already be used in forest management strategy (Mathias et al. 2015).

2.1.1 Hypothesis and objectives of the study

The limit ofthis kind of studies is their computational cost, and the need for a simple model, which means a compromise between complexity and realism. Our first hypothesis is that we can use a theoretical model to explore the effect of diversity on ecosystem services, and that the results will be transferable to more complex models. The advantages of this approach is that we can explore a large range of possibilities and test new hypothesis that could not be tested with more complex models. The second hypothesis is that diversity can be used as a management tool to maintain ecosystem services. This is a new way to think about diversity in forest management, and could be a way to change the paradigm of forest management.

3 Methods

3.1 Very short history on forest models

Forest models are very diverse, they evolved with need, understanding of ecosystem processes, and technological innovations. They are applied at different spacial scales from tree, to stand to landscape level. They integrate different processes as growth, regeneration, mortality, management,

photosynthesis, evapotranspiration, disturbances with more or less details. Numerous types of forest model classification exist (Porté and Bartelink 2002), but for this short exploration only a simple classification in two groups will be useful (Fontes et al. 2011) : first there are the empirical models that are developed on experimental data (and then theoretical models which are the continuous equivalent with differential equation), secondly there are the process based models (PBM) that infer dynamics from underlying processes at community,individual or cellular level. Amongst PBM, the biggest family is formed by Gap-models (Bugmann 2001), built upon the assumption that most of forest dynamic is the result of competition for light. Although gap models show promise, a significant drawback is their complexity, especially when defining the system state. This complexity surpasses our capacity for analysis. However, it is possible to reduce dimensions (and runtime to 5%) while making minimal assumptions with model aggregation, achieved through tools like DisCForM and TreeMig (Lischke, Löffler, and Fischlin 1998; Lischke, Zimmermann, et al. 2006) by height discretization. On the other hand theoretical models are derived from theoretical considerations, and not from detailed mathematical models of tree population dynamics such as gap models. However both of this approach show a remarkable congruence in their formulation (Bugmann 2001). For this study the needs for stand-level mixed-species size structured forest with a limited number of state variables and the possibility to apply management strategies, led us to the choice of a theoretical model. The model is based on the work of Kohyama and associates (T. Kohyama and Takada 2009; T. S. Kohyama and Takada 2012).

3.2   Our model

Our choice of model was highly constrained by the computational memory and capacity needed by a viability analyses. The model had to be simple enough to be sumarized by a small number of state variables, but also complex enough to be able to test different management strategies.For this purpouse theorical models are a good compromise.

The theoretical model described below comes from the study of multiple articles from Kohyama and associates (T. Kohyama and Takada 2009; T. S. Kohyama and Takada 2012). It is a compartment based model with multi species and multi layers structure Figure 1. The dynamic is influenced by growth, regeneration, mortality as well as competition processes. There are some differences between the models present in Kohyama 2009 and 2012, in particular definition of birth and competition. We chose to define birth as in Kohyama 2009 as a negative linear, or Verhulst function (and not as a negative exponential, or Ricker function in Koyama 2012). The only difference is that birth in our study is concidere on independant from the number of adult tree. This is

the same hypothesis as in the gap-model ForCEEPS (Xavier Morin, Damestoy, et al. 2020) with which we want to parameterize our model. Even if Kohyama 2009 propose a way to add competition for resources by layers below, we chose a strictly one-sided competition from the above layers as in Kohyama 2012.

Fig. 1. Dynamics of tree populations in a two-storeyed forest of model eqn 2. Owing to the one-sided competition for light, species-additive canopy foliage density regulates demographic processes of trees in canopy, whereas the overall foliage density affects understorey mortality.
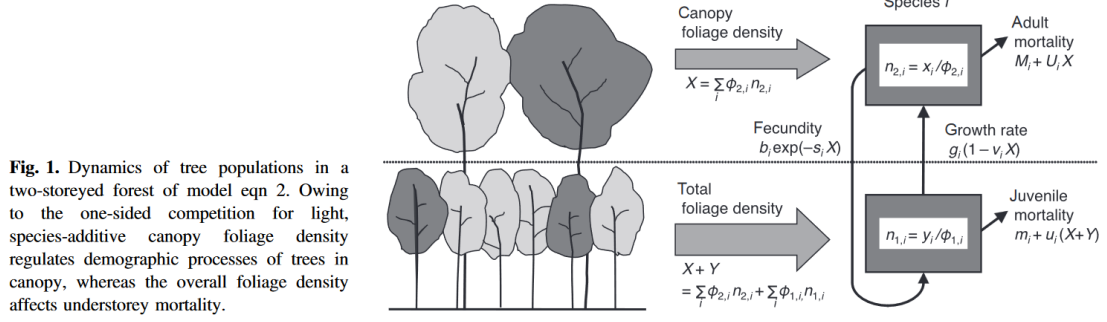
Figure 1: Figure from (T. S. Kohyama and Takada 2012)

Dynamic of each layer is driven by the competition from above layers foliage density (assimilated to the basal area) $\sum_{i=l}^{L} X_i$ with X_i being the foliage density of layer i :

$$X_l = \sum_{sp} x_{sp,l} = \sum_{sp} \phi_{sp,l} n_{sp,l} \tag{2}$$

The various processes are influenced by competition, with a linear negative relationship. Optimal probabilities are determined for each processes (birth b, growth g and mortality m) without competition. These probabilities are then adjusted based on the process sensitivity (Cb, Cg, Cm) of the layer and species to foliage density.

The model can be summarised with one differential equation :

$$\begin{aligned}
\frac{dn_{sp,l}}{dt} =& b_{sp,l}(1 - Cb_{sp,l} \sum_{i=1}^{L} X_i) \\
&+ g_{sp,l-1}\, n_{sp,l-1}(1 - Cg_{sp,l-1} \sum_{i=l-1}^{L} X_i) \\
&- g_{sp,l}\, n_{sp,l}(1 - Cg_{sp,l} \sum_{i=l}^{L} X_i) \\
&- m_{sp,l}\, n_{sp,l}(1 + Cm_{sp,l} \sum_{i=l}^{L} X_i)
\end{aligned} \tag{3}$$

And some special cases for lower and upper layers :

$$b_{sp,l} = 0 \text{ for } l > 1$$

$$g_{sp,L} = 0$$

$$g_{sp,0} = 0$$

Population densities and demographic parameters are defined in 1 and are all positive.

Abbreviation	Meaning	Unit
l	layer index	
L	number of layer (i.e. maximum layer)	
sp	species index	
SP	number of species	
$n_{sp,l}$	number of trees of species sp in layer l	ha^{-1}
$x_{sp,l}$	foliage density of species sp in layer l	$m^2.ha^{-1}$
$\phi_{sp,l}$	mean basal area of tree from species sp in layer l	m^2
X_l	foliage density of layer l	$m^2.ha^{-1}$
$\sum_{i=l}^{L} X_i$	foliage density above layer l	$m^2.ha^{-1}$
b_{sp}	optimal birth rate per tree in layer L	
Cb_{sp}	birth susceptibility to superior foliage density	$ha.m^{-2}$
$g_{sp,l}$	growth susceptibility to superior foliage density	
$m_{sp,l}$	probability of intrinsic mortality	
$Cg_{sp,l}$	growth susceptibility to superior foliage density	$ha.m^{-2}$
$Cb_{sp,l}$	mortality susceptibility to superior foliage density	$ha.m^{-2}$

Table 1: Parameters for the model

3.3   Model parametrisation

We are starting with a 3 layers 3 species system with a mixture of possible species : *Abies alba*, *Betula pendula*, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *Quercus pubescens*. The layers are defined by simplifying the IGN (French National Institute for Geographic and Forestry Information) 4-dimensional wood classification used in national forest inventory into 3 classes : dbh (cm) in [0,22.5] for small wood, [22.5,67.5] for medium and large, and [67.5+[for very large. We have to define all parameters from the model.

Litterature and ForCEEPS simulations where used to adjust the dynamic of the system on a constant climate. (see appendix on parametrisation (Bugmann 1965; Xavier Morin, Bugmann, et al. 2021)). Giving the parameters in Table S.5.

After looking at the results of our model compared to ForCEEPS we choose to concentrate our analyses on *Abies alba* and *Fagus sylvatica* as their dynamic was the most similar to ForCEEPS and they can be found together in mixed stand in France.

3.4 Control theory and viability

Viability theory provides a framework for management of dynamic systems. The challenge lies in finding management strategies ($u(t)$) that perpetually keep the system within a space of chosen constraints. Rather than fixating on a single optimal state, the approach is to navigate within a spectrum of acceptable outcomes, preventing irreversible negative impacts. In our case, the control is discrete and can happen every five years (Δt), mathematically, this is articulated as a controlled discrete-time dynamical system:

$$N(t + \Delta t) = g(N(t), u(t), \Delta t),$$

where $N(t)$ is the system state at time t, $u(t)$ is the control applied at time t, and g is the state transition function.

The resulting viability kernel ($Viab(K)Viab(K)$), which includes states where a management strategy can keep the system within desirable states, is formally described as:

$$Viab(K) = \{N_0 \in K \mid \exists u(\cdot), \forall t \in \mathbb{N}_5, N(t) \in K\},$$

where N_0 denotes an initial state of the system in our constraints K. Within the viability kernel, at least one control strategy $u(\cdot)$ can maintain the system in a desirable state K. After the delimitation of the viability kernel all viable controls (u_v) can be determined and analysed.

To approach the viability kernel we used an algorithm inspired by Saint-Pierre ((Saint-Pierre 1994)).

4 Control theory and viability : study case

In our case the state of the system, $N(t)$, is defined by the matrix of the number of trees in each layer and for each species:

$$N(t) = [n_{sp,l}(t)]_{SP \times L}$$

. The space of possible control is defined by the number of trees that are going to stay after a cut in the two higher layer :

$$U = \{u \in \mathbb{N}^{sp*Ncut} \mid \forall sp \in \mathbb{N}_{[1,SP]} \,\&\, l \in \mathbb{N}_{[c,L]}, u_{sp,l} \leq n_{sp,l}\}$$

The space of possible control is then all the possible compositions of cut layers ($Ncut$ being the number of layers that are cut, 2 in our study, then the first layer cut is $c = L - Ncut + 1$) such as

the number of trees left is inferior to the number of trees present before the cut in the layer. The transitionform t to $t + \Delta t$, $g(.)$ is defined by the model (Eq. 3).

To define the desirable states we chose constraints on wood extraction and diversity. The first one allow to take into account the economic aspect of forest management. The metrics for diversity were included as a way to take into account the diversity aspect of forest management and it's impact on other services. We chose to use the Shannon index as a measure of species and vertical diversity, as it is a common metric in ecology.

After defining the viability kernel for : species... Known limitation of the viability analyses (harware -> perhaps in discussion) On a machin RAM, turning for blabla time with , code accessible at github; Everything ran with R 4 and analyses where also done with R. We got the results :

5 Results

6 Discussion for now random text on reflexion I had and may be incliduded or not

Landscape diversity

Limit of parametrisation : other possibilities : data/ easy abc, error, sensitivity analysis, and also more generally simplified model truthtfullness

Limit : choice of diversity index, sensibility and Hill number, Gini...

6.1 Forest diversity, may be more complex than diversity drives diversity

In forests diversity can be define in different ways : Composition or structural diversity. And at different scale from the stand to the landscape.

Work on composition diversification and its effects is mainly driven by the first work on biodiversity ecosystem functioning (BEF) from grassland studies in the 70's (Tilman 1996).They showed that there was a positive link between biodiversity and ecosystem functioning. But the mechanisms behind this link are still not well understood. Numerous hypothesis were made to explain this link: competitive exclusion, niche complementary, sampling effect, etc. (Ali 2023). This uncertainty makes it difficult to predict the impact of biodiversity loss, and even more in other ecosystems than grasslands. While the hypothesis of BEF relationship, and its relevance is still debated, it fuels an

entire segment of research. The study of BEF in forest is more recent and mainly focused on the link between species diversity and productivity. A positive relattionship has been demonstrated at a global scale (Liang et al. 2016), but also in specific forest (X. Morin et al. 2011; Paquette and Messier 2011; Jourdan et al. 2021). But as for grassland the mechanisms are not understood and the interaction is not positive in every forest type. (Forrester and Bauhus 2016). However one of the way to explain the contrasting results could be that the biodiversity-productivity interaction is context dependant. The relationship seems to be mostly positive in harsh climate and low tree density but negative in suitable environment (Jucker et al. 2016). It is also reductive to consider productivity as the only characteristic of forest ecosystems, and many other should be accounted for : support of habitat and biodiversity, regulation of flood, carbon storage and also cultural and aesthetic values. All of them might not be impacted in the same way. For example there doesn't seem to be an effect of mixture on other soil biodiversity (Korboulewsky, Perez, and Chauvat 2016). To have a better understanding of the impact of biodiversity on forest functioning it seems necessary to study multiple functions at the same time. It has been shown that diversity can increase multi-functionality by the jack-of-all-trades mechanism (Van Der Plas et al. 2016) while not optimizing any of them. This compromise can be seen in the balance between young and old grown forests, if the firsts are more productive, they store less carbon than the last (Caspersen and Pacala 2001). It is thus important to define the functions that we want to preserve as well as threshold for each of them.

Actually species diversity is not the only way to bring back diversity in forest and recently vertical diversity in forest have also been advocated to be a possible solution to the increasing fralgility of this ecosystem (Guldin 1996). Today only 25% of managed forest in europe is composed of uneven aged stand (foresteurope.org), but the actual effect of such management is hardly consensual. In his review in 2017 Nolet (Nolet et al. 2018) concludes that "overall, the complexity of comparing even- and uneven- aged silviculture may explain the surprisingly limited number of studies that compare ecological effects of even- and uneven- aged silviculture".

6.2 Management for diversity

Forest management is inextricably linked to the evolving understanding of ecological dynamics and global shifts. In addressing the question of how to manage diversity in managed forests, several propositions or practice philosophies have been put forth. The first is avoiding clear-cutting which can be done in a number of ways. First retention forestry (Gustafsson et al. 2012; Rosenvald and Lõhmus 2008) aims at maintaining the structure and composition of the forest by leaving a certain proportion of trees in the stand after harvesting. This approach is based on the assumption that

the forest will regenerate naturally, and that the retained trees will provide a seed source for the next generation, it is also a way to keep a certain diversity on the stand. The second is the choice of an irregular Shelterwood Systems (also called uneven aged forest or continuous cover forestry) (Sinha et al. 2017; Schall et al. 2018; Nyland 2003; Nolet et al. 2018; Duduman 2011) which aims to maintain a continuous cover of trees in the stand, and some vertical diversity. The second thing to rely on mixture of species (X. Morin et al. 2011; Jourdan et al. 2021), while eventually consideration the plantation of tree species resilient to future climate conditions (Webster et al. 2018).

The complexity of these approaches underscores the need for a comprehensive study of forest management practices to ascertain their effectiveness while mitigating drawbacks.

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Appendix

A Kohyama model parametrisation

We are starting with a 3 layers 3 species system with a mixture of possible species : *Abies alba, Betula pendula, Fagus sylvatica, Picea abies, Pinus sylvestris, Quercus pubescens*. The layers are defined by dbh (cm) interval : [0,22.5], [22.5,67.5], [67.5+[. We have to define all parameters in Table 2.

By species, sp		
$b_{sp,1}$	optimal birth probability	$ha^{-1}.year^{-1}$
$Cb_{sp,1}$	birth susceptibility to superior foliage density	$ha.m^{-2}$
m_{sp}	probability of intrinsic mortality	$year^{-1}$
Cg_{sp}	growth susceptibility to superior foliage density	$ha.m^{-2}$
Cm_{sp}	mortality susceptibility to superior foliage density	$ha.m^{-2}$
By layer l		
ϕ_l	mean basal area per tree in layer l	$m^2.ha^{-1}$
By species sp **and layer** l		
$g_{sp,l}$	optimal probability of transition from layer l to the next	$.year^{-1}$

Table 2: Parameters that we have to define numerically

A.1 Parameters deduced form litterature of ForCEEPS and ForClim

A.1.1 Basal area

Basal area is defined as the area of the cross subsection of the tree at breast height (1.3m). It is a good indicator of the density of the forest. It is defined as :

$$\phi_l = \frac{\pi}{4} * \overline{D_l}^2 \tag{4}$$

With $\overline{D_l}$ the mean diameter in layer l. (i.e. 11.25, 45, 100 cm).

A.1.2 Intrinsec Mortality

Mortality was defined axactly as in ForCEEPS, as the inverse of the life expectancy of the species (A_{max}) multiplied by a factor $c_{mort} = 4.605$.

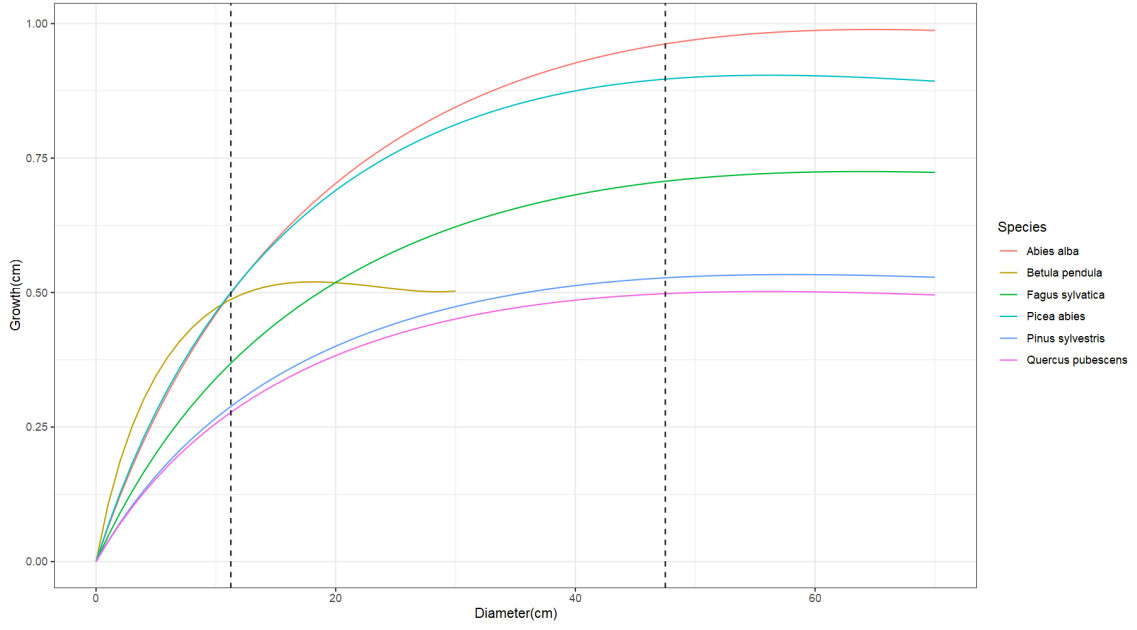$$m_s = \frac{c_{mort}}{A_{max_s}} \tag{5}$$

Figure 2: Growth as a function of diameter for the 5 species

$A_m ax$ can be found in the thesis on ForClim (Bugmann 1965) or the supplementary data of ForCEEPS (Xavier Morin, Bugmann, et al. 2021)

A.1.3   Optimal Growth

Optimal growth is defined in ForCEEPS (Xavier Morin, Bugmann, et al. 2021) as :

$$\Delta D_{\text{opt}_i}(t+1) = g_s \frac{D_i(t)\left(1 - \frac{H_i(t)}{H_{\max_s}}\right)}{2H_{\max_s} - b_{\max_s} \times \exp\left(\left(\frac{-s_s}{b_{\max_s}}D_i(t)\right) \times \left(\frac{-s_s}{b_{\max_s}}D_i(t) + 2\right)\right)} \tag{6}$$

With g_s the growth rate, D_i the diameter of the tree, H_i the height of the tree, $H_{\max_s}$ the maximum height of the species, $b_{\max_s}$ the maximum heigth of the species above breast ($b_{\max_s} = H_{\max_s} - 1.37$), and s_s the shape parameter of the species. g_s, $H_{\max_s}$, and s_s can be found in the appendix (Xavier Morin, Bugmann, et al. 2021). H_i is also defined as a function of D_i :

$$H_i(t) = b + b_{\max_s}\left(1 - \exp\left(-\frac{s_s}{b_{\max_s}}D_i(t)\right)\right) \tag{7}$$

This gives a function $f(D_i) = \Delta D_{\text{opt}_i}(t+1)$, which is the growth of the tree as a function of its diameter.

As our model does not account for a change of growth with diameter we took the growth from the mean diameter of our two interval : $[0, 22.5]$ and $[22.5, 67.5]$ (i.e. 11.25 and 45). It gives :

Species	Growth 1	Growth 2
Abies alba	0.5	0.96
Betula pendula	0.5	0
Fagus sylvatica	0.37	0.71
Picea abies	0.5	0.9
Pinus sylvestris	0.29	0.53
Quercus pubescens	0.28	0.5

Table 3: Growth for the 5 species and two below layers

Growth is the number of cm added to the diameter of the tree each year. To get the transition probability to the next layer with the assumption that tree dbh are uniformly distributed in each layer we need to divide this value by the diameter difference of the layer (See Tab. **??**).

A.1.4 Optimal Esthablishment

Establishment is a process that is still not well understood. In ForCEEPS optimal establishment (if all the threshold for establishment are met) is the same for every species : 0.006 individu/m2/year. We will use this value for our model for every species.

A.1.5 Light competition

Proportionality between the species is known (see ForClim Ly (growth) and La(birth)), as mortality due to light competition is due to the absence of growth we used the same proportionality between species.

Species	Ly (growth, mortality)	La (birth)
Abies alba	0.05	1
Betula pendula	0.3	9
Fagus sylvatica	0.05	1
Picea abies	0.1	5
Pinus sylvestris	0.3	9
Quercus pubescens	0.3	7

Table 4: Sensitivity for light competition

If we have a relative sensitivy of our species to light availability we still have to get the global coefficient linked to this sensitivity for growth, birth and mortality. We cannot extract the parameters from a simplification as we used a negative linear function, which is not the case in ForCEEPS. We will use the data from ForCEEPS to fit our parameters.

A.2 ForCEEPS input data and results

ForCEEPS simulations where used to adjust the dynamic of the system. 6 species where chosen to do so : *Abies alba, Betula pendula, Fagus sylvatica, Picea abies, Pinus sylvestris.* We chose a constant climate for 300 years drawn randomly from meteorologic data from Bern between 1950 and 2000 (resulting climate can be found in Fig. 3). We used the same initial forest structure for all simulations : 10 trees per species per layer. We did 20 simulations of 1000m2 patch for each species association. We then took the mean of the 20 simulations and multiplied it by 10 to get the number of trees per hectare. We then fitted the parameters of the model to get the same dynamic as the ForCEEPS simulations.

A.2.1 Climate

Climate was taken randomly for each months in the climate data from 1950 to 2000 (Bern), to get a constant climate. To be sure to have non limiting precipitation they were all multiplied bya factor 10.
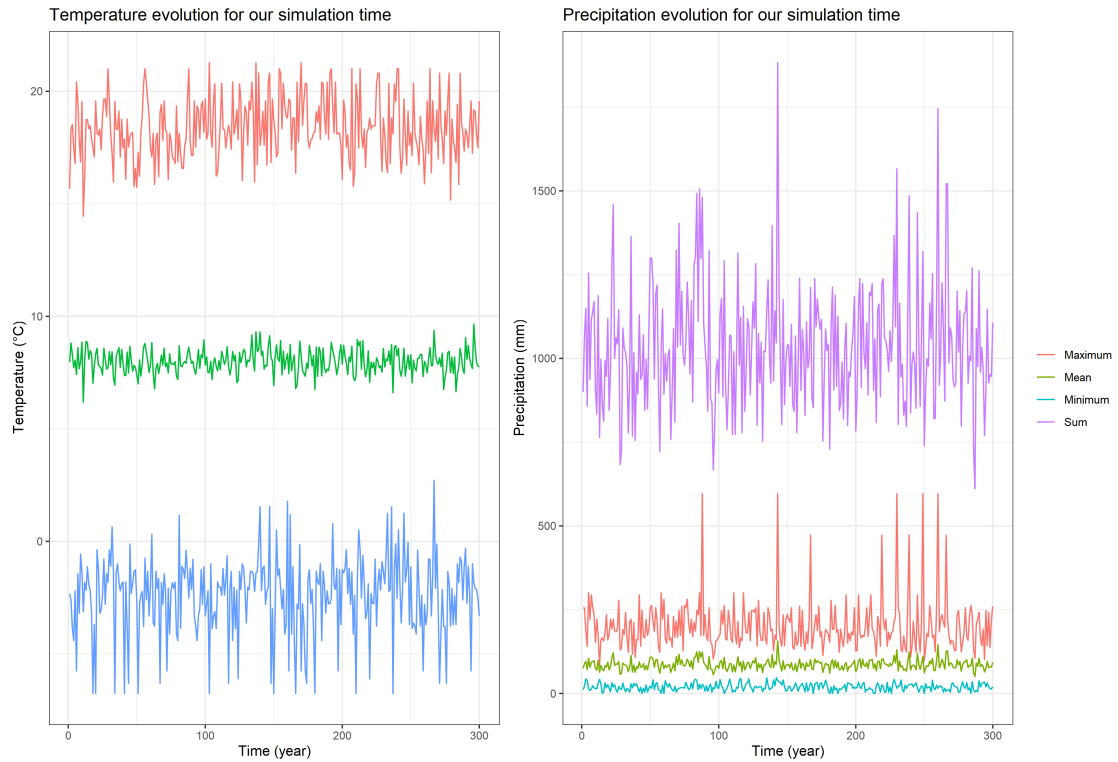

Figure 3: Climate for our ForCEEPS simulation

A.2.2 setup parameters

For the setup parameters we used non limiting values for water and nitrogen. The parameters can be found in the github documents (file Basic.setup), and are the same for all simulations.

Result of the simulation are in color in Fig. 4.

A.2.3 Fitting the parameters

To fit the parameter we used the function optim in R with the following parameters :

> result <- optimParallel(start point, function to minimize, lower = rep(0,3), upper = rep(0.1,3), method = "L-BFGS-B")

Method "L-BFGS-B" (see optim documentation `https://www.rdocumentation.org/packages/stats/versions/3.6.2/topics/optim`) allows box constraints, that is each variable can be given a lower and/or upper bound. The initial value must satisfy the constraints. This uses a limited-memory modification of the BFGS quasi-Newton method. "BFGS" is a quasi-Newton method (also known as a variable metric algorithm), specifically that published simultaneously in 1970 by Broyden, Fletcher, Goldfarb and Shanno. This uses function values and gradients to build up a picture of the surface to be optimized.

I only fit three non specific parameters LCg (light competition for growth), LCm (light competition for mortality) and LCb (light competition for birth). In the model they are then multiplied by the sensitivity of the species to light competition (see Tab. 4).

A.2.4 Results

Species	b (/ha/an)	m (/year)	g1 (/year)	g2 (/year)	LCb	LCm	LCg
Abies alba	60	0.013	0.022	0.021	0.0059	0.0046	0.0059
Betula pendula	60	0.031	0.022	0	0.0295	0.0229	0.0295
Fagus sylvatica	60	0.012	0.016	0.016	0.0531	0.0413	0.0531
Picea abies	60	0.015	0.022	0.02	0.0531	0.0413	0.0531
Pinus sylvestris	60	0.023	0.013	0.012	0.0059	0.0046	0.0059
Quercus pubescens	60	0.008	0.012	0.011	0.0413	0.0321	0.0413

Table 5: Parameters found for the 5 species

A.3 Volume allometry

Volume was calculated with the formula from (Deleuze et al. 2014) :

$$\text{VolTot} = \frac{h_{\text{tot}} \cdot c_{130}^2}{4\pi \left(1 - \frac{1.3}{h_{\text{tot}}}\right)^2} \left(a + b \cdot \frac{\sqrt{c_{130}}}{h_{\text{tot}}} + c \cdot \frac{h_{\text{tot}}}{c_{130}}\right) \tag{8}$$

With h_{tot} the total height of the tree, c_{130} the diameter at 130cm, and a, b, and c the coefficients for each species. The coefficients can be found in (Deleuze et al. 2014). h_tot was defined as a function of c_{130} like in equation 7.

Species	Volume layer 1	Volume layer 2	Volume layer 3
Abies alba	0.007624415	0.2518305	1.724068
Picea abies	0.009195898	0.2779880	1.697751
Pinus sylvestris	0.005440307	0.1669922	1.134001
Betula pendula	0.004805793	0.1585726	0.947111
Fagus sylvatica	0.005384323	0.2140528	1.681878
Quercus pubescens	0.004872535	0.1729537	1.281115

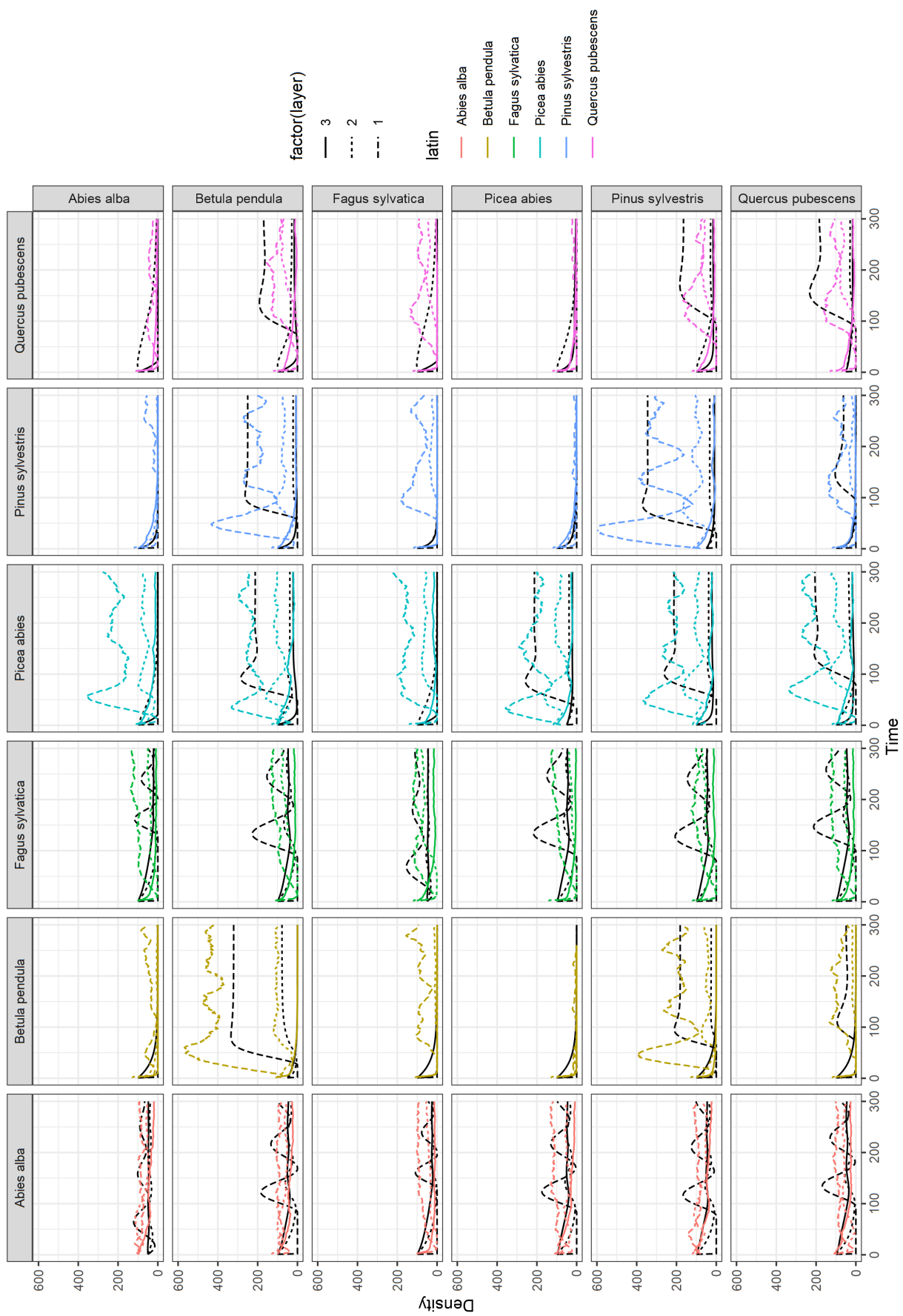Table 6: Volume of the 6 species in the 3 layers (m3/tree)

Figure 4: Fit Kohyama model (color) on ForCEEPS simulation (black) for individual species