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Sylvain SCHMITT

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Sylvain SCHMITT

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Titre Prénom NOM	Examinateur
Titre Prénom NOM	Examinateur
Titre Prénom NOM	Enseignant-référent

Contents

Résumé et Abstract

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Acknowledgments

I would like to thank...

Introduction

Sutainable forest management in the tropics (i.e. managed selective harvesting of timber) has been widely promoted internationnaly to combat tropical deforestation and degradation [Zimmerman and Kormos, 2012]. Currently tropical logging accounts for one eight of global timber production [Blaser et al., 2011] and is still increasing. Most tropical timber production originates from selective logging, the targeted harvesting of timber from commercial species in a single cuttint cycle [Martin et al., 2015].

On the other hand, tropical rainforests have fascinated ecologists due to their outstanding diversity [Connell, 1978]. Effectively tropical forests host over half of the Earth's biodiversity [Scheffers et al., 2012]. High biodiversity from tropical rainforests is the source of many ecosystem functions. Amongst others, tropical forests play a key role in biogeochemical cycles, including carbone storage [Lewis et al., 2004]. **Add insights into carbon storage role of tropical forest.** Ecosystem functions from tropical forests support numerous ecosystem services, such as timber production and climate regulation.

But several authors argue that selective logging represents a major threat to biodiversity [Carreño-Rocabado et al., 2012, de Avila et al., 2015, Gibson et al., 2013, Martin et al., 2015, Zimmerman and Kormos, 2012], challenging the sustainable definition from current selective logging. We consequently need to assess both short and long term impacts of selective logging on tropical forest ecosystems to implement better syslvicultural practives in order to reach sustainability.

The question of selective logging impact on tropical forest can be directly related to the emerging field of biodiversity and ecosystem functionning [Loreau, 2000]. Tropical forest outstanding biodiversity will be both a factor and a result of forest ecosystem response to logging disturbance. And forest ecosystem response to logging disturbance will directly modify ecosystem functionning in both short and long term. Consequently assessing selective logging effect on tropical forest linking biodiversity and ecosystem seems an obvious and promising way [Loreau, 2010]. **Paragraph to fully review !**

Negative short term impacts of selective logging have been assessed [Carreño-Rocabado et al., 2012; de Avila et al., 2015; but see Martin et al., 2015]. Much less is known about the long term impact [Osazuwa-Peters et al., 2015]. The main reason is the difficulty to conduct long term empirical study [but see Herault et al., 2010], which can be completed by the use of forest simulators [Huth et al., 2004, Köhler and Huth, 2004, Rüger et al., 2008, Tietjen and Huth, 2006]. Individual-based models of forest dynamics present the perfect framework to develop such joint biodiversity-ecosystem approaches [Maréchaux and Chave]. Individual-based models describe forest 'patches' accumulating carbon through time, assessing tree growth within the patch, or releasing carbon through gap opening [Bugmann, 2001]. Up to several dozens of different Plant Functional Types (PFTs) are generally defined and models can sometimes be fully spatially explicit [Pacala et al., 1996]. Recently, the forest growth simulator TROLL [Chave, 1999], an individual-based and spatially explicit forest model, was developped to introduce recent advances in plant physiological community. TROLL model relates physiological processes to species-specific functional traits [Maréchaux and Chave]. Consequently, TROLL model allow to simulate fully a neotropical forest biodiversity to study biodiversity-ecosystem functionning link response to logging disturbance.

Major question greater diversity (taxonomic and functional) brought a better resilience to disturbance ?

1 Model description

1.1 Overview

TROLL model each tree indivdually in a located environment. Thus TROLL model, alongside with SORTIE [Pacala et al., 1996, Uriarte et al., 2009] and FORMIND [Fischer et al., 2016, Köhler and Huth, 1998], can be defined as an individual-based and spatially explicit forest growth model. TROLL simulates the life cycle of individual trees from recruitment, with a diameter at breast height (dbh) above 1 cm, to death with growth

Table 1: Species-specific parameters used in TROLL from @Li. Data originates from the BRIDGE [@Baraloto2010] and TRY [@Kattge2011] datasets.

Abbreviation	Description	Units
LMA	leaf mass per area	$g.m^{-2}$
N_m	leaf nitrogen content per dry mass	$mg.g^{-1}$
P_m	leaf phosphorous content per dry mass	$mg.g^{-1}$
wsg	wood specific gravity	$g.cm^{-3}$
dbh_{thresh}	diameter at breasth height threshold	m
h_{lim}	asymptotic height	m
a_h	parameter of the tree-height-dbh allometry	m

and seed production. Trees are growing in a located light environment explicitly computed witin voxels of 1 m^3. Each tree is consistently defined by its age, diameter at brest height (dbh), height (h), crown radius (CR), crown depth (CD) and leaf area (LA) (see figure 1). Tree geometry is calculated with allometric equations but leaf area vary dinamically within each crown following carbon allocations. Voxels resolution of 1 m^3 allow the establishment of maximum one tree by 1x1 m pixels. Each tree is flagged with a species label inherited from the parent tree through the seedling recruitment. A species label is associated to a number of species specific parameters (see table 1) related to functional trait values which can be sampled on the field.

Carbon assimilation is computed over half-hourly period of a representative day. Then allocation is computed to simulate tree growth from an explicit carbone balance (in contrast to previous models). Finally environment is updated at each timestep set to one month. Seedlings are not simulated explicitly but as a pool. In addition belowground processes, herbaceous plants, epiphytes and lianas are not simulated inside TROLL. The source code is written in C++ and available upon request. All analyses were conducted in R version 3.4.0 **Cite R, add entry in Mendeley**.

1.2 Abiotic environment

A voxel space, with a resolution of 1 m^3, is used to explicilty model the abiotic environment. For each tree crown, leaf area density is calculated on tree geometry assuming a uniform distriution across voxels occupied by the crown. Leaf area density is computed within each voxel summing all tree crowns inside the voxel v, and is denoted $LAD(v)$ (leaf area per voxel in $mš.m^{-3}$). The vertical sum of LAD from voxel v to the ground level defines $LAI(v)$ (leaf area per fround area in $m^2.m^{-2}$ commonly called leaf area index):

$$LAI(v) = \sum_{v'=v}^{\infty} LAD(v') \tag{1}$$

Daily variations in light intensity (photosynthetic photon flux density PPFD in $\mu mol_{photons}.m^{-2}.s^{-1}$), temperature (T in degrees Celsius), and vapor pressure deficit (VPD in kPA) are computed to assess carbon assimilation within each voxel of the canopy and for a representative day per month (see Appendix 1 from Maréchaux and Chave for further details). Variation of PPFD Within the canopy is calculated as a loacal Beer-Lambert extinction law:

$$PPFD_{max,month}(v) = PPFD_{top,max,month} * e^{-k*LAI(v)} \tag{2}$$

The daily maximum incident PPFD at the top of canopy $PPFD_{top,max,month}$ is given as input. The extinction rate k is assumed as constant, besides is variation with zenith angle and species leaf inclination angle [Meir et al., 2000]. Moreover only vertical light diffusion is considered ignoring lateral light diffusion, which can have an important role especially in logging gaps. Finally, intra-day variation at half hour time steps t for a representative day every month are used to compute $PPFD_{month}(v,t)$, $T_{month}(v,t)$ and $VPD_{month}(v,t)$. Water and nutrient process both in soil and inside trees are not simulated.

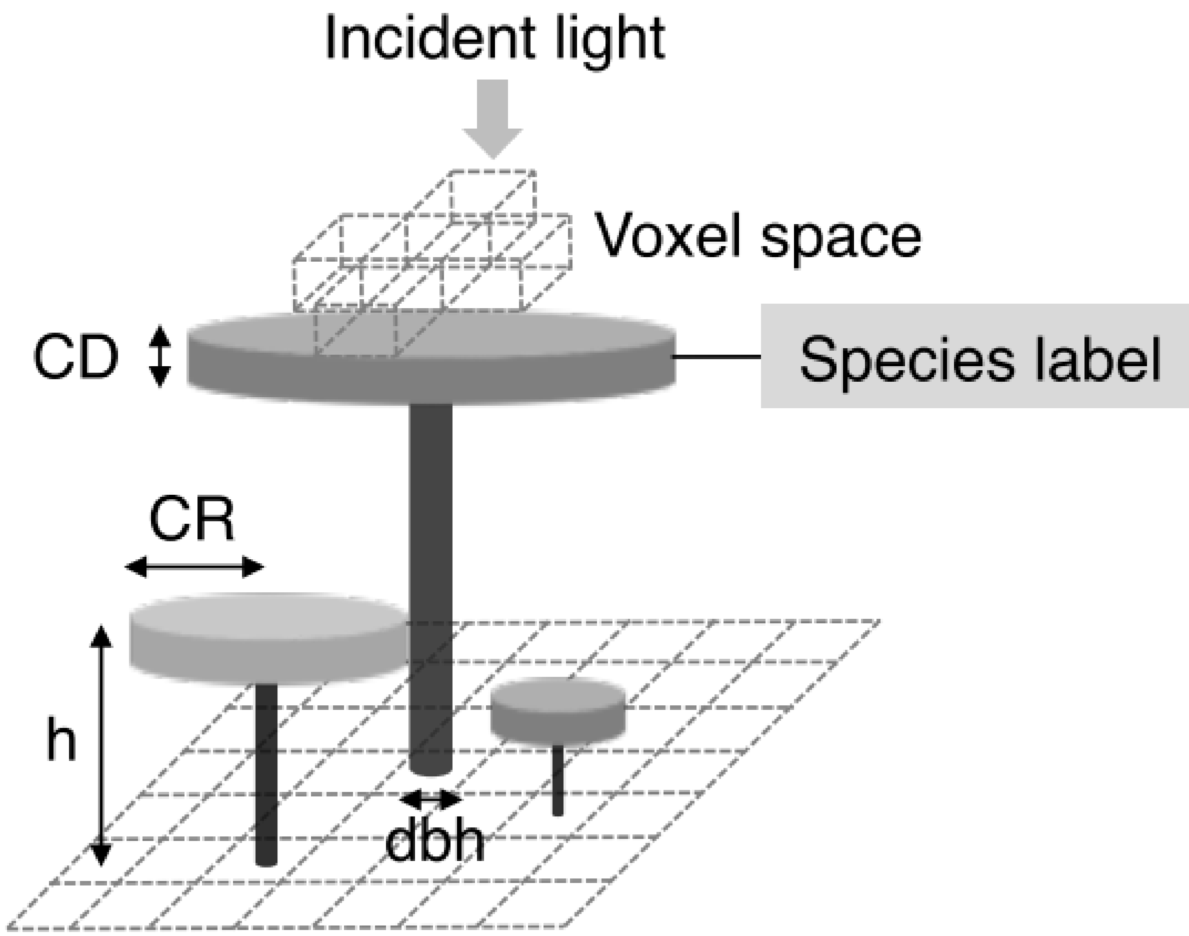

Figure 1: Individuals tree inside TROLL explicit spatial grid from Maréchaux and Chave. Tree geometry (crown radius CR, crown depth CD, height h, diameter at breast height dbh) is updated at each timestep following allometric relationship with assimilated carbon allocated to growth. Each tree is flagged with a species label linking to its species-specific attributes. Light is compputed explicitly at each timestep for each voxel.

1.3 Photosynthesis

1.3.1 Theory

Troll simulates the carbon uptake of each individual with the Farquhar, von Caemmerer and Berry model of C3 photosynthesis [Farquhar et al., 1980]. Gross carbon assimilation rate (A in $\mu mol\ CO_2.m^{-2}.s^{-1}$) will be the minimum of eiter Rubisco activity (A_v) or RuBP generation (A_j):

$$A = min(A_v, A_j) \mid A_v = V_{cmax} * \frac{c_i - \Gamma^*}{c_i + K_m} \ ; \ A_j = \frac{J}{4} * \frac{c_i - \Gamma^*}{c_i + 2 * \Gamma^*} \tag{3}$$

V_{cmax} is the maximum rate of carboxylation ($\mu mol\ CO_2.m^{-2}.s^{-1}$). c_i is the CO_2 partial pressure at carboxylation sites. Γ^* is the CO_2 compensation point in absence of dark respiration. K_m is the apparent knietic constant of the Rubisco. And J is the electron transport rate ($\mu mole^-.m^{-2}.s^{-1}$). J depends on the light intensity with $PPFD$:

$$J = \frac{1}{2 * \theta} * [\alpha * PPFD + J_{max} - \sqrt{(\alpha * PPFD + J_{max})^2 - 4 * \theta * \alpha * PPFD * J_{max}}] \tag{4}$$

J_{max} is the maximal electron transport capacity ($\mu mole^-.m^{-2}.s^{-1}$). θ is the curvature factor. And α is the apparent quantum yield to electron transport ($mole^-.mol\ photons^{-1}$).

Carbon assimilation by photosynthesis will then be limited by the CO_2 partial pressure at carboxylation sites. Stomata controls the gas concentration at carboxylation sites throught stomatal transport:

$$A = g_s * (c_a - c_i) \tag{5}$$

g_s is the stomatal conductance to CO_2 ($molCO_2.m^{-2}.s^{-1}$). TROLL simulates stomatal conductance g_s with the model from [Medlyn et al., 2011]:

$$g_s = g_0 + (1 + \frac{g_1}{\sqrt{VPD}}) * \frac{A}{c_a} \tag{6}$$

g_0 and g_1 are parameters from the model. TROLL model assume $g_0 \approx 0$ (empirically tested and considered as reasonable).

1.3.2 Parametrization

Leaf traits can be used as proxy of photosynthesis, especially leaf nutrient content which directly play a role in it [Wright et al., 2004]. Domingues et al. [2010] suggested that V_{cmac} and J_{max} were both limited by the leaf concentration of nitrogen N and phosphorus P ($mg.g^{-1}$):

$$log_{10}V_{cmax-M} = min(\begin{array}{c} -1.56 + 0.43 * log_{10}N - 0.37 * log_{10}LMA \\ -0.80 + 0.45 * log_{10}P - 0.25 * log_{10}LMA \end{array}) \tag{7}$$

$$log_{10}J_{max-M} = min(\begin{array}{c} -1.50 + 0.41 * log_{10}N - 0.45 * log_{10}LMA \\ -0.74 + 0.44 * log_{10}P - 0.32 * log_{10}LMA \end{array}) \tag{8}$$

V_{cmax-M} and J_{max-M} are the photosynthetic capacities at $25°C$ of mature leaves per leaf dry mass (resp. $\mu molCO_2.g^-1.s^{-1}$ and $\mu mole^-.g^{-1}.s^{-1}$). LMA is the leaf mass per are ($g.cm^{-2}$). V_{cmax} and J_{max} are calculated by multiplying V_{cmax-M} and J_{max-M} by LMA. V_{cmax} and J_{max} variation with temperature are caluclated with Bernacchi et al. [2003] (see Appendix 2 from Maréchaux and Chave for further details).

TROLL computes leaf carbon assimilation A_l combining equations from (3) to (8) for each tree crown voxel within in each crown layer l:

$$A_l = \frac{1}{n_v * t_M} * \sum_v \sum_{t=1}^{t_M} A(PPFD_{month}(v,t), VPD_{month}(v,t), T_{month}(v,t)) \quad (9)$$

$PPFD_{month}(v,t)$, $VPD_{month}(v,t)$, and $T_{month}(v,t)$ are derived from microclimatic data. n_v is the number of voxels within crown layer l. And the sum is calculated over the t_M half-hourly intervals t of a tipical day.

1.4 Autotrophic respiration

A large fraction of plants carbon uptake is actually used for plant maintenance and growth respiration. The autotrophic respiration can represents up to 65% of the gross primary productivity but varies strongly among species, sites, and environnements.

TROLL uses Atkin et al. [2015] database of mature leaf dark respiration and associated leaf traits to compute leaf maintenance respiration:

$$R_{leaf-M} = 8.5431 - 0.1306 * N - 0.5670 * P - 0.0137 * LMA + 11.1 * V_{cmax-M} + 0.1876 * N * P \quad (10)$$

R_{leaf-M} si the dark respiration rate per leaf dry mass at a temperaure of $25°C$ ($nmolCO_2.g^{-1}.s^{-1}$). The other terms are in equations (7) and (8). TROLL assume leaf respiration during day light to be 40% of leaf dark respiration, and computes total leaf respiration by accounting for the legnth of daylight.

TROLL model stem respiration (R_{stem} in $\mu molC.s^{-1}$) with a constant respiration rate per volume of sapwood:

$$R_{stem} = 39.6 * \pi * ST * (dbh - ST) * (h - CD) \quad (11)$$

dbh, h, CD and ST are tree diameter at breast height, height, corwn depth and sapwoond thickness, respectively (m). TROLL assumes $ST = 0.04\ m$ when $dbh > 30\ cm$ and an increasing ST for lower dbh.

Finally, TROLL computes both fine root maintenance respiration, as half of the leaf maintenance respiration. Whereas coarse root and branch maintenance respiration is computed as half of the stem respiration. And growth respiration (R_{growth}) is assumed to account for 25% of the gross primary productivity minus the sum of maintenance respirations.

1.5 Net carbon uptake

Net primary production of carbon for one individual NPP_{ind} (gC) is computed by the balance between gross primary production GPP_{ind} and respirations R:

$$NPP_{ind} = GPP_{ind} - R_{maintenance} - R_{growth} \quad (12)$$

TROLL partitions individuals total leaf area LA into three pools for different leaf age classes corresponding to different photosynthesis efficiency (young, mature and old leaves with LA_{young}, LA_{mature}, and LA_{old} respectivelly). Consequently we can compute growth primary production for one individual as:

$$GPP_{ind} = 189.3 * \Delta t * \sum_{l=\lfloor h-CD \rfloor+1}^{\lfloor h \rfloor} [A_l] * (\frac{LA_{young}}{2} + LA_{mature} + \frac{LA_{old}}{2}) \quad (13)$$

h and CD are tree height and crown depth, repectivelly (m). $\lfloor x \rfloor$ is the rounding function. Δt is the duration of a timestep ($year$).

Thus, TROLL can compute carbon allocation to wood into an increment of stem volume ΔV (m^3):

$$\Delta V = 10^{-6} * \frac{f_{wood} * NPP_{ind}}{0.5 * wsg} * Senesc(dbh) \tag{14}$$

f_{wood} is the fixed fraction of NPP allocated to stem and branches. wsg is the wood specific gravity ($g.cm^{-3}$, see 1). TROLL assume large trees less efficient to convert NPP as growth by using a size-related growth decline with function $Senesc$ after a specific diameter at brest height threshold dbh_{thresh}:

$$Senesc(dbh) = max(0; 3 - 2 * \frac{dbh}{dbh_{thresh}}) \tag{15}$$

Finally, TROLL can compute carbon allocation to canopy with canopy NPP fraction denoted f_{canopy} and decomposed into leaf, twig and fruit production. Carbon allocation to leaf results in a new young leaf pool, whereas other leaf pools are updated as follow:

$$\begin{aligned} \Delta LA_{young} &= \tfrac{2*f_{leaves}*NPP_{ind}}{LMA} - \tfrac{LA_{young}}{\tau_{young}} \\ \Delta LA_{mature} &= \tfrac{LA_{young}}{\tau_{young}} - \tfrac{LA_{mature}}{\tau_{mature}} \\ \Delta LA_{old} &= \tfrac{LA_{mature}}{\tau_{mature}} - \tfrac{LA_{old}}{\tau_{old}} \end{aligned} \tag{16}$$

τ_{young}, τ_{mature}, and τ_{old} are species residence times in each leaf pools ($years$). The sum of residency time thus defined the leaf lifespan $LL = \tau_{young} + \tau_{mature} + \tau_{old}$ ($years$). τ_{young} is set to one month and τ_{mature} is set to a third of leaf lifespan LL. Previous implementation of TROLL model used Reich et al. [1991] allometry to infer leaf lifespan LL from species leaf mass per area LMA [Maréchaux and Chave]. But the use of the allometrie from Reich et al. [1991] with current implementation of the TROLL model resulted in an underestimation of leaf lifespan for low LMA species. Consequently in the following paragraph we suggest a new allometry. Belowground carbon allocation is not simulated inside TROLL.

1.6 Leaf lifespan

The underestimation of leaf lifespan for low LMA species with the allometry from Reich et al. [1991] resulted in indivduals unealistic early death from carbon starvation. We gathered data from TRY[Kattge et al., 2011], DRYAD [Chave et al., 2009] and GLOPNET [Wright et al., 2004] datasets. We used an out of the bag method applied on a random forest to select variables with highest importance to explain leaf lifespan. We thus selected leaf mass per are LMA, leaf nitrogen content N and wood specific gravity wsg. We then used a bayesian approach to test different models with growing level of complexity. The model with the best tradeoff between complexity (number of parameters), convergence, likelihood, and prediction quality (root mean square error of prediction RMSEP) was kept. We selected following model with a maximum likelihood of 13.6 and a RMSEP of 12 months:

$$LL_d \sim \updownarrow\wr\}\mathcal{N}(\beta_{1_d} * LMA - \beta_{2_d} * N * \beta_3 * wsg, \sigma) \tag{17}$$

Leaf lifespan LL follows a lognormal law with location infered from leaf lifespan LMA, nitrogen content N and wood specific gravity wsg and a scale σ. Each β_{i_d} is following a normal law located on β_i with a scale of σ_i. All β_i, σ_i, and σ are assumed without presemption following a gamma law. d represents the dataset random effects and encompass environmental and protocol variations. The sampling of model (17) resulted in the following allometry:

$$LL = e^{0.017*LMA - 0.103*Nmass + 1.94*wsg} \tag{18}$$

1.7 Tree growth

Once the increment of stem volume ΔV calculated with equation (14), TROLL convert it into an increment of tree diameter at breast height denoted Δdbh. TROLL infer tree height from dbh using a Michaelis-Menten equation:

$$h = h_{lim} * \frac{dbh}{dbh + a_h} \tag{19}$$

On the other hand, we have the trunk volume $V = C * \pi * (\frac{dbh}{2})^2 * h$, thus:

$$\begin{aligned} \Delta V = C * \tfrac{1}{2} * \pi * h * dbh * \Delta dbh + C * \pi * (\tfrac{dbh}{2})^2 * h \\ \Delta V = V * \tfrac{\Delta dbh}{dbh} * (3 - \tfrac{dbh}{dbh+ah}) \end{aligned} \tag{20}$$

Next, TROLL used the new trunk dimension (dbh and h) to update tree crown geometry using allometric equations [Chave et al., 2005]:

$$\begin{aligned} CR = 0.80 + 10.47 * dbh - 3.33 * dbh^2 \\ CD = -0.48 + 0.26 * h \; ; \; CD = 0.13 + 0.17 * h \; (h < 5 \; m) \end{aligned} \tag{21}$$

Finally, TROLL computes the mean leaf density within the crown (LD in $m^2.m^{-3}$) assuming a uniform distribution:

$$LD = \frac{LA_{young} + LA_{mature} + LA_{old}}{\pi * CR^2 * CD} \tag{22}$$

1.8 Mortality

Mortality is partitioned in three factors inside TROLL: background death d_b, treefall death d_t and negative density dependent death d_{NDD}. Because density dependent death d_{NDD} is still in development inside TROLL we did not used it, so we will not detail is computation.

Chave et al. [2009] advocated for a wood economics spectrum opposing fast growing light wood species species with high risk of mortality to slow growing dense wood species with reduced risk of mortality. Hence, background mortality is derived from wood specific gravity wsg inside TROLL:

$$d_b = m * (1 - \frac{wsg}{wsg_{lim}}) + d_n \tag{23}$$

m ($events.year^{-1}$) is the reference background death rate for lighter wood species (pioneers). d_n represents death by carbohydrates shortage. If the number of consecutive day with $NPP_{ind} < 0$ (12) is superior to tree leaf lifespan d_n is set to 1 and remains null in other cases.

Mortality by treefall inside TROLL depends on a specifric stochastic threshold θ:

$$\theta = h_{max} * (1 - v_T * |\zeta|) \tag{24}$$

h_{max} is the maximal tree height. v_T is the variance term set to 0.3. $|\zeta|$ is the absolute value of a random centered and scaled Gaussian. If the tree hieght h is superior to θ then the tree may fall with a probability $1 - \theta/h$ [Chave, 1999]. The treefall direction is random (drawn from a uniform law ($\mathcal{U}[0, 2\pi]$). All tree in the trajectory of the falling tree will be hurted through a variable denoted $hurt$, incremented by fallen tree height h. If a tree height is inferior than its $hurt$ values then it may die with a probability $1 - \frac{1}{2}\frac{h}{hurt}$. $hurt$ variable is reset to null at each timestep ($month$).

1.9 Recruitment

Once the tree became fertile they will start to disperse seeds. TROLL consider tree as fertile after a specific height threshold h_{mature} [Wright et al., 2005]:

$$h_{mature} = -11.47 + 0.90 * h_{max} \tag{25}$$

But TROLL is not considering seed directly through a seedbank, instead seed might be interpreted as a seedling recruitment opportunity. The number of reproduction opportunities per mature tree is denoted n_s and set to 10 for all species. This assumption originates from a trade-off between seed number and seed size resulting in equivalent survival and recruitment probability. All n_s events are dispersed with a distance randomly drawn from a Gaussian distribution. Additionally, TROLL model consider external seedrain through n_{ext} events of seed immigration:

$$n_{ext} = N_{tot} * f_{reg} * n_{ha} \tag{26}$$

N_{tot} is the external seedrain per hectare (number of reproduction opportunities). f_{reg} is the species regional frequency. n_{ha} is the simulated plot size in ha.

Finally, a bank of seedlings to be recruited is defined for each pixel. If the ground-level light reaches a species light compensation point LCP the species will be recruited:

$$LCP = \frac{R_{leaf}}{\phi} \tag{27}$$

R_{leaf} is the leaf respiration for maintenance (see (10)). ϕ is the quantum yield ($\mu molC.\mu mol\ photon$) set to 0.06. If several species reach their LCP, one is picked at random. Seedlings are recruited with following intial geometry:

$$\begin{gathered} dbh = \frac{a_h}{h_{max}-1} \\ h = 1\ m \\ CR = 0.5\ m \\ CD = 0.3\ m \\ LD = 0.8\ m^2.^{-3} \end{gathered} \tag{28}$$

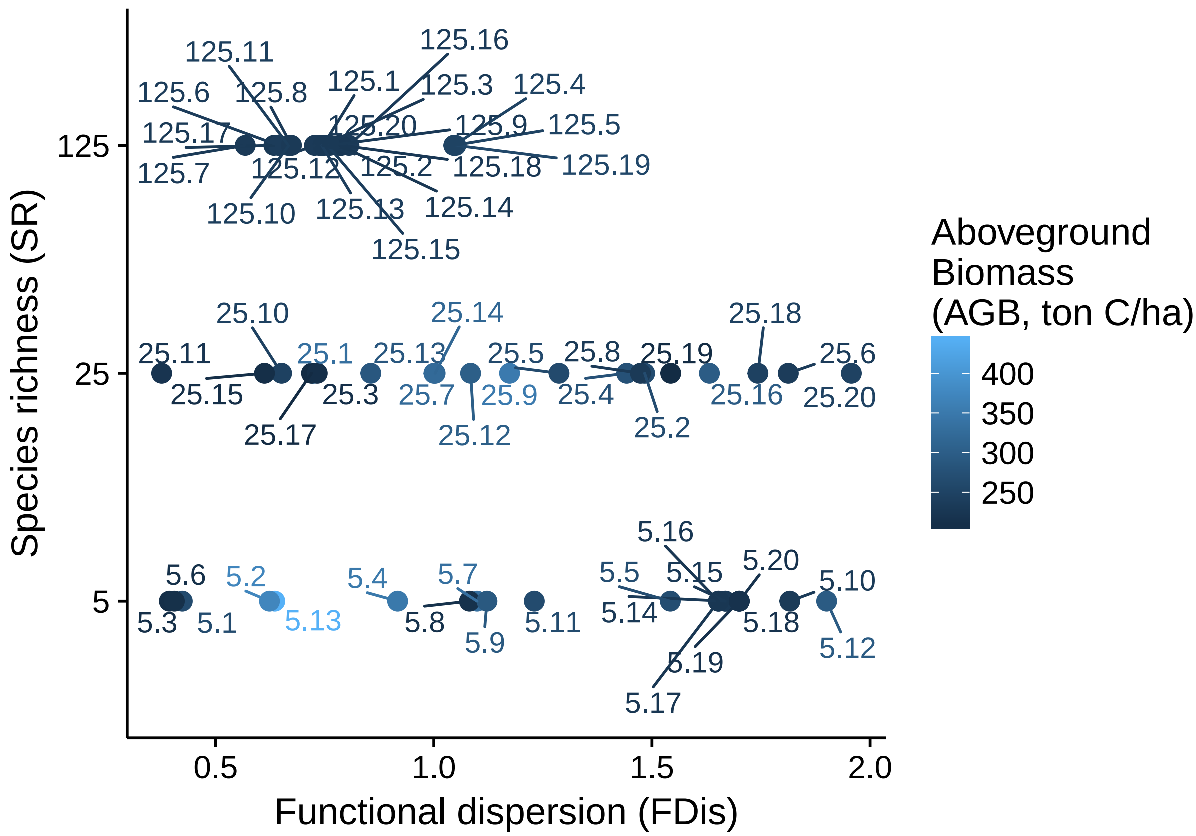

Figure 2: Experimental design before disturbance. Communities are implemented along a gradient of species richness (SR) and functional dispersion (FDis) resulting in a broad range of aboveground biomass (AGB). FDis was caluclated based on 4 functional traits (leaf mass per area, wood specific gravity, maximum diameter, maximum height).

2 Sensitivity analysis

2.1 Functional traits

2.2 Seed rain

3 Disturbance

3.1 Model description

3.2 Design of experiment

3.3 Outputs anlaysis ?

3.3.1 Resistance and resilience metrics

3.3.2 Biodiversity partitioning

4 Selective logging

4.1 Model description

4.1.1 Designation

4.1.2 Selection

4.1.3 Rotten trees

4.1.4 Felling

4.1.5 Tracks

4.1.6 Gap damages

4.2 Design of experiment

4.3 Outputs analysis ?

4.3.1 Resistance and resilience metrics

4.3.2 Biodiversity partitioning

5 Results

5.1 Sensitivity

5.2 Disturbance

5.3 Sylviculture

6 Discussion

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