Finite mixture of size projection matrix models for highly diverse rainforests in a variable environment

F. MORTIER, D.-Y. OUÉDRAOGO & N. PICARD

with S. Gourlet-Fleury and V. Freycon

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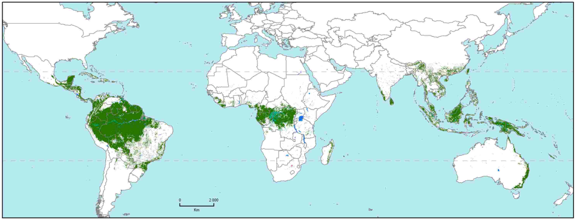
Outline

1. Ecological Context
2. Forest dynamics models
   - The Usher model
   - Environmental variability
   - High biodiversity
3. The M'Baïki experimental site: unique data in Central Africa
   - Mixture models outputs
   - Dynamics species groups
4. Conclusions

outline

Tropical forests I



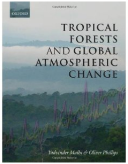
Generality and Specificity

1. 6% of the worlds surface area
2. 50% of all living organisms on Earth
3. more than 1.5b people depending on the forest

Tropical forests II

Multiple uses and actors

- local: resource (wood, NWFP)
- national: foreign exchange (timber)
- global scale: CO_2 concentration regulation through carbon sequestration
  (Millennium Ecosystem Assessment, 2005)



Tropical forests III

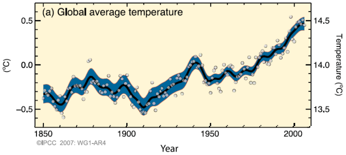
Conservation and management

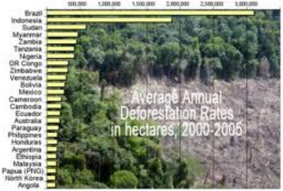
increasing atmospheric CO_2 concentration:

- increasing global temperatures
- climate change Solomon et al. (2007)

increasing land uses

- Agricultural, fuel
- ... FAO (2010)





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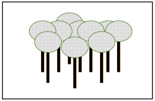
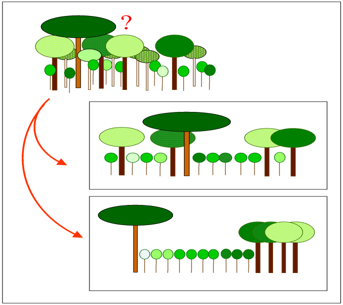
Different type of models I

Stand models: all trees are equivalents

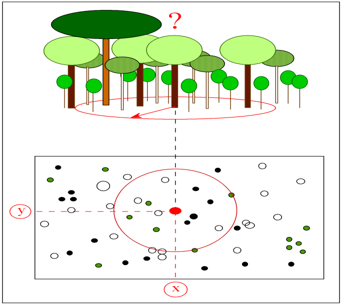


(V, G, N) = f(age, species, site, density)

Individual tree models



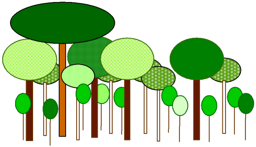
distance independant

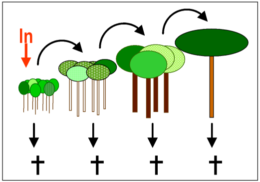


distance dependent

Different type of models II

Size projection matrix





Discrete distributions: tree equivalents inside class

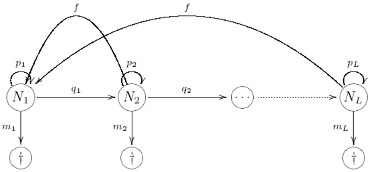
The Usher matrix I

The Usher model (Usher, 1966, 1969)

- matrix population model for size-structured populations
- describes the evolution of the population by a vector $N(t)$
- $N(t)$ vector of the number of individuals in L ordered state class at discret time t.
- This matrix population model relies on the four following hypotheses:
  - Hypothesis of independence: evolution of individuals is independent.
  - Markov hypothesis: evolution of an individual between two time steps t and $t+1$ only depends on its state at t.
  - Usher hypothesis: during each time step, an individual can stay in the same class, move up a class, or die; each individual may give birth to a number of offspring.
  - Hypothesis of stationarity: evolution of individuals between two time steps is independent of time.

The Usher matrix II

graphical representation of the Usher model



$$\mathbb{E}(\mathbf{N}_{t+1}|\mathbf{N}_t) = \mathbf{PS}\mathbb{E}\mathbf{N}_t + \mathbf{R}$$

$$\mathbf{P} = \begin{pmatrix} 1-q_2^\bullet & & 0 & 0 \\ q_2^\bullet & \ddots & & \vdots \\ & \ddots & 1-q_l^\bullet & 0 \\ 0 & & q_l^\bullet & 1 \end{pmatrix} \quad \mathbf{S} = \begin{pmatrix} 1-m_1 & & 0 \\ & \ddots & \\ 0 & & 1-m_l \end{pmatrix} \quad \mathbf{R} = \begin{pmatrix} r \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

- $q_{i+1}^\bullet$ conditional upgrowth rate
- m_i probability to die
- r number of recruited trees

Environment and Usher model I

Temporal changes of the diameter distribution of a tree population

$$\mathbf{N}(t+1) = \mathbf{P}(X_t)\mathbf{S}(X_t)\mathbf{N}(t) + \mathbf{R}(X_t)$$

$$\mathbf{P}(X_t) = \begin{pmatrix} 1 - q_2^{\bullet}(X_t) & & 0 & 0 \\ q_2^{\bullet}(X_t) & \ddots & & \vdots \\ & \ddots & 1 - q_l^{\bullet}(X_t) & 0 \\ 0 & & q_l^{\bullet}(X_t) & 1 \end{pmatrix}$$

$$\mathbf{S}(X_t) = \begin{pmatrix} 1 - m_1(X_t) & & 0 \\ & \ddots & \\ 0 & & 1 - m_l(X_t) \end{pmatrix}$$

$$\mathbf{R}(X_t) = \begin{pmatrix} r(X_t) \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

- $q_{i+1}^{\bullet}(X_t)$ conditional upgrowth rate
- $m_i(X_t)$ probability to die
- $r(X_t)$ number of recruited trees

Regression estimator

(Rogers-Bennett and Rogers, 2006; Picard et al., 2008; Zetlaoui, 2006)

$$q_{i+1}^{\bullet}(X_t) = \frac{\Delta D_i(X_t)}{d_i}$$

$\Delta D_i(X_t)$ "typical" dbh growth rate
d_i width of diameter class i

Environment and Usher model II

Modeling growth, mortality and recruitment

- Let ΔD be the Diameter increment,

$$\Delta D_{sti} = \mathbf{X}_{ti}^{D}\beta_s + \varepsilon_s$$

  where β_s is the vector of unknown parameters, $\mathbf{X}^D = (\mathbf{X}_{ti}^{D})_{t,i}$ the kown incidence

- Let N_{st} be the number of recruits:

$$\begin{aligned} N_{st} &\sim \mathcal{P}\left(r_{st}\right) \\ \log(r_{st}) &= \mathbf{X}_{t}^{N}\gamma_s \end{aligned}$$

- Let M_{sti} be the mortality

$$\begin{aligned} M_{sti} &\sim \mathcal{B}er\left(m_{sti}\right) \\ \mathrm{logit}(m_{sti}) &= \mathbf{X}_{ti}^{M}\alpha_s \end{aligned}$$

Main concern with tropical forests: high specific richness

+ 300 species/ha

- many species with very few individuals
- high intra specific variability of dynamic variables
- ➥ one species one model: poor fit of models

☞ **building groups of species according to their dynamics**

Mixture of growth, mortality and recruitment processes

Mixture models

- For growth and mortality processes, let assumed:

$$\ell_n(\psi|\mathbf{Y}) = \sum_{s=1}^{S}\sum_{t=1}^{T}\sum_{i=1}^{n_{st}} \log\left[\sum_{k=1}^{K} \pi_k\, f(Y_{sti}|\mathbf{X}, \psi_k)\right]$$

  with f Gaussian density and $Y_{sti} = \Delta D_{sti}$ or the masse function associated to the Bernoulli distribution and $Y_{sti} = M_{sti}$.

- For the recruitment process, let assumed

$$\ell_n(\psi|\mathbf{Y}) = \sum_{s=1}^{S}\sum_{t=1}^{T} \log\left[\sum_{k=1}^{K} \pi_k\, f(N_{st}|\mathbf{X}, \psi_k)\right]$$

  where f is the masse function associated to the Poisson distribution.

Mixture Models and variable selection

Co-variates can differ from a group to another
stepwise selection can be computational intensive
- LASSO (**L**east **A**bsolute **S**hrinkage & **S**election **O**perator)

Selection (Khalili and Chen, 2007)

The estimator $\hat{\psi}$ of the model's parameters ψ corresponds to the maximum of a penalized version of the log-likelihood:

$$\hat{\psi} = \arg\max_{\psi} \left\{ \ell_n(\psi|\mathbf{Y}) - p_n(\psi) \right\}$$

where p_n is a penalty. We used the lasso penalization to perform variable selection in each component:

$$p_n(\psi) = \sum_{k=1}^{K} \pi_k \left(\sum_{j=1}^{p+1} \gamma_{nk} \sqrt{n} |\beta_{kj}| \right)$$

where β_{kj} is the jth element of $\boldsymbol{\beta}_k$ and γ_{nk} is a tuning parameter.

EM algorithm with LASSO

- **Estimate** $\hat{c}_{sik} = P\{$ tree of species s $\in k|$ data $(\mathcal{X})$, parameters$(\psi)\}$
  to start we choose randomly $\hat{c}_{sik}$

- **Maximise** the penalized log likelihood (Khalili and Chen, 2007)

$$\log L^*(\psi|\mathcal{X}) = \log L(\psi|\mathcal{X}) - p(\psi|\mathcal{X})$$

with $p(\psi|\mathcal{X})$ penalty term

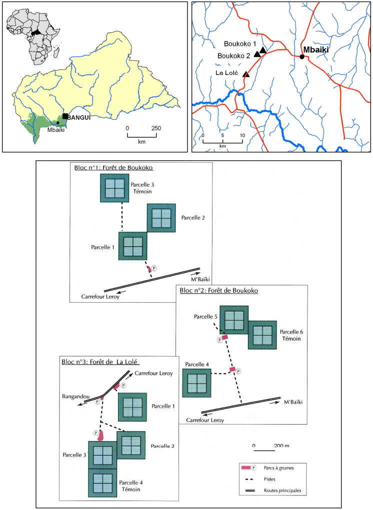
covariates selection by shrinkage : coefficient $\beta_{kp} <$ threshold $= 0$

$\rightarrow \hat{\psi}_k \rightarrow \hat{\pi}_k$

- **Classification** of **species** (not individuals) into groups
  $\rightarrow$ tree i of species s belongs to groups k for $\max(\hat{c}_{sik})$

outline

The M’Baïki experimental site (Central African Republic)



N. Fauvet CIRAD - UR 105
Septembre 2011

- Permanent sample plots (annual)
- 1982
- 40 ha
- semi-deciduous forest
- 239 species / morphospecies
- silvicultural treatments (undisturbed, logging, logging + thinning)
  $\rightarrow$ disturbance gradient

The M'Baïki experimental site (2)

Every year since 1982 (except in 1997, 1999, 2001), all trees $\geq$ 10 cm diameter at breast height (dbh)

- individually marked
- measured for dbh
- mapped
- identified

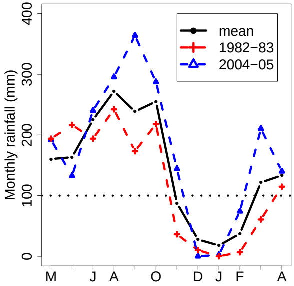
+ inventory of dead trees and newly recruited trees with dbh $\geq$ 10 cm
annual diameter growth, mortality, and recruitment

Data

- growth, mortality more than 200,000 observations
- recruitment more than 100,000 observations
- more than 200 species

Covariates (1) : Drought indices

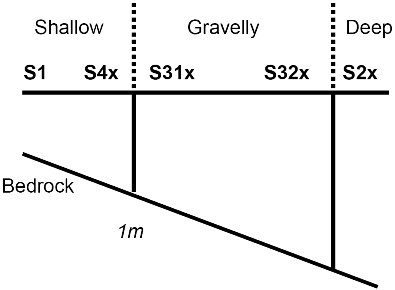
- Length of *the dry season* (**LDS**, nb months)
- Average rainfall during *the dry season* (**RDS**, mm)



Positive correlation

- Average annual soil water content (**MSW**, mm)
  simple water balanced model
  5 soil depth categories

$$SW_{t+1} = SW_t + P_t - E_t$$



Covariates (2): Light availability indices

Indirectly measured

- stand basal area (**BAst**, $m^2\ ha^{-1}$)
- stand density (**Dst**, number of stems ha^{-1})

Positive correlation

Covariates (3): Tree development stage

- tree diameter (**Di**, cm)

Mixture models outputs I

Separate species groups for growth, mortality, recruitment

- Species groups **characteristics**

- Species groups **response to drought**

Coefficients

$$\begin{aligned} \Delta D_{kti} &= \mathbf{X}_{ti}^{D} \beta_k + \varepsilon_k \\ \mathrm{logit}(m_{kti}) &= \mathbf{X}_{ti}^{M} \alpha_k \\ \log(r_{kt}) &= \mathbf{X}_{t}^{N} \gamma_k \end{aligned}$$

Covariates

Length of the dry season (**LDS**)

Average rainfall during the dry season (**RDS**)

Average annual soil water content (**MSW**)

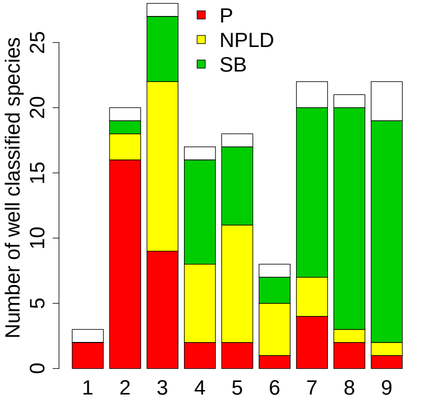
Mixture models outputs II

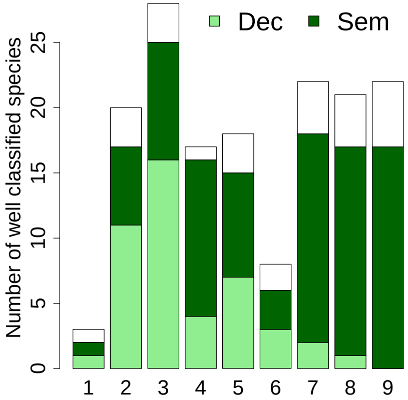
Classification results

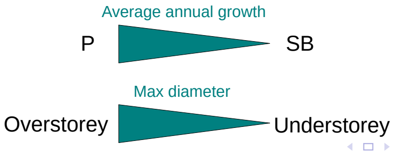
- 9 **growth species groups**
- 3 **mortality species groups**
- 5 **recruitment species groups**

54 non-empty matrix population groups

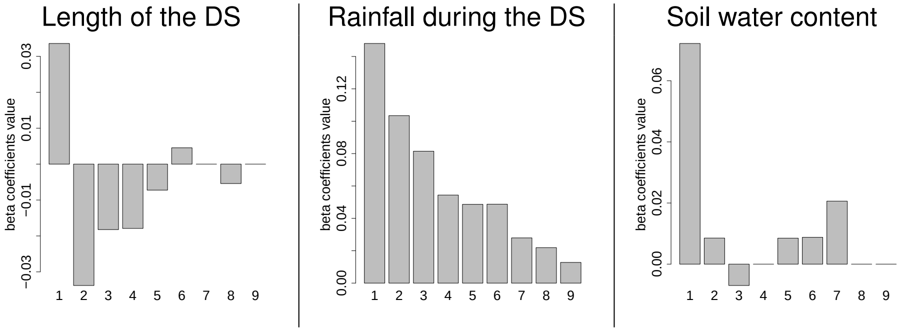
9 growth species groups

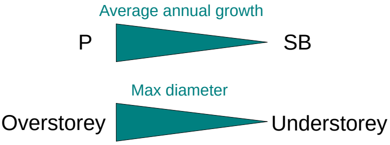






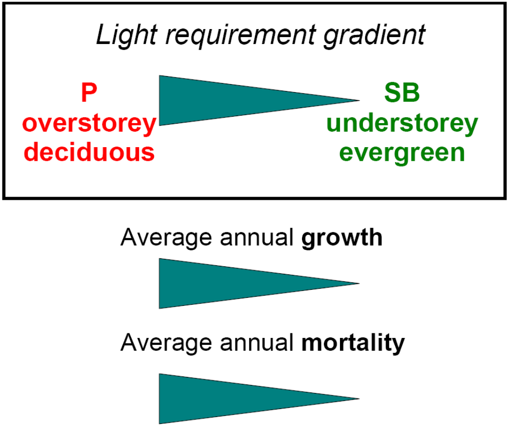
Growth species groups response to drought





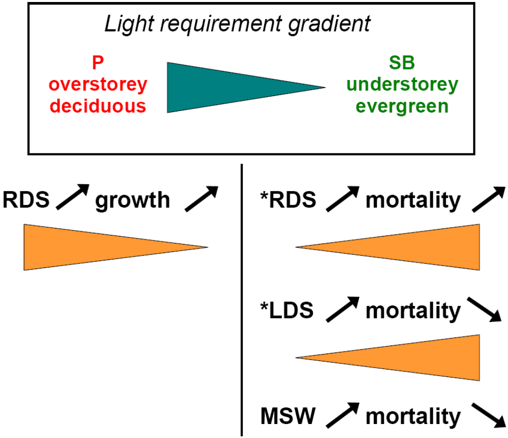
Comments I

Drought indices: capture several effects



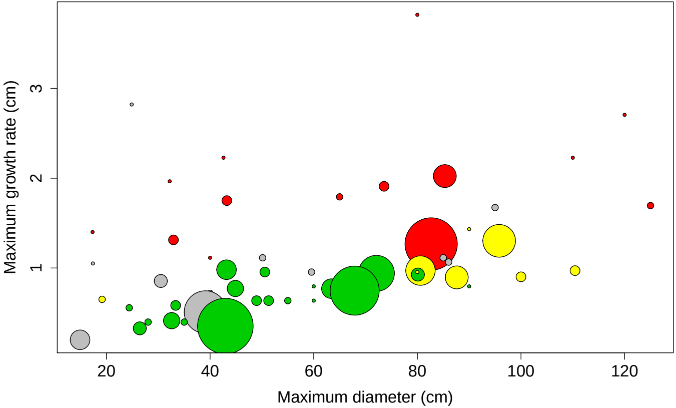
Comments II

Drought indices: capture several effects

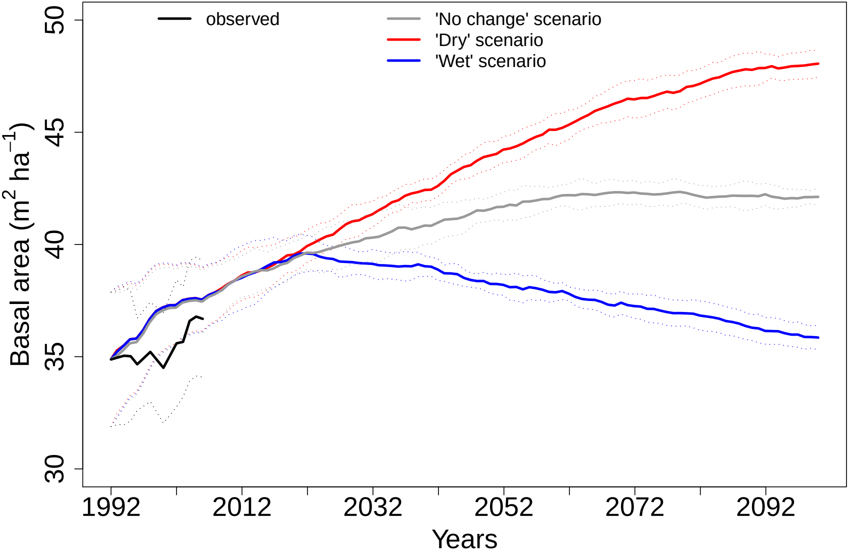


- **LDS/RDS**
  indirect measure of light availability for the understorey
  (Lingenfelder and Newbery, 2009; Newbery et al., 2011)
- **MSW**
  measure of water stress

Dynamics species groups



Dynamics response to drought: basal area



outline

Conclusions I

- **A species classification without *a priori***

  based on (growth + mortality + recruitment) response to

  light, drought (+ size)

$\Rightarrow$ leads to ecological groups of tree species

- M'Baïki **undisturbed** forest seems to be resilient to drought

+ pioneer trees more sensitive to drought
Disturbance increased the proportion of pioneer trees

Ouédraogo et al. (2011)

$\hookrightarrow$ **combination of logging + drought disturbance?**

Conclusions II

- **A powerful method for species classification**
  - species classification
  - estimation of the response to light, drought, and size
  - covariates selection

simultaneously!

- but Estimation and selection realized process by process

➳How to combine estimation, classification ans selection for the three processes simultaneously?

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