Grouping species to model forest dynamics: a case study of a forest in the Central African Republic

Gaëlle Lahoreau
Nicolas Picard
Sylvie Gourlet-Fleury
CIRAD-Forêt
Programme forêts naturelles
TA 10/D
Campus international de Baillarguet
34398 Montpellier Cedex 05
France

The authors propose to group species on the basis of ecological and commercial criteria, and to validate them through the construction of a forest dynamics model. This strategy is applied to data recorded in a stand at M'Baïki station (Central African Republic).

Access to a fruiting experiment set up with the main commercial species close to Berbérati.
Accès à un dispositif d'étude de la fructification des principales espèces commerciales installé près de Berbérati.
Photo L. Durrieu de Madron.

RÉSUMÉ

CONSTITUTION DE GROUPES D'ESPÈCES POUR LA MODÉLISATION DE LA DYNAMIQUE FORESTIÈRE : UN EXEMPLE EN RÉPUBLIQUE CENTRAFRICAINE

Les modélisateurs ont pour habitude de simplifier la diversité spécifique des forêts denses tropicales humides en regroupant les espèces. Les groupes ainsi constitués peuvent être des groupes écologiques possédant une signification biologique, ou bien, de manière plus pratique, des groupes commerciaux présentant un intérêt économique. Sur le dispositif de M'Baïki, en République centrafricaine, sept groupes d'espèces résultant d'un croisement entre cinq groupes écologiques et cinq catégories commerciales ont été définis. Les groupes écologiques ont été constitués par la classification automatique sur la base des variables accroissement diamétrique, taux de mortalité et taux de recrutement évaluées espèce par espèce. Un modèle matriciel de dynamique forestière a ensuite été construit afin d'évaluer la pertinence des sept groupes finalement retenus. De fait, l'état stationnaire du peuplement constitué de ces groupes est correctement prédit par le modèle, excepté pour un groupe qui se révèle rassembler des espèces dont les tempéraments sont trop contrastés.

Mots-clés : groupe d'espèces, groupe écologique, catégorie commerciale, modèle matriciel, République centrafricaine.

ABSTRACT

GROUPING SPECIES TO MODEL FOREST DYNAMICS: A CASE STUDY OF A FOREST IN THE CENTRAL AFRICAN REPUBLIC

Modellers usually define groups of species to deal with tree species diversity in tropical rainforests. They may be ecological groups with a biological interest or commercial categories with a practical interest. At M'Baïki station in the Central African Republic, seven groups of species are defined at the intersect of five ecological groups and five commercial categories. The ecological groups were obtained by a cluster analysis based on species diameter growth rates, their mortality rates and recruitment rates. A forest dynamics matrix model was then built to assess the relevance of the groups. The stationary state of the stand is well predicted by the model except for one group that appears to pool species with contrasted ecological behaviours.

Keywords: species group, ecological group, commercial category, matrix model, Central African Republic.

RESUMEN

CONSTITUCIÓN DE GRUPOS DE ESPECIES PARA LA MODELIZACIÓN DE LA DINÁMICA FORESTAL: UN EJEMPLO EN LA REPÚBLICA CENTROAFRICANA

Los modelizadores suelen simplificar la diversidad específica de los bosques densos tropicales húmedos agrupando las especies. Los grupos así formados pueden ser grupos que tengan un significado biológico o bien, de manera más práctica, grupos comerciales con un interés económico. En el diseño de M'Baïke en la República Centroafricana, se definieron siete grupos de especies resultantes de un cruce entre cinco grupos ecológicos y cinco categorías comerciales. Los grupos ecológicos se constituyeron mediante la clasificación automática basada en las variables de crecimiento diamétrico, tasa de mortalidad y tasa de reclutamiento evaluadas especie a especie. Seguidamente, se construyó un modelo matricial de dinámica forestal para evaluar la pertinencia de los siete grupos finalmente elegidos. De hecho, el estado estacionario del rodal constituido por estos grupos está correctamente predicho por el modelo, exceptuando un grupo que agrupa especies con naturalezas demasiados diferentes.

Palabras clave: grupo de especies, grupo ecológico, categoría comercial, modelo matricial, República Centroafricana.

Species group definitions

When focusing on timber, sustainable management of tropical forests is based on an assumed balance between logging and tree natural mortality on one hand, and recruitment and growth on the other. It is essential to be able to predict the future state of the stand before assessing whether management operations respect this balance. Forest dynamics models are tools that facilitate such forecasts (LOFFEIER, FAVRICHON, 1996). In tropical forests, the task of the modeller is complicated by the great number of tree species, thus contributing to the variability of measurements, which in turn reduces prediction reliability.

Some modellers actually try to parameterise every single species (e.g. SHUGART et al., 1980), but defining groups of species is the solution usually adopted to deal with species diversity in tropical forest dynamics modelling (FAVRICHON, 1994). Apart from a few marginal methods (e.g. groups based on plant functional attributes, see VANCLAY et al., 1997), there are two main approaches used to define species groups. The most natural one involves building groups on the basis of some ecological characteristics of the species, in relation with functions required in the model (FAVRICHON, 1994; FINEGAN et al., 1999; KÖHLER et al., 2000). For instance, species may be partitioned according to their diameter growth rate if the model strongly relies on diameter growth rates (VANCLAY, 1991).

This approach efficiently accounts for specific variability, but it may not be practical for management purposes. Imagine, for instance, that a commercial category of trees of particular interest for the forest manager encompasses several ecological groups. Then, provided the model is built on the basis of ecological groups, it may turn out to be difficult to simulate and monitor variations in the commercial category. Some authors have thus deliberately favoured groups based on commercial or technological criteria (BOSCOLO, VINCENT, 1998; VANCLAY, 1989; WAN RAZALI, 1986).

The commercial categories may overlap with the ecological groups. For instance, in dipterocarp forests, dipterocarps represent both a commercial category and a group of species with relative ecological homogeneity (BOSCOLO, VINCENT, 1998; FAVRICHON, YOUNG CHEOL, 1998). However, the modeller generally has a difficult choice to make: either use ecological groups with a biological interest, or favour commercial groups with a practical interest.

In this study, we propose to build species groups using both ecological and commercial criteria, and to validate them through the construction of a forest dynamics model. The groups are obtained at the intersect of two sets of groups, i.e. some ecological groups and some commercial categories provided by Dr. Marco Boscolo from the Harvard Institute for International Development (Harvard University, Cambridge, Mass., USA). The model that we shall build is a density-dependent matrix model. Matrix models are indeed valuable tools for forest management, since they are both robust and may be built from common inventory data (BOSCOLO, VINCENT, 1998; FAVRICHON, 1996). The overall approach is tested on the M'Baïki stand in the Central African Republic, where 40 ha of logged and undisturbed forest have been inventoried for 18 years (BEDEL et al., 1998).

Iroko *(Milicia excelsa)* log abandoned at a timber site because it split during felling.
Bille d'iroko (Milicia excelsa) *abandonnée sur le lieu de coupe à cause de son éclatement lors de l'abattage.*
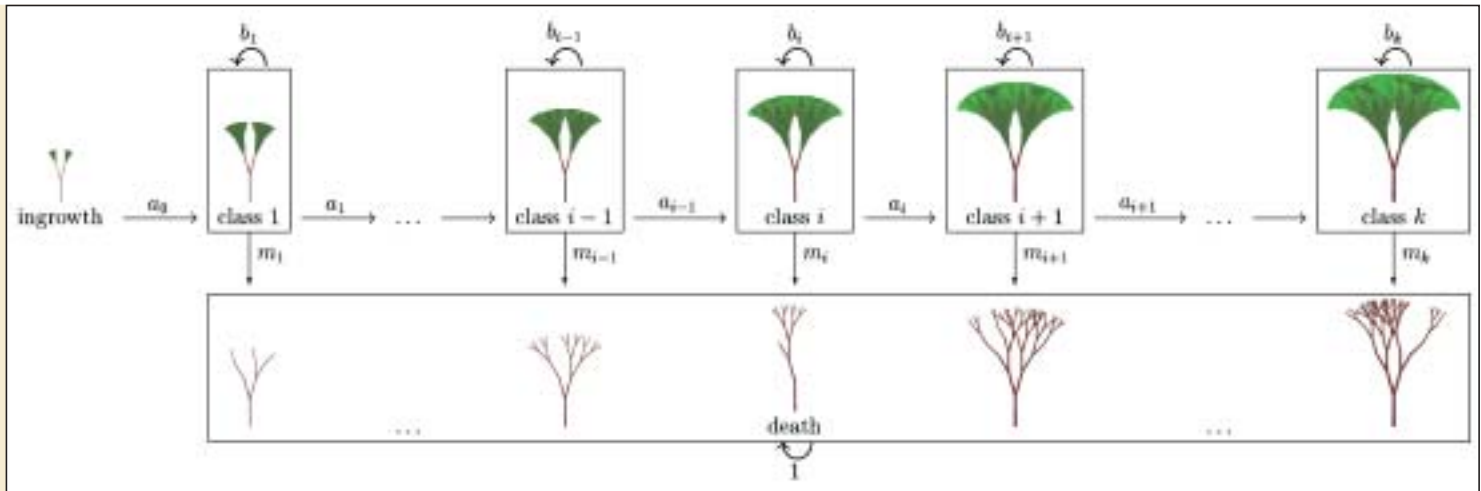Photo L. Durrieu de Madron.

Figure 1.

The Markov chain that corresponds to the growth of a tree in the matrix model: m_i, a_i and b_i are probabilities (respectively to die, to grow to the next diameter class, and to stay in the same class) that sum up to one.

Chaîne de Markov correspondant à la croissance d'un arbre dans le modèle matriciel : m_i, a_i et b_i sont des probabilités (respectivement de mourir, de passer dans la classe de diamètre suivante et de rester dans la même classe de diamètre) dont la somme vaut 1.

Materials and methods

M'Baïki station

M'Baïki station was settled in 1981 in Lobaye province, 120 km southwest of Bangui (3°50' N, 18° E) in the Central African Republic (BEDEL *et al.*, 1998). It consists of ten 4 ha square permanent plots surrounded by a buffer zone 50 m wide. Every year since 1982, all trees greater than 10 cm DBH (diameter at breast height) have been inventoried and their girth measured. Newly recruited trees are also listed, as well as dead trees. The database built from field measurements thus encompasses more than 34 800 trees (NARBONI, 2000).

In 1984-85, seven out of the ten plots were logged with a mean intensity of 4 trees/ha (50 m³/ha). The three remaining plots were left as control. In 1986, four of the seven logged plots underwent an additional systematic thinning with 20 trees/ha (51 m³/ha) removed on average. In 1991 a botanical inventory of all individuals was conducted, identifying 260 tree species. Trees that died before 1991 were therefore not botanically inventoried.

Species grouping

Four species groups have already been defined at M'Baïki:

▪ Commercial categories that were defined prior to settlement of the M'Baïki plots (BEDEL *et al.,* 1998): A. Commercial species (15 species); B. Potentially commercial species (25 species); C. Non-commercial species.

▪ Boscolo's commercial categories, based on economic-policy criteria (five categories, denoted I to V).

▪ Ecological groups defined by FAVRICHON (1991) for 18 species only.

▪ Ecological groups defined by MOREL & TANDEAU DE MARSAC (1995), based on mean diameter, mortality and recruitment rates, and diameter growth rates of each species. One hundred species are thus partitioned into nine groups.

We defined our species groups by intersecting Boscolo's categories with ecological groups obtained by cluster analysis. A preliminary correlation analysis enabled us to select five variables to characterize the species: the average diameter growth rate on logged plots; the average diameter growth rate on logged and thinned plots; the average diameter on control plots; the mortality rate on control plots; and the recruitment rate on control plots. All variables were computed on the basis of the 1991-93 period to ensure the shortest time from the 1984-86 treatments while benefiting from the 1991 botanical inventory. We tested several clustering methods and finally retained the *k*-means algorithm (procedure FASTCLUS of SAS, SAS Institute Inc., or function KMEANS of S-PLUS, MathSoft Inc.) as the most relevant.

The species groups were built using species that had no missing data, and that were represented by at least 15 individuals in 1991 (however, sipo, *Entandrophragma utile* Spra., was included due to its economic importance, even though only seven boles remained in 1991). Three further species were eliminated because they had outlier characteristics, i.e. parasolier (*Musanga cecropioides* R. Br.), bassala (*Macaranga paxii* Prain) and essessang (*Ricinodendron heudelotii* Pierre). The cluster analysis was thus restricted to 72 species out of the 260 listed in the database. The 188 remaining species were *a posteriori* assigned to the closest species group in the following way: let d_{ij} be the Euclidean distance in the five-dimension space of species characteristics between species *i* and the centroid of species group *j*. Species *i* is assigned to the group for which d_{ij} is minimum.

Matrix model

Matrix models in forestry date back to the seminal work of USHER (1966). Their principle is presented, for instance, in FAVRICHON (1996). Individual trees are broken down by species group and diameter class. Time is discrete and varies by a quantity Δt. According to the Markov chain interpretation illustrated in Figure 1, a tree of species group s in diameter class i at time t has three possible futures at time $t + \Delta t$:

▪ either it dies, with probability m_{sit}

▪ or it stays alive and grows to the next diameter class, with probability a_{sit}

▪ or it stays alive and remains in the same diameter class, with probability $b_{sit} = 1 - m_{sit} - a_{sit}$.

At the stand level, the diametric structure of the forest stand is represented by a vector $\mathbf{N}_t = [n_{sit}]$, where n_{sit} is the number of trees per hectare of species group s in diameter class i at time t. The individual trajectories can be summarised by a matrix relationship:

$$\mathbf{N}_{t+\Delta t} = \mathbf{A}_t \mathbf{N}_t + \mathbf{R}_t$$

where the transition matrix $\mathbf{A}_t$ is a block matrix, each block being the transition matrix for a given species group:

$$\mathbf{A}_t = \begin{bmatrix} \mathbf{A}_{1t} & & \mathbf{o} \\ & \ddots & \\ \mathbf{o} & & \mathbf{A}_{St} \end{bmatrix} \quad \text{and} \quad \mathbf{A}_{st} = \begin{bmatrix} b_{s1t} & & & \mathbf{o} \\ a_{s1t} & b_{s2t} & & \\ & \ddots & \ddots & \\ \mathbf{o} & & a_{s,k-1,t} & b_{skt} \end{bmatrix}$$

and $\mathbf{R}_t$ is a vector that gives the number of recruited trees in the first diameter class of each species group:

$$\mathbf{R}_t = \begin{bmatrix} \mathbf{R}_{1t} & \dots & \mathbf{R}_{St} \end{bmatrix}' \quad \text{and} \quad \mathbf{R}_{st} = \begin{bmatrix} r_{st} & \mathbf{o} & \dots & \mathbf{o} \end{bmatrix}'$$

In these equations, S stands for the number of species groups and k for the number of diameter classes. The matrix relationship can alternatively be written as (FAVRICHON, 1996):

$$\mathbf{N}_{t+\Delta t} = \mathbf{P}_t (\mathbf{I} - \mathbf{M}_t) \mathbf{N}_t + \mathbf{R}_t$$

where $\mathbf{P}_t$ is a matrix analogous to $\mathbf{A}_t$ with a_{sit} being replaced by $a^{\bullet}_{sit} = a_{sit}/(1 - m_{sit})$, and $b_{sit} = 1 - m_{sit} - a_{sit}$ being replaced by $b^{\bullet}_{sit} = b_{sit}/(1 - m_{sit}) = 1 - a^{\bullet}_{sit}$, $\mathbf{M}_t$ is a diagonal matrix with the death probabilities on its diagonal, and $\mathbf{I}$ is the identity matrix. It is important to certify that $\mathbf{P}_t$ is the transition matrix with the conditional probabilities that a tree grows from a diameter class to the next one *knowing that* it is alive, whereas $\mathbf{A}_t$ is the transition matrix with the unconditional probabilities that a tree grows from a diameter class to the next one *and* stays alive. The estimates of a_{sit} and $a^{\bullet}_{sit}$ are therefore not the same, up to a multiplicative coefficient representing the survival probability.

The upgrowth probabilities a_{sit} may be straightforwardly estimated as the proportions of trees that move up to the next diameter class between time t and $t + \Delta t$. Let $\hat{a}_{sij}$ be the estimate of the 1991 to 1993 upgrowth transition probability between diameter classes i and $i + 1$ for species group s, in plot j at M'Baïki station. The density dependence of a_{sit} is accounted for by a linear relationship that

links the probability to a global tree interaction variable, namely the B_t/B_0 ratio, where B_t is the total basal area at time t and B_0 is the total basal area at steady state. The growth coefficients were estimated through the regression:

$$\hat{a}_{sij} = \alpha_{s0} + \alpha_{s1}D_i + \alpha_{s2}D_i^2 - \alpha_{s3}B_j/B_0 + \varepsilon_{sij}$$

where D_i is the mean diameter of class i and B_j is the basal area of plot j in 1991, taking into account all 40 plots of the station.

The number of recruited trees r_{st} in species group s at time t is also modelled as a linear function of the B_t/B_0 ratio. The recruitment coefficients were estimated through the regression:

$$\hat{r}_{sj} = \beta_{s0} - \beta_{s1}B_j/B_0 + \varepsilon_{sj}$$

where $\hat{r}_{sj}$ is the estimate of the number of recruited trees between 1991 and 1993 in species group s and plot j.

To estimate the mortality rates, we use an approach that is described in HOUDE, LEDOUX (1995). It simply involves checking that the diameter distribution, upgrowth probabilities and mortality rates are functionally linked at steady state. The matrix relationship can indeed be developed as:

$$n_{si,t+\Delta t} = (1 - m_{sit} - a_{sit})n_{sit} + a_{s,i-1,t} \, n_{s,i-1,t}$$

At steady state, all variables and coefficients turn out to be independent of time, and this relationship can be rewritten as:

$$m_{si} = a_{s,i-1}\frac{n_{s,i-1}}{n_{si}} - a_{si}$$

where, for convenience, we note $a_{s0}n_{s0}$ instead of r_s. Provided that the stationary diameter distribution complies with a negative exponential law with parameter λ, the equation can eventually be written as:

$$m_{si} = a_{s,i-1} \exp(\lambda\Delta) - a_{si}$$

where Δ is the diameter class width, except for the first diameter class, for which:

$$m_{s1} = r_s/n_{s1} - a_{s1}$$

and for the last one, for which:

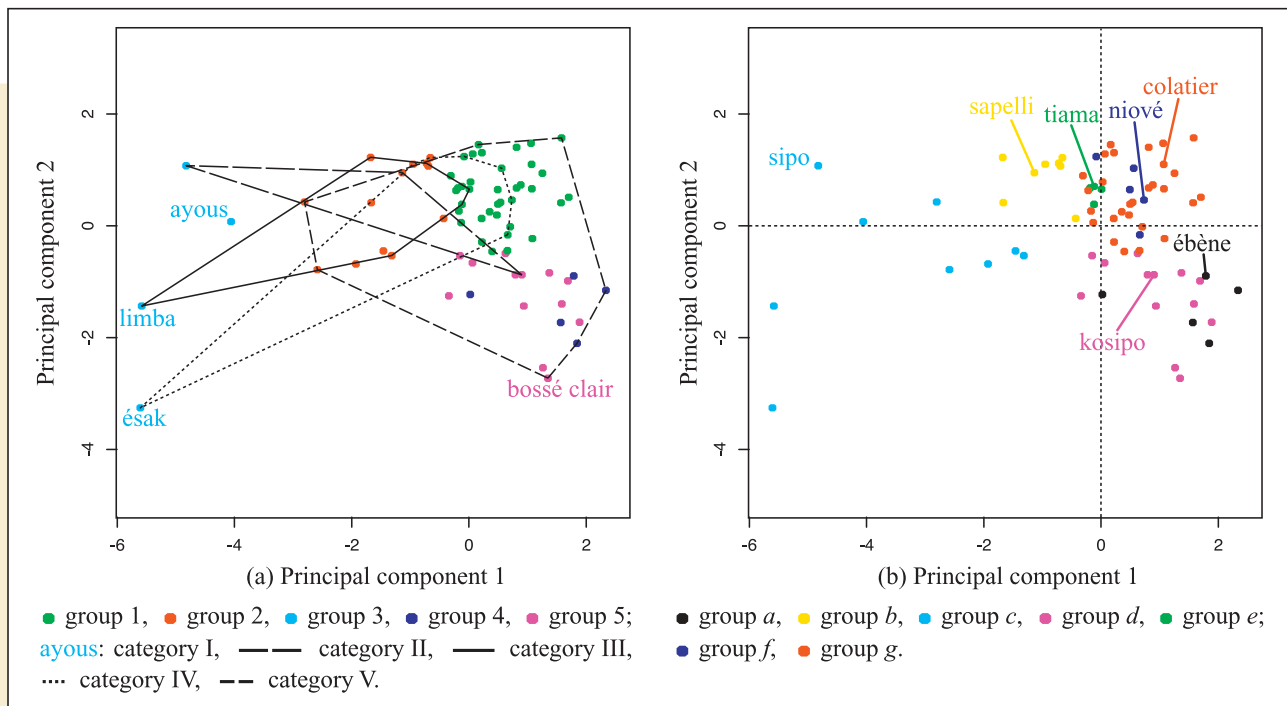$$m_{sk} = a_{s,k-1}[\exp(\lambda\Delta) - 1]$$

Parameter λ was estimated from its maximum likelihood estimator, using diameter data restricted to control plots.

Sapelli *(Entandrophragma cylindricum)* disc cut for ring counting. First assessment before sanding.
Rondelle de sapelli (Entandrophragma cylindricum) *prélevée pour un comptage de cernes. Premier examen avant le ponçage.*
Photo L. Durrieu de Madron

Figure 2.
Projection on the first two axes of the PCA of the species together with the groups they belong to: (a) the five groups are the ecological groups obtained by cluster analysis; (b) the seven groups are obtained by intersecting the ecological groups with the commercial categories.
Projection, sur les deux premiers axes de l'ACP, des espèces ainsi que des groupes auxquels elles appartiennent : (a) les cinq groupes sont les groupes écologiques obtenus par classification automatique ; (b) les sept groupes sont obtenus en croisant les groupes écologiques avec les catégories commerciales.

Results

Groups of species

The cluster analysis yielded five groups of species. They are represented in Figure 2a, as a projection on the first two axes of a principal component analysis (PCA) with respect to the species characteristics. Groups 4 and 5, that seem to overlap, are discriminated on the third axis of the PCA. The boundaries of Boscolo's five commercial categories are superimposed over the species projections. The striking feature is that there is absolutely no match between the ecological groups and the commercial categories: each commercial category overlaps several ecological groups. The intersection between the ecological groups and Boscolo's categories actually yields 14 distinct groups (Table I). Sufficient numbers of individuals in each group are required to estimate the parameters of the matrix model. We then focused on groups that contained at least 100 individuals, which eventually led to seven groups,

denoted *a* to *g* (Table I). Species of the remaining seven groups (9 species overall) were pooled with the 188 species that had been disregarded from the start, and were *a posteriori* reattached to the groups in the same way as the 188 species.

The seven groups are represented (Figure 2b) as a projection again on the first two axes of the PCA. The group interpretation is derived from the principal component analysis illustrated in Figure 3. The first axis reflects the potential size of the species, as well as their growth rates. It thus opposes slow growing species with a small average diameter to fast growing species with a high average diameter. The second axis reflects the species turnover rate. It opposes species with high mortality and recruitment rates to species with low mortality and recruitment rates.

The seven groups may then be interpreted as follows:

▪ Group *a*: understorey species with a medium to high turnover rate (e.g. ebony, *Diospyros canaliculata* De Wild.).

▪ Group *b*: medium-sized species with a low turnover rate (e.g. sapelli, *Entandrophragma cylindricum* Spra.).

▪ Group *c*: overstorey species with a variable turnover rate e.g. sipo (*Entandrophragma utile* Spra.), ayous (*Triplochiton scleroxylon* K.Sch.), limba (*Terminalia superba* Engl./Diel.), ésak (*Albizia glaberrima* Bent.).

▪ Group *d*: medium-sized to understorey species with a medium to high turnover rate, e.g. kosipo (*Entandrophragma candollei* Harms), bossé clair (*Guarea laurentii* Pell.).

▪ Group *e*: medium-sized species with a low turnover rate (e.g. tiama, *Entandrophragma angolense* C. DC.).

▪ Group *f*: understorey species with a low turnover rate (e.g. niové, *Staudtia kamerunensis*).

▪ Group *g*: medium-sized to understorey species with a low turnover rate (e.g. colatier, *Cola nitida* Scho./Endl.).

This interpretation, however, is based on the 72 core species retained for the cluster analysis. It does not take into account the 188 species *a posteriori* assigned to the seven species groups *a* to *g*.

Table I.

Intersection of ecological groups determined by cluster analysis and Boscolo's commercial categories, and the resulting seven species groups denoted *a* to *g*. In each cell, the two numbers in parenthesis are respectively the number of species and the number of trees in 1991.

Ecological Group	Commercial category I	II	III	IV	V
1	-	-	*e* (4-258)	*f* (5-888)	*g* (28-2141)
2	-	(1-79)	(3-91)	*b* (5-817)	*c* (4-300)
3	(1-45)	(1-5)	(1-32)	(1-33)	-
4	-	-	-	-	*a* (5-270)
5	-	(1-24)	-	-	*d* (12-877)

Table II.

Parameters of the matrix model. The upgrowth transition probability for a given species group is computed as: $a_i = \alpha_0 + \alpha_1 D_i + \alpha_2 D_i^2 - \alpha_3 B/B_0$. The recruitment is computed as: $r = \beta_0 - \beta_1 B/B_0$.

Group 1

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	− 0.0109	0.0036	0	0	11.2695	8.3916	0.2391
Std. Error	0.0393	0.0016			2.4060	2.6284	
Pr (> |t|)	0.781	0.025			< 0.001	0.003	

$R^2 = 0.03$, F-statistic = 5.09, df = 1 and 174, p-value = 0.025 $R^2 = 0.21$

Group 2

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	0.0685	0.0021	0	0	3.5000	0	0.0637
Std. Error	0.0282	0.0008					
Pr (> |t|)	0.016	0.009					

$R^2 = 0.02$, F-statistic = 6.87, df = 1 and 357, p-value = 0.009

Group 3

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	1.3339	0.0140	− 0.0002	1.2336	74.6815	63.6688	0.0382
Std. Error	0.2057	0.0053	0.0001	0.1926	10.2681	11.2176	
Pr (>|t|)	< 0.001	0.009	0.003	< 0.001	< 0.001	< 0.001	

$R^2 = 0.12$, F-statistic = 17.07, df = 3 and 378, p-value < 0.001 $R^2 = 0.46$

Group 4

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	0.3643	0	0	0.3092	17.7202	12.8268	0.1652
Std. Error	0.1165			0.1185	3.2357	3.5349	
Pr (> |t|)	0.002			0.010	< 0.001	0.001	

$R^2 = 0.02$, F-statistic = 6.81, df = 1 and 266, p-value = 0.010 $R^2 = 0.26$

Group 5

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	0.4144	0.0046	0	0.4287	5.5018	4.7690	0.1095
Std. Error	0.2239	0.0017		0.2245	1.0921	1.1931	
Pr (> |t|)	0.066	0.007		0.058	< 0.001	< 0.001	

$R^2 = 0.05$, F-statistic = 5.37, df = 2 and 207, p-value = 0.005 $R^2 = 0.30$

Group 6

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	0.0537	0	0	0	11.0960	8.4209	0.1251
Std. Error					2.1412	2.3392	
Pr (> |t|)					< 0.001	0.001	

$R^2 = 0.25$

Group 7

Parameter	α_0	α_1 (cm⁻¹)	α_2 (cm⁻²)	α_3	β_0	β_1	λ (cm⁻¹)
Value	0.0084	0.0017	0	0	21.5212	15.8211	0.1493
Std. Error	0.0215	0.0006			3.8208	4.17432	
Pr (> |t|)	0.697	0.006			< 0.001	< 0.001	

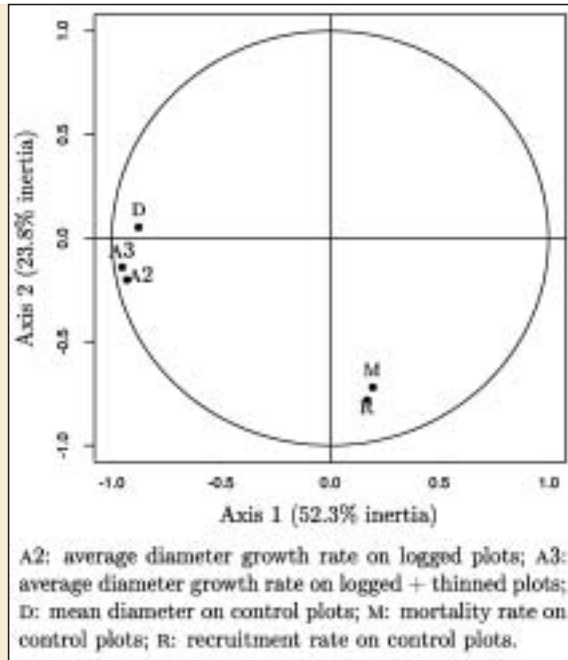$R^2 = 0.02$, F-statistic = 7.78, df = 1 and 336, p-value = 0.006 $R^2 = 0.27$

Figure 3.
Correlations between species characteristics and the first two principal components of the PCA.
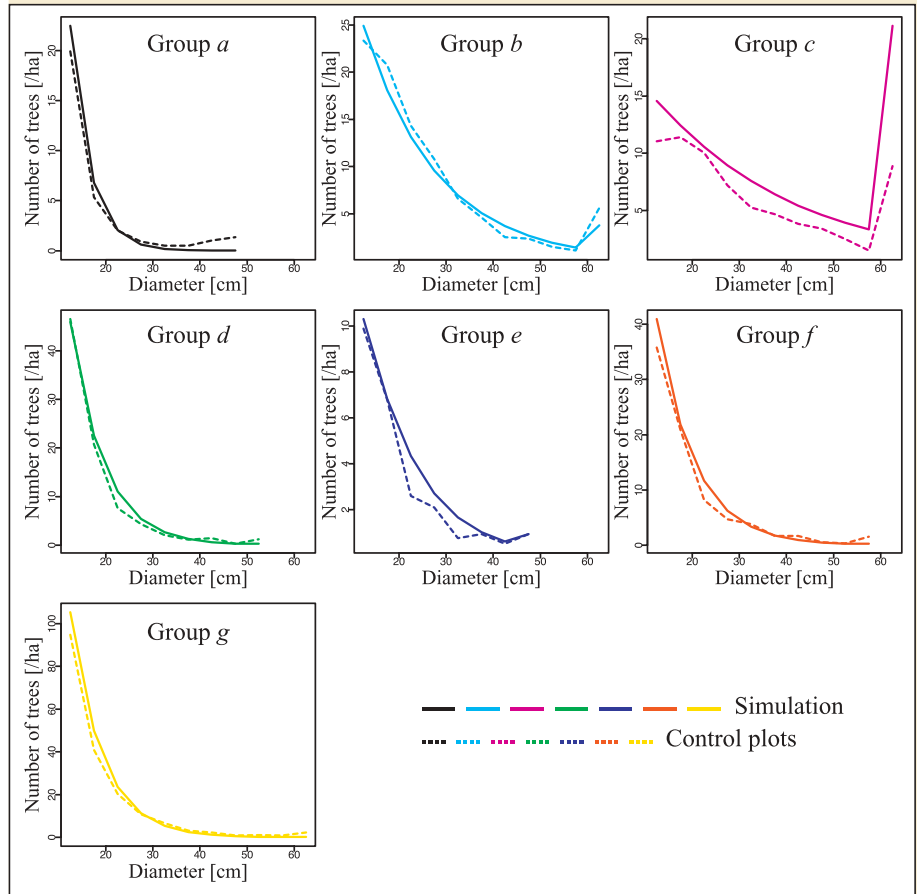*Corrélations entre les caractéristiques des espèces et les deux premières composantes principales de l'ACP.*

A2: average diameter growth rate on logged plots; A3: average diameter growth rate on logged + thinned plots; D: mean diameter on control plots; M: mortality rate on control plots; R: recruitment rate on control plots.

Figure 5.
Diameter distributions of each species group at steady state as predicted by the matrix model and as observed on control plots in 1991.
Distribution diamétrique de chaque groupe d'espèces lorsque le peuplement est à l'équilibre : comparaison entre les valeurs prédites par le modèle matriciel et les valeurs observées sur les parcelles témoins, en 1991.
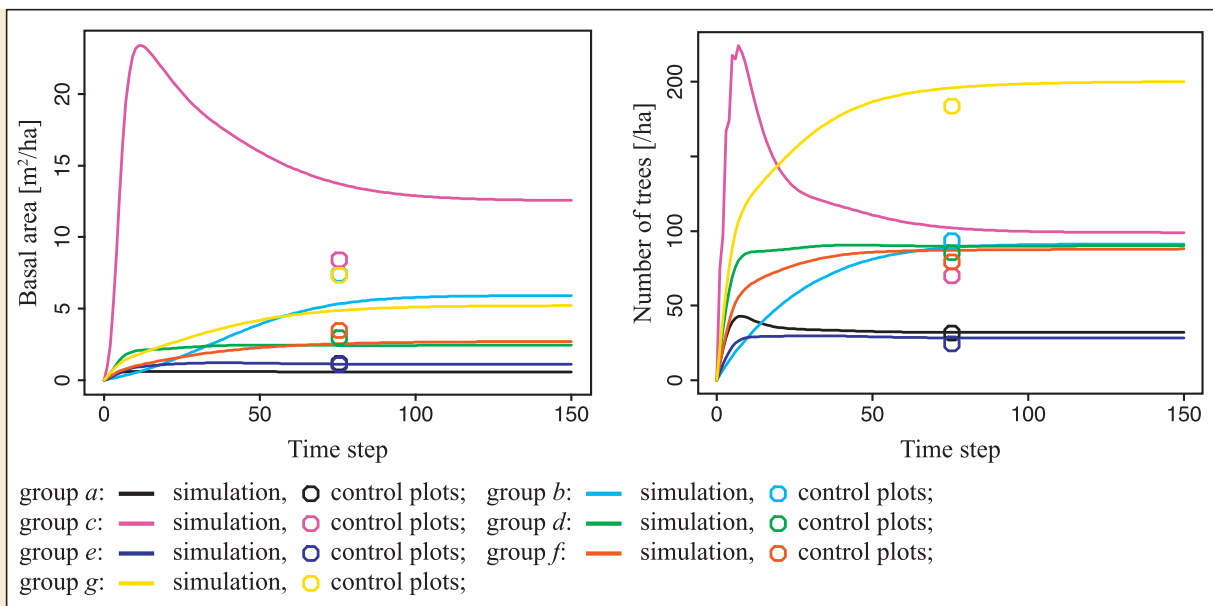

Figure 4.
Simulation over 300 years starting from an empty plot: (left) basal area of each group, (right) number of trees of each group. Values obtained on control plots in 1991 are superimposed.
Simulation sur 300 ans, à partir d'une parcelle « vide » (coupe à blanc étoc) : (à gauche) surface terrière de chaque groupe, (à droite) nombre d'arbres dans chaque groupe. On a superposé les valeurs réelles observées sur les parcelles témoins, en 1991.

Forest-savanna interface near Berbérati.
Collection of charred wood after a brush fire.
Limite forêt-savane près de Berbérati.
Récupération de bois brûlés lors du passage
des feux de brousse.
Photo L. Durrieu de Madron.

Forest dynamics

The time step was set at $\Delta t = 2$ years. Diameter classes are 5 cm wide and range from 10 cm DBH to 60 cm (the last class includes all trees greater than 60 cm DBH). The matrix model was built using the seven previously defined species groups. The parameter values are given in Table II.

Figure 4 shows a simulation, over 300 years, starting from an empty plot. The order of prevalence of the groups varies with time until it stabilises as the steady state is reached. In addition, Figure 5 shows the diameter distribution of each species group at steady state, as simulated and as observed at M'Baïki (assuming that the control plots are representative of the stand steady state, which is not a strong hypothesis as the plots were set up in undisturbed forest).

Globally, the model predictions are in agreement with the observations, even though for all groups except group *e*, the χ^2 test rejects (at the 5% level) the adjustment between the observed diameter distribution and the predicted distribution at steady state. However, the basal area of groups *b*, *c* and *g* is overestimated. The most serious disagreement concerns group *c* whose total number of trees is also underestimated. Figure 5 shows that the predicted diameter distribution for species group *c* lies well above its observed distribution.

Discussion

The ecological groups that were determined at M'Baïki turned out to be independent of Boscolo's commercial categories. Intersecting the ecological groups with the commercial category was thus a necessary step to get species groups that are both biologically meaningful and practical for management issues. The intersection was, however, only partially successful: seven out of the fourteen groups obtained at the intersect were retained, due to the low number of trees in the seven remaining groups (Table I). In particular the commercial categories I and II, that are the most interesting, are not represented by any final group, whereas category V corresponds to four groups (*a*, *c*, *d* and *g*).

The problem with commercial categories I and II is that they contain too few species: category I contains one species only (the ayous), whose number of trees was too low to adjust a matrix model. Category II contains three species: sapelli, sipo and kosipo. All together, these three species are numerous enough to estimate the matrix model parameters, but separately they are not. Unfortunately, the three species are split by the cluster analysis into three different ecological groups (Table I)!

We still have to determine a way to deal with these four species separately. One solution could be to make a separate matrix for each of these species, and copy the upgrowth and mortality probabilities from the group to which they belong (sapelli is currently assigned to group *b*, sipo to group *c* and kosipo to group *d*). Then we just have to estimate the recruitment rates from the species specific data. Another solution could be to enlarge the diameter class width, in order to have fewer parameters to estimate. Then fewer data are required, but the price to pay is a lower model prediction accuracy.

The role of the matrix model with respect to this species grouping approach was mainly to validate the relevance of the groups obtained. All groups except group *c* are presumably acceptable, even though matrix models are in essence robust and may erase minor imperfections. Let us focus more closely on the behaviour of species group *c*: starting from an empty plot, the number of trees in group *c* increases very sharply at the beginning (Figure 4, left), which indicates a pioneer behaviour. But at the same time group *c* has a high number of trees and a large basal area at steady state (Figure 4, right), which is typical of a shade-tolerant, slow-growing behaviour. This "schizophrenic" character of group *c* is confirmed by the inspection of its specific composition. Group *c* contains species with markedly different ecological behaviours, such as:

▪ sipo, a large overstorey tree with a high diameter growth rate,

▪ essessang, emien (*Alstonia boonei* De Wild.), and fromager (*Ceiba pentandra* Gaer.), that have an L-shaped diameter distribution,

▪ parasolier, pioneer species.

The irregular diameter distribution of group *c* at steady state, with a peak at 20 cm (Figure 5), may thus result from the mixing of several different types of diametric structures. The matrix model, which approximates the distribution by an exponential function, then has a serious shortcoming.

The heterogeneity of group *c* is certainly a consequence of the way disregarded species are *a posteriori* assigned to the seven groups. Note that the seven final groups are built from a core of 72 species. The remaining 188 species are *a posteriori* attached by proximity. This method does not require any expert knowledge and can deal with missing data, but it does not ensure that similar species will be assigned to the same group. For instance, sipo, kosipo and sapelli fall into three different groups, although the three of them were classified in the same ecological group by MOREL & TANDEAU DE MARSAC (1995). In a similar way, the three ebony species (*Diospyros crassiflora* Hiern,

Diospyros iturensis R. Let./F. Whi., *Diospyros canaliculata* De Wild.) do not fall into the same group.

We used almost the same variables to build the groups as MOREL & TANDEAU DE MARSAC (1995). However, to assign the disregarded species, such as sipo, kossipo and sapelli that have just been mentioned, they relied on their ecological knowledge of the species. They thus obtained groups that make sense with respect to the species' ecological behaviours. In a similar way, FAVRICHON (1994) used an empirical clustering method based on his ecological knowledge of the species and on a PCA, to define species groups in a French Guiana forest. This suggests that methodological developments are to be made to deal with rare species, which are numerous in tropical rainforests, and that cannot be processed by standard statistical analysis. At present, clustering methods must be supplemented with expert knowledge to get reliable groups. However, expert knowledge — which is not quantifiable — does not ensure that the group construction will be repeatable.

Conclusion

Intersecting ecological groups with commercial categories is a valuable way to define species groups that are both biologically meaningful and practical for management purposes. Our case study demonstrated that (i) balanced commercial categories in terms of number of species, and (ii) a sound ecological classification, are recommended to get relevant groups. The group definition is usefully complemented by a matrix model of forest dynamics, that enables the assessment of group consistency. It may thus serve as a forest management tool.

We shall now estimate the robustness of the cluster analysis by varying the number of variables that characterise the species. In particular, we shall build the groups without taking mortality rates into account so as to estimate its impact on group definition. Another prospect would be to try to benefit from the repetition of measurements. So far, only the 1991-93 period of the database has been assessed, whereas 16 inventories are available at M'Baïki. Thus a longitudinal data analysis could be achieved to derive more accurate estimations.

Forest growing in a permanently flooded lowland region. Bambio, Lobaye region.
Forêt développée sur un bas-fond inondé en permanence. Bambio, région de la Lobaye.
Photo L. Durrieu de Madron.

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Essessang *(Ricinodendron heudelotii)* regeneration at the foot of a logged ayous *(Triplochiton scleroxylon)* stump.
Régénération d'essessang (Ricinodendron heudelotii) *au pied d'un ayous* (Triplochiton scleroxylon) *exploité.*
Photo L. Durrieu de Madron.

Synopsis

GROUPER LES ESPÈCES POUR MODÉLISER LA DYNAMIQUE FORESTIÈRE : UN EXEMPLE EN RÉPUBLIQUE CENTRAFRICAINE

Gaëlle Lahoreau,
Nicolas Picard,
Sylvie Gourlet-Fleury

La modélisation de la dynamique forestière peut être un outil d'aide à l'aménagement forestier. Dans les forêts tropicales humides, le modélisateur est confronté au nombre considérable d'espèces d'arbre présentes. La solution couramment adoptée consiste à définir des groupes d'espèces. Il peut s'agir de groupes écologiques, construits à partir de caractéristiques telles que l'accroissement diamétrique moyen, le taux de mortalité… ou de catégories commerciales, qui n'ont pas d'interprétation biologique mais qui présentent un intérêt pratique évident pour l'aménagement forestier.

Dans cette étude, on se propose de définir des groupes d'espèces en utilisant, à la fois, des critères écologiques et des critères commerciaux, puis de construire un modèle de dynamique forestière pour évaluer la pertinence des groupes obtenus. La démarche est appliquée aux données du dispositif de M'Baïki, en République centrafricaine, où 40 ha de forêt exploitée et non perturbée ont été inventoriés annuellement depuis 1982.

Matériel et démarche

Les groupes d'espèces sont obtenus par intersection de groupes écologiques et de cinq catégories commerciales données *a priori*. Les groupes écologiques ont été formés par la classification automatique (méthode des nuées dynamiques) des espèces, caractérisées par cinq variables : leur accroissement diamétrique moyen sur la période 1991-1993 dans les parcelles traitées, leur diamètre moyen, leur taux de mortalité et leur taux de recrutement sur des parcelles témoins. On s'est limité aux espèces représentées par un nombre suffisamment élevé d'individus (72 espèces sur les 260 recensées à M'Baïki).

Le modèle retenu pour simuler la dynamique forestière est un modèle matriciel à coefficients densité dépendants. Le domaine de variation du diamètre est discrétisé en classes, et le peuplement est décrit par un vecteur d'effectif par classe de diamètre et groupe d'espèce. Une matrice de transition, dont les coefficients s'interprètent comme des probabilités de mourir et des probabilités de passer dans la classe supérieure en restant vivant, permet de calculer le vecteur des effectifs au temps $t + 1$ en fonction des effectifs au temps t. Une relation linéaire relie la valeur des coefficients à la surface terrière de la parcelle.

Résultats

La classification automatique donne cinq groupes écologiques. Leur intersection avec les cinq catégories commerciales produit 14 groupes d'espèces, dont sept sont finalement retenus, qui présentent un effectif suffisamment élevé pour estimer les paramètres du modèle matriciel. Les sept groupes se distinguent par leur taille et leur vitesse de croissance d'une part (espèces de grande taille et à fort accroissement diamétrique opposées aux espèces de petite taille et à faible accroissement diamétrique) et, d'autre part, par leur taux de renouvellement (espèces aux taux de mortalité et de recrutement élevés, opposées aux espèces aux taux de mortalité et de recrutement faibles). Les 188 espèces qui n'ont pas servi à la définition des groupes leur sont rattachées *a posteriori* par proximité au barycentre des groupes. En se fondant sur ces sept groupes d'espèces, le modèle matriciel est construit. L'état stationnaire prédit par le modèle est globalement en bon accord avec l'état observé dans les parcelles témoins du dispositif. La surface terrière de trois des groupes est cependant surestimée, et l'un de ces groupes a de plus un effectif sous-estimé par le modèle.

Discussion et conclusion

Les cinq groupes écologiques obtenus par classification automatique ne coïncident pas avec les cinq catégories commerciales, d'où la nécessité de croiser ces deux regroupements. Toutefois, cette démarche n'est efficace que dans la mesure où la répartition des espèces (et surtout du nombre d'individus) dans chacune des modalités est équilibrée.

Le modèle matriciel révèle que l'un des sept groupes d'espèces ainsi obtenus a un comportement ambigü : certaines de ses caractéristiques le rapprochent des espèces pionnières, d'autres le font assimiler aux espèces de la canopée, tolérantes à l'ombre. Un examen approfondi montre qu'effectivement ce groupe rassemble des espèces présentant des comportements écologiques contrastés. L'étape de la démarche à remettre en cause est vraisemblablement celle du rattachement *a posteriori* des 188 espèces rares qui n'ont pas participé à la définition des groupes. En effet, la méthode utilisée n'assure pas que deux espèces ayant des comportements écologiques proches seront affectées au même groupe. Pour pallier cette faiblesse du traitement statistique des espèces rares, il faut faire appel à l'expertise d'un écologue.