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SPLITTING SPECIES GROUPS BETWEEN MODEL COMPONENTS TO MODEL THE DYNAMICS OF A TROPICAL RAIN-FOREST

Nicolas Picard, Sylvie Gourlet-Fleury, Plinio Sist Cirad-forêt, Montpellier, France

Abstract

Tropical forests are known for their tree species diversity, that is difficult to take into account in models. Even if some authors do not renounce to model separately every species, the usual solution consists in defining groups of species, then adjusting a set of parameters for each group. Groups may be built from ecological characteristics of the species, thus providing so-called 'functional groups', but they may also take into consideration extraneous information such as commercial categories.

Defining groups in relation to a model of forest dynamics is however uneasy, as two species may appear similar with respect to a biological function, and at the same time different with respect to another function. Crossing all causes of singularities among species then brings a diversity of groups that is comparable to the species diversity itself.

In this study, we address this issue by allowing a species to move from one species group to another, depending on the biological process that is concerned. We developed this approach with a matrix model of forest dynamics, for a tropical rain-forest in French Guiana, at Paracou, focusing on the methodological aspects. As in other matrix models, forest dynamics is split into three components: recruitment, growth, and mortality. Five groups of species were defined at Paracou from species characteristics, in a previous study; we re-analyzed these data to build 5 recruitment groups, 5 growth groups, and 5 mortality groups.

One species is then characterized by its recruitment group, its growth group and its mortality group, thus yielding at total $5 \times 5 \times 5 = 125$ possibilities, which brings a more realistic view of the floristic composition of the

forest, as if each species had been modelled separately. The resulting matrix model however do not have more parameters than it would have with 5 global species groups: if r, g and m are the numbers of parameters required to model recruitment, growth and mortality for one species, then in both cases the total number of parameters of the model is 5(r + g + m). So the parameters can be estimated as easily as in the usual approach.

As a conclusion, allowing a species to shift from one species group to another depending on the model component ensures a richness similar to the species richness, without increasing the number of parameters to estimate. As prospects, we shall investigate the ecological significance of the species groups thus obtained.

1 Introduction

When trying to model the dynamics of a tropical rain-forest, one is confronted to the huge diversity of the tree species. Even if some authors do not renounce to treat separately every single species (e.g. Shugart et al., 1980), the usual solution consists in building ad hoc groups (generally by cluster analysis) from species characteristics that are in use in the model, and then adjusting a set of parameters for each group (Favrichon, 1998; Finegan et al., 1999; Huth and Ditzer, 2001; Köhler and Huth, 1998; Köhler et al., 2000, 2001). Groups may be built from ecological characteristics of the species, thus providing so-called 'functional groups', but they may also take into consideration extraneous information such as commercial categories (Boscolo and Vincent, 1998; Vanclay, 1989; Wan Razali, 1986). Still, defining groups in relation to a model of forest dynamics remains uneasy, as two species may appear similar with respect to a biological function, and at the same time different with respect to another function. For instance, species groups that are homogeneous with respect to growth may be built, but it is likely that these groups will be heterogeneous with respect to recruitment or mortality. Crossing all causes of singularities among species to get species groups that are homogeneous with respect to the different process of the dynamics then brings a number of groups that allows to better account for the floristic composition of the stands

In this paper, we address this issue by defining three distinct species groupings: one is growth-specific and split the species along their growth characteristics; the second is recruitment-specific and gathers species with similar recruitment characteristics; the third one is mortality-specific. The key point is that the model of forest dynamics allows a species to shift from one species group to another depending on the biological process (growth, recruitment or mortality) that is concerned. A species may thus take its recruitment parameters from a species group, its growth parameters from another one, and its mortality parameters from a last one. The resulting model thus has as many parameters as in the classical approach, but their combinations give a much higher richness of modelled species.

We developed this approach with a matrix model of forest dynamics, for a tropical rain-forest in French Guiana, at Paracou. We deliberately focused on the methodological aspects in this paper, leaving the study of the ecological relevance for future work. We analyzed the Paracou data to build 5 growth-specific groups, 5 recruitment-specific groups, 5 mortality-specific groups, and 5 comprehensive species groups that simultaneously rely on growth, recruitment and mortality. Two matrix models were then developed: one is classical and is based on the 5 comprehensive species groups; the other one illustrates the proposed new approach and makes use of the three process-specific groupings into 5 groups. The predictions of the two matrix models are then confronted.

2 Material and methods

2.1 The Paracou plots

The matrix models were built from the data of the Paracou forest, in French Guiana, 40 km West from Kourou (5°15'N, 52°55'W). The climate is equatorial with an average annual rainfall of 3160 mm and an average temperature of 26°C. On this site twelve 6.25 ha plots of natural rain forests were settled in 1984 by the Cirad-Forêt. Nine plots underwent silvicultural treatments in 1987-88, and three plots were left as controls. The girth of every tree greater than 10 cm DBH (diameter at breast height) was measured, and a taxonomic information was noted too. As the botanical inventory did not enable to identify every tree to the species level, a tree was characterized either by its species or by a group of species. Measurements have been carried annually from 1984 to 1995, and once every two years since. At total, more than 46,000 trees have been inventoried and 202 species or groups of species (SGS) have been identified. More details about the Paracou experimental station may be found in Schmitt and Bariteau (1990). Favrichon (1998) built a matrix model for the Paracou forest, showing that growth was related to the total basal area on 1.5625 ha subplots (one quarter of the plot, 48 subplots at total).

2.2 Characterizing SGS

Each SGS was first characterized by a set of parameters that describe its growth, its recruitment and its mortality. On each of the 48 subplots and at years t = 1984, 1988, 1990 and 1992, we computed the average diameter increment, the mortality rate and the recruitment flux between year t and t + 2. Let us denote a_{nts} the average diameter increment of the SGS s (= 1...202) between year t and t + 2 in subplot n, y_{nts} the number of trees of the SGS s that are alive in subplot n at year t, z_{nts} the number of trees of the SGS s that die in subplot n between year t and t + 2, and r_{nts} the number of trees of the SGS s that are recruited in subplot n between year t and t + 2.

We supposed, as in Favrichon's model, that growth and recruitment are density-dependent, whereas mortality is not. The stocking of a subplot at year t is quantified by the ratio b of its basal area at year t over its basal area in 1984 (assuming that 1984 characterizes the steady state of the subplot):

$$b_{nt} = \frac{B_{nt}}{B_{n,1984}}\tag{1}$$

where B_{nt} is the basal area of subplot n at year t. The growth of the SGS s was then characterized by the parameters α_{0s} and α_{1s} of the regression:

$$a_{nts} = \alpha_{0s} - \alpha_{1s}b_{nt} + \varepsilon_{nts}$$

Similarly the recruitment of the SGS s was characterized by the parameters β_{0s} and β_{1s} of the regression:

$$r_{nts} = \beta_{0s} - \beta_{1s}b_{nt} + \varepsilon_{nts}$$

As the diameter increments or the recruitment fluxes on a same subplot at two consecutive years are not independent, a standard linear regression (that would assume that the ε_{nts} are independent) cannot be achieved. A regression for repeated measurements (Diggle et al., 1996) is required. A preliminary analysis showed that an exponential model (Diggle et al., 1996, p.57) could adequately fit the variance-covariance structure of the residuals. The variance-covariance matrix of the ε_{nts} was thus modelled by:

The parameters α_0 , α_1 , β_0 , β_1 were then estimated by maximizing the loglikelihood (Diggle et al., 1996, p.63). As mortality was supposed density-independent, the mortality rate m_s of the SGS s was simply estimated as:

$$m_s = \frac{\sum_{n,t} z_{nts}}{\sum_{n,t} y_{nts}}$$

The computations were actually achieved for all SGS with at least 15 individuals (on average between 1984 and 1992) in at least three subplots. At this step, we thus have got the set of dynamics parameters $(\alpha_0, \alpha_1, \beta_0, \beta_1, m)$ for a subset of SGS.

2.3 Building species groups

This set of parameters was used to build the species groups. In a comprehensive approach, the dissimilarity $d_{ss'}$ between any two SGS s and s' was defined as the Euclidian distance between the standardized vector of their dynamics parameters:

$$d_{ss'} = \left[(\alpha_{0s}^* - \alpha_{0s'}^*)^2 + (\alpha_{1s}^* - \alpha_{1s'}^*)^2 + (\beta_{0s}^* - \beta_{0s'}^*)^2 + (\beta_{1s}^* - \beta_{1s'}^*)^2 + (m_s^* - m_{s'}^*)^2 \right]^{0.5}$$

where for any parameter x, $x_s^* = (x_s - \bar{x})/\sqrt{s_x}$, \bar{x} is the empirical mean of x_s over all SGS and s_x is the empirical variance of x_s . A hierarchical cluster analysis using Ward's minimum variance method was then used to define five comprehensive species groups.

Species groups that are specific to a process of the forest dynamics were also defined by restricting the parameters used to compute the dissimilarity between SGS. Five growth-specific groups were thus obtained in the same way from the following dissimilarity:

$$d_{ss'} = \left[(\alpha_{0s}^* - \alpha_{0s'}^*)^2 + (\alpha_{1s}^* - \alpha_{1s'}^*)^2 \right]^{0.1}$$

Five recruitment-specific groups were also obtained from the dissimilarity:

$$d_{ss'} = \left[(\beta_{0s}^* - \beta_{0s'}^*)^2 + (\beta_{1s}^* - \beta_{1s'}^*)^2 \right]^{0.1}$$

and five mortality-specific groups were obtained from the dissimilarity:

$$d_{ss'} = |m_s^* - m_{s'}^*|$$

Let g_s (= 1...5), $g_s^{\rm gr}$, $g_s^{\rm rc}$ and $g_s^{\rm mt}$ be respectively the comprehensive species group to which the SGS s belongs, the growth-specific group to

which it belongs, the recruitment-specific group to which it belongs, and the mortality-specific group to which it belongs. The dynamical behaviour of a species can be characterized either by its comprehensive species group g_s , or by the combination $(g_s^{\rm gr}, g_s^{\rm rc}, g_s^{\rm mt})$ of its process-specific groups. The former characterization encompasses five categories, whereas the latter potentially encompasses $5 \times 5 \times 5 = 125$ categories.

2.4 Matrix model

The model is a Usher model with species groups and density-dependent coefficients. Its principle has been exposed in Buongiorno and Michie (1980); Favrichon (1998); Usher (1969). The trees of the stand are broken down by diameter class and species group. Time is discrete with a time step Δt . Between time t and $t+\Delta t$, a tree of species group s and diameter class i has three possibilities: (1) it dies, with probability $p_{si\dagger}(t)$, (2) it stays alive and moves up to the next diameter class, with probability $p_{sii+1}(t)$, (3) it stays alive in the same diameter class, with probability $p_{sii}(t) = 1 - p_{sii+1}(t) - p_{sii+1}(t)$.

Let $N_{si}(t)$ be the number of trees of species group s in diameter class i at time t. Its equation of evolution is:

$$N_{si}(t + \Delta t) = p_{sii}(t)N_{si}(t) + p_{si-1i}(t)N_{si-1}(t) \quad (i > 1)$$
(2)

This equation is complemented for the first diameter class (i = 1) by an equation that gives the recruitment $R_s(t)$:

$$N_{s1}(t + \Delta t) = p_{s11}N_{s1}(t) + R_s(t)$$
(3)

Equations (2) and (3) can be condensed in a matrix equation:

$$\mathbf{N}(t + \Delta t) = \mathbf{A}(t)\mathbf{N}(t) + \mathbf{R}(t)$$

where \mathbf{A} is a block diagonal matrix with diagonal elements \mathbf{A}_s that are the transition matrices for each species group:

$$\mathbf{A} = \begin{bmatrix} \mathbf{A}_1 & \mathbf{0} \\ & \ddots & \\ & \mathbf{A}_s \\ \mathbf{0} & & \ddots \end{bmatrix} \quad \text{and} \quad \mathbf{A}_s = \begin{bmatrix} \ddots & \mathbf{0} \\ & p_{sii} \\ & p_{sii+1} \\ \mathbf{0} \\ & & \ddots \\ \mathbf{0} \end{bmatrix}$$

and N is the concatenated vector obtained from the species diameter distribution vectors N_s , and, similarly, R is the concatenated vector obtained from the recruitment vectors \mathbf{R}_s of each species group:

$$\mathbf{N} = \begin{bmatrix} \vdots \\ \mathbf{N}_{s} \\ \vdots \end{bmatrix}, \quad \mathbf{N}_{s} = \begin{bmatrix} \vdots \\ N_{si} \\ \vdots \end{bmatrix}, \quad \mathbf{R} = \begin{bmatrix} \vdots \\ \mathbf{R}_{s} \\ \vdots \end{bmatrix} \text{ and } \mathbf{R}_{s} = \begin{bmatrix} R_{s} \\ 0 \\ \vdots \end{bmatrix}$$

Provided that there are *n* diameter classes and *p* species groups, \mathbf{A}_s is a $n \times n$ matrix and \mathbf{A} is a $np \times np$ matrix, \mathbf{N}_s and \mathbf{R}_s are vectors of length *n*, and \mathbf{N} and \mathbf{R} are vectors of length np.

A linear relationship between the p_{sii+1} 's and the ratio b(t) of the subplot basal area at year t over its basal area in 1984 (see (1)) was selected:

$$p_{sii+1}(t) = \delta_{0sii+1} - \delta_{1sii+1}b(t)$$

For recruitment, a linear relationship between b(t) and either the recruitment flux $R_s(t)$ or its log-transform was selected:

$$R_s(t) = \gamma_{0s} - \gamma_{1s}b(t)$$

or $\ln R_s(t) = \gamma_{0s} - \gamma_{1s}b(t)$

2.5 Parameter estimation

Given two inventories at year t and $t+\Delta t$, the upgrowth transition probability p_{sii+1} can readily be estimated as the proportion of trees of species group s and diameter class i that moves up to diameter class i + 1. Similarly, the mortality rate $p_{si\dagger}$ can readily be estimated as the proportion of trees of species group s and diameter class i that dies. Let $p_{sii+1nt}$ (resp. $p_{si\dagger nt}$) be the estimate of p_{sii+1} (resp. $p_{si\dagger}$) obtained from the subplot n (= 1...48) and from the inventories t and $t + \Delta t$.

To reduce the number of parameters of the model and to ensure the smoothness of the transition probabilities, the following regressions were actually performed:

$$p_{sii+1nt} = \delta_{0s} + \delta_{1s}D_i + \delta_{2s}D_i^2 + \delta_{3s}D_i^3 - \delta_{4s}b_{nt} + \varepsilon_{sint}$$
(4)

$$p_{si\dagger nt} = \mu_{0s} + \mu_{1s}D_i + \mu_{2s}D_i^2 + \varepsilon_{sint} \tag{5}$$

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where D_i is the average diameter of diameter class *i* and b_{nt} is given by (1).

As in Favrichon's model, we selected a time step $\Delta t = 2$ years. We then used the data at t = 1984, 1988, 1990, 1992. Each subplot thus appears four times in (4) or (5), so that the residuals ε_{sint} cannot be considered as independent, and a longitudinal data analysis is again required. Again an exponential model was selected for the variance-covariance structure:

$$\begin{array}{rcl} \operatorname{Cov}(\varepsilon_{sint},\varepsilon_{si'n't'}) &=& 0 & \text{if } n \neq n' \text{ or } i \neq i', \ \forall (t,t') \\ \operatorname{Cov}(\varepsilon_{sint},\varepsilon_{sint'}) &=& \sigma_s^2 \rho_s^{|t-t'|} \end{array}$$

and the parameters were estimated by maximizing the log-likelihood (Diggle et al., 1996).

Similarly for recruitment: let R_{snt} be the number of trees of species group s that are recruited between years t and $t + \Delta t$ on subplot $n \ (= 1...48)$. The following regressions were performed:

$$R_{snt} = \gamma_{0s} - \gamma_{1s}b_{nt} + \varepsilon_{snt}$$
$$\ln R_{snt} = \gamma_{0s} - \gamma_{1s}b_{nt} + \varepsilon_{snt}$$

As each subplot appears four times, a regression for repeated measurements using the same variance-covariance structure as before was achieved.

In regressions (4) and (5), all the subplots have the same weight. This can lead to some distortions as a subplot with a low number of trees (and thus imprecise estimates of $p_{sii+1nt}$ and $p_{si\dagger nt}$) will have the same weight as a subplot with a high number of trees (and thus accurate estimates of $p_{sii+1nt}$ and $p_{si\dagger nt}$). For a few species groups containing few species and few individuals, we indeed obtained very unrealistic mortality rates. In those cases we used in place of (5) an a posteriori estimate of the mortality rates that is derived from (2). Eq. (2) may be written as:

$$N_{si}(t + \Delta t) = [1 - p_{sii+1}(t) - p_{si\dagger}(t)] N_{si}(t) + p_{si-1i}(t) N_{si-1}(t)$$

At steady state all the quantities are independent of time, which yields:

$$p_{si\dagger} = p_{si-1i} \frac{N_{si-1}}{N_{si}} - p_{sii+1} \quad (i > 1)$$

Similarly for the first diameter class, we obtain from (3):

$$p_{s1\dagger} = \frac{R_s}{N_{s1}} - p_{s12}$$

These two equations enable to compute the mortality rates from the diameter distribution, the upgrowth transition probabilities and the recruitment flux at steady state.

A set of parameters $(\delta_{0s}, \delta_{1s}, \delta_{2s}, \delta_{3s}, \delta_{4s}, \mu_{0s}, \mu_{1s}, \mu_{2s}, \gamma_{0s}, \gamma_{1s})_{s=1...5}$ is associated with each species grouping. The complete parameter set was estimated for the comprehensive species grouping. The parameters $(\delta_{0s}, \delta_{1s}, \delta_{2s}, \delta_{3s}, \delta_{4s})_{s=1...5}$ were then estimated for the growth-specific grouping, $(\mu_{0s}, \mu_{1s}, \mu_{2s})_{s=1...5}$ were estimated for the mortality-specific grouping, and $(\gamma_{0s}, \gamma_{1s})_{s=1...5}$ were estimated for the recruitment-specific grouping.

3 Results

3.1 Species groups

One hundred and fifty two SGS, out of the 202 that are present in the database (75%), have enough data for their dynamics parameters to be estimated. Table 1 shows the correlation matrix between the five parameters: α_0 and β_0 are strongly correlated with α_1 and β_1 respectively; α_0 and β_0 (or α_1 and β_1) are positively correlated, which means that the slow growing species tend to have a smaller recruitment. On the contrary there is no marked correlation between m and any other parameter.

Table 1: Correlation matrix between the five dynamics parameters α_0 , α_1 (growth parameters), β_0 , β_1 (recruitment parameters), and m (mortality rate). * indicates a significant departure from zero at the 5% level.

	$lpha_0$	α_1	β_0	β_1	m
α_0	1	0.95*	0.26*	0.27*	-0.04
α_1	0.95^{*}	1	0.14	0.14	-0.04
β_0	0.26^{*}	0.14	1	1.00*	0.00
β_1	0.27^{*}	0.14	1.00^{*}	1	-0.03
m	-0.04	-0.04	0.00	-0.03	1

The five comprehensive groups that are derived from all parameters may be described as follows (Table 2):

- Group 1: low α 's, medium β 's; this group thus gathers slow-growing species that are hardly sensitive to a change of the stand stocking;
- Group 2: medium α 's and medium β 's; this group thus gathers species with an intermediate behaviour in every respect;
- Group 3: high α 's, medium β 's; this group thus gathers fast-growing trees that are sensitive to a change of the stand stocking;
- Group 4: low β 's, medium α 's and high mortality rate; this group thus gathers the species that require a stand stocking large enough to recruit young trees;
- Group 5: very high α 's and very high β 's; this group thus gathers the species that grow very fast and have a high recruitment when the stand is open (pioneer species).

Group 4 and 5 gather species with outlying characteristics and thus encompass a little number of species.

Table 2: Mean values of the dynamics parameters α_0 , α_1 (growth parameters), β_0 , β_1 (recruitment parameters), and m (mortality rate) in the 5 comprehensive species groups. S is the number of species in the groups.

\overline{g}	α_0	α_1	β_0	β_1	m	S
1	0.64	0.40	0.70	0.56	0.024	46
2	1.33	1.04	0.28	0.20	0.010	75
3	2.76	2.24	0.90	0.84	0.016	25
4	0.95	0.76	-0.54	-1.05	0.184	4
5	3.15	1.57	24.29	25.09	0.027	2

The growth-specific groups discriminate the species along a gradient from slow-growing density-independent species (group 1 with low α 's) to fastgrowing density-dependent species (group 5 with high α 's), see Table 3. Similarly the recruitment-specific groups discriminate the species along a gradient from low to high recruitment (Table 3), and the mortality-specific groups discriminate the species along a gradient from low to high mortality.

When crossing the 5 growth-specific groups with the 5 recruitment-specific groups and the 5 mortality-specific groups, 43 combinations out of the 125 possible combinations are observed (one third). The number of observed combinations is less than 125 because the specific groups are not independent from each other. A χ^2 test shows indeed that there is a relationship between the growth-specific groups and the recruitment-specific groups (p-value = 0.04). On the contrary there is no relationship between the growth- and mortality-specific groups (χ^2 test, p-value = 0.82) or between the recruitment- and mortality-specific groups (χ^2 test, p-value = 0.13). These dependencies reflect the correlations between the dynamics parameters (Table 1).

3.2 Model predictions

As in Favrichon's model, 11 diameter classes were defined, ranging from 10 to 60 cm with a constant width of 5 cm, the last diameter class grouping all the trees greater than 60 cm DBH. The parameters for the classical matrix model based on comprehensive species groups are given in Table 4. A posteriori estimates of the mortality rates were used for species group 4 and 5: for

Table 3: Mean values of the growth parameters α_0 , α_1 in the 5 growth-specific groups, of the recruitment parameters β_0 , β_1 in the 5 recruitment-specific groups, and of the mortality rates m in the 5 mortality-specific groups. S is the number of species.

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$g^{ m gr}$	α_0	α_1	S	$\overline{g^{r}}$	с	β_0	β_1	S	g^{mt}	t	m	S
1	0.42	0.17	35		1	0.15	0.08	117	1	L	0.014	34
2	1.67	1.31	46		2	1.01	0.81	23	2	2	0.005	71
3	1.04	0.80	51	1	3	2.83	2.43	9	3	3	0.025	32
4	2.73	2.19	17		4	7.80	8.03	1	4	1	0.060	11
5	5.67	4.90	3		5	24.29	25.09	2	Ę	5	0.184	4

species group 4, $p_{i\dagger} = 0.0224$, $\forall i$; for species group 5, $p_{1\dagger} = 0.2381$, $p_{2\dagger} = 0.0505$, $p_{3\dagger} = 0.1258$, and $p_{i\dagger} = 1 \forall i \ge 4$.

The matrix model was then used to predict the stationary state of a 1.5625 ha subplot of the Paracou forest. Figure 1 shows the predicted number of trees and the predicted basal area of each species group, and confront these numbers to their observed distributions on the 48 Paracou subplots in 1984.



Figure 1: Predicted versus observed number of trees and basal area on a 1.5625 ha subplot, for the matrix model based on comprehensive species groups: • predictions of the matrix model; the box-and-whisker plots indicate the observed distributions on the 48 subplots in 1984; g1...g5 designates the comprehensive species groups.

The predicted number of trees in each species group are in good agreement with the observations, whereas the basal area is less well predicted, with an over-estimation of the basal area of the species groups 2 and 3, and an underestimation of the basal area of the species group 1. Moreover the predicted

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g	Growth	·** .		ρR^2 (%	6) Recruitn	nent	$ ho R^2$ (%)	Mortality		ρ	R^2 (%)
1	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 - \delta_2 D_i^2$	$\delta_4 b$	0.17 3	$.8 R = \gamma_0 -$	$-\gamma_1 b = -0.$	03 41.5	$p_{i\dagger} = \mu_0 + \mu_1$	D_i	0.13	7.1
2	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 +$	$\delta_3 D_i^3 - \delta_4 b$	0.02 12	$.4 R = \gamma_0 -$	$-\gamma_1 b = -0.$	01 30.6	$p_{i\dagger} = \mu_0 + \mu_1$	D_i	-0.11	0.5
3	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 +$	$\delta_3 D_i^3 - \delta_4 b$	-0.09 7	$.9 \ln R = \gamma_0$	$0-\gamma_1 b = 0.3$	24 40.2	$p_{i\dagger} = \mu_0 + \mu_1$	D_i	-0.05	0.2
- 4	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 +$	$\delta_3 D_i^3$	-0.04 2	.1 $\ln R = \gamma_0$	$b_0 - \gamma_1 b = -0.4$	44 8.3	$p_{i\dagger} = \mu_0 + \mu_1$	D_i	0.00	1.3
5	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 - \delta_2 D_i^2$	$\delta_4 b$	0.13 14	$.6 \ln R = \gamma_0$	$p-\gamma_1 b = 0.$	12 43.7	$p_{i\dagger} = \mu_0 + \mu_1$	$D_i + \mu_2 D_i^2$	-0.03	3.7
		Group 1			Group 2			Group 3			
	Estimate	Std. error	p-value	Estimate	Std. error	p-value	Estimate	Std. error	p-value	_	
δ_0	2.04810^{-2}	1.37110^{-2}	0.068	2.70210^{-1}	2.84310^{-2}	< 0.001***	5.29210^{-1}	6.92210^{-2}	< 0.001***		
δ_1	3.04610^{-2}	6.55010^{-4}	< 0.001***	-9.36910^{-3}	2.66710^{-3}	< 0.001***	-1.97610^{-2}	6.57310^{-3}	0.001**		
δ_2	-4.95310^{-5}	8.77510^{-6}	< 0.001***	3.45810^{-4}	7.75410^{-5}	< 0.001***	7.26510^{-4}	1.95710^{-4}	< 0.001***		
δ_3	-	-		-3.67110^{-6}	6.87010^{-7}	< 0.001***	-7.47010^{-6}	1.76710^{-6}	< 0.001***		
δ_4	1.87510^{-2}	1.03210^{-2}	0.035^{*}	1.41510^{-1}	1.05410^{-2}	< 0.001***	2.90010^{-1}	2.78210^{-2}	< 0.001***		
20	32.169	1.795	< 0.001***	21.265	1.364	$< 0.001^{***}$	3.844	0.271	< 0.001***		
γ_1	25.680	2.161	< 0.001***	15.207	1.640	< 0.001***	3.140	0.330	< 0.001***		
μ_0	-4.84010^{-2}	1.12510^{-2}	< 0.001***	5.78310^{-3}	3.22310^{-3}	0.036*	1.29510^{-2}	5.78210^{-1}	0.013^{*}		
μ_1	3.36110^{-3}	2.96810^{-4}	< 0.001***	2.78910^{-4}	8.03810^{-5}	$< 0.001^{***}$	2.85410^{-4}	1.58810^{-4}	0.036*		
μ_2					-	-	-		-	-	
		Group 4	5		Group 5	=					
	Estimate	Std. error	p-value	Estimate	Std. error	p-value					
δ_0	1.28810^{-1}	3.84610^{-2}	< 0.001***	1.350	1.79610^{-1}	< 0.001***					
δ_1	-1.28610^{-2}	4.01810^{-3}	< 0.001***	-4.59510^{-2}	1.10310^{-2}	$< 0.001^{***}$					
δ_2	4.51410^{-4}	1.23010^{-4}	< 0.001***	5.19710^{-4}	1.68110^{-4}	$< 0.001^{***}$					
03	-4.47510^{-6}	1.12910^{-6}	$< 0.001^{***}$	1		-					
δ_4	-	-	-	3.50910^{-1}	1.60510^{-1}	0.014**					
· ~0	-0.100	0.233	0.333	5.549	0.422	< 0.001***					
γ_1	-0.942	0.290	0.001***	5.276	0.010	< 0.001***					
μ_0	4.90410^{-1}	$2.805 10^{-2}$	< 0.001***	1.47910^{-1}	5.21410^{-2}	0.002**					
μ_1	-3.11210^{-5}	8.453 10	< 0.001	-1.41010^{-2}	3.84710^{-6}	0.008**					
μ_2				3.441 10	1.00010	0.013	e e e e e e e e e e e e e e e e e e e				

Table 4: Selected regression equations and parameter values of the matrix model for the comprehensive species grouping. Levels of significance: *** 1 permil, ** 1%, * 5%.

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diameter distribution of each species group falls within the range of observed diameter distributions on the 48 subplots in 1984.

The parameters for the matrix model based on growth-, recruitment- or mortality-specific groups are given in Table 5. Each of the 43 species groups that result from the crossing of these three groupings can be specified by a triplet $(g^{\text{gr}}, g^{\text{rc}}, g^{\text{mt}})$. For instance (1,3,2) will specify the group of species that belong to the first growth-specific group, to the third recruitment-specific group and to the second mortality-specific group. The transition matrix of such a group will take its upgrowth transition parameters from group 1 for growth (Table 5); it will take its recruitment parameters from group 3 for recruitment, and it will take its mortality parameters from group 2 for mortality. The resulting matrix model thus behaves like a matrix model with 43 species groups.

This matrix model was again used to predict the stationary state of a 1.5625 ha subplot of the Paracou forest. Figure 2 shows the predicted number of trees and the predicted basal area of each species group, and confront these numbers to their observed distributions on the 48 Paracou subplots in 1984.



Figure 2: Predicted versus observed number of trees and basal area on a 1.5625 ha subplot, for the matrix model based on growth-, recruitment- and mortality-specific groups: the whiskers indicate the empirical 95% confidence interval of the observed quantities; --- line of slope 1.

Once again, the number of trees is better predicted than basal area. However the discrepancy between predictions and observations is greater than for the classical matrix model based on 5 species groups. The gain of precision in species description (43 groups instead of 5) is compensated by a loss of precision in quantitative predictions. From the 43 species groups it is possible to re-compose larger species groups. For instance Figure 3 shows the predicted

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g	Growth			ρR	2 (%)	Recruitn	nent	ρ	R^2 (%)	Mortality	ρ	R^2 (%)
1	$p_{ii+1} = \delta_0 - \delta_4$	b		0.14	1.5	$\ln R = \gamma_0$	$\gamma_1 - \gamma_1 b$	0.18	16.5	$p_{i\dagger} = \mu_0$		
2	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 +$	$\delta_3 D_i^3 - \delta_4 b$	0.02	10.4	$\ln R = \gamma_0$	$-\gamma_1 b$	0.18	41.2	$p_{i\dagger} = \mu_0$	-	-
3	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 - \delta_2 D_i^2$	$\delta_4 b$	0.01	9.0	$\ln R = \gamma_0$	$-\gamma_1 b$	0.18	43.2	$p_{i\dagger} = \mu_0 + \mu_1 D$	i -0.04	1.3
4	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 - \delta_2 D_i^2$	$\delta_4 b$	-0.02	7.1	$\ln R = \gamma_0$	$\gamma_0 - \gamma_1 b$	0.01	41.8	$p_{i\dagger} = \mu_0 + \mu_1 D$	i 0.11	3.3
5	$p_{ii+1} = \delta_0 + \delta_1$	$D_i + \delta_2 D_i^2 +$	$\delta_3 D_i^3 - \delta_4 b$	0.01	14.8	$\ln R = \gamma_0$	$\gamma_1 - \gamma_1 b$	0.12	43.7	$p_{i\dagger} = \mu_0 + \mu_1 D$	i 0.00	1.3
		Group 1				Group 2				Group 3		
	Estimate	Std. error	p-value	Estima	ate	Std. error	p-v	alue	Estima	te Std. error	p-value	
δ_0	9.58910^{-2}	1.26010^{-2}	< 0.001***	3.41910	-1 2	4.07610^{-2}	< 0.00	1***	8.228 10	$^{-2}$ 1.094 10 $^{-2}$	< 0.001***	
δ_1	-			-1.05910	-2	3.83110^{-3}	0.00	3**	2.35410^{-1}	-3 5.210 10 ⁻⁴	< 0.001***	
δ_2	-	-		3.96910	4 -	1.11610^{-4}	< 0.00	1***	-4.37410^{-1}	$^{-5}$ 6.885 10 ⁻⁶	$< 0.001^{***}$	
δ_3	-	-		-4.30910	-6 (9.91310^{-7}	< 0.00	1***	-	-		
δ_4	6.55510^{-2}	1.48010^{-2}	< 0.001***	1.80310	-1	1.52110^{-2}	< 0.00	1***	5.94510^{-1}	-2 8.111 10 -3	< 0.001***	
γ_0	3.186	2.04210^{-1}	< 0.001***	3.965	1	2.07610^{-1}	< 0.00	1***	4.148	2.27110^{-1}	< 0.001***	
γ_1	1.343	2.42010^{-1}	$< 0.001^{***}$	2.644	1	2.46310^{-1}	< 0.00	1***	3.030	2.70610^{-1}	< 0.001***	
μ_0	1.52210^{-2}	5.42810^{-2}		9.29310	-3 [5.61710^{-2}	-	*	1.82110^{-1}	-3 6.473 10 ⁻³	0.389	
μ_1	-	-	. –			-,	-		8.425 10-	-4 1.71410 ⁻⁴	< 0.001***	_
		Group 4				Group 5	1					
	Estimate	Std. error	p-value	Estima	ite	Std. error	p-v	alue				
δ_0	3.12010^{-1}	4.36010^{-2}	< 0.001***	2.219	2	2.74410^{-1}	< 0.00	1***				
δ_1	8.03010^{-3}	2.05010^{-3}	< 0.001***	-1.64310	-1 2	2.90510^{-2}	< 0.00	1***				
δ_2	-1.16910^{-4}	2.81510^{-5}	< 0.001***	5.33510	-3 (9.71610^{-4}	< 0.00	1***				
δ_3				-5.04410	-5 (9.54710^{-6}	< 0.00	1***				
δ_4	3.21310^{-1}	3.33710^{-2}	< 0.001***	5.04310	-1]	1.20610^{-1}	< 0.00	1***				
γ_0	3.785	4.61210^{-1}	$< 0.001^{***}$	5.549	4	4.22310^{-1}	< 0.00	1***				
γ_1	4.138	7.21510^{-1}	< 0.001***	5.276	(6.10510^{-1}	< 0.00	1***				
μ_0	1.07610^{-2}	1.33810^{-2}	0.211	4.90410	-1 2	2.80510^{-2}	< 0.00	1***				
μ_1	2.67110^{-3}	3.55010^{-4}	< 0.001***	-3.11310	-3 8	8.45310^{-4}	< 0.00	1***				

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Table 5: Selected regression equations and parameter values of the matrix model for the growth-, recruitment- and mortality-specific groupings. Levels of significance: *** 1 permil, ** 1%, * 5%.

number of trees and the predicted basal area of each of the 5 growth-specific group, and confront these numbers to their observed distributions on the 48 Paracou subplots in 1984. This Figure is deduced from Figure 2 by splitting the 43 species groups into the 5 growth-specific groups. It is not possible however to compute in this way the characteristics of the 5 comprehensive species groups, as the 43 species groups are not a subdivision of the 5 comprehensive groups.



Figure 3: Predicted versus observed number of trees and basal area on a 1.5625 ha subplot, for the matrix model based on growth-, recruitment- and mortality-specific groups: • predictions of the matrix model; the box-and-whisker plots indicate the observed distributions on the 48 subplots in 1984; $g1 \dots g5$ designates the growth-specific groups.

4 Discussion and conclusion

Allowing the species to shift from a species grouping to another one depending on the biological process under concern thus enables to get a finer description of the species richness. To each species grouping is associated a set of parameters, and this approach may also be seen as a crossing over of parameter sets. The resulting model has as many parameters as in the classical approach where species belong to a unique species group. This approach is quite general and could be applied to several types of models.

In the case of the Paracou forest, the matrix model based on the different combinations of growth-, recruitment- and mortality-specific groups yields less accurate predictions of the stationary state than the classical matrix model based on five comprehensive species groups. This raises questions about (1) the construction of the species groups, (2) the estimation of the model parameters.

First, species groups could be built from other parameters than the ones that we used. The parameter α_0 can be interpreted as the diameter growth rate in an empty plot (when b = 0), whereas α_1 represents the sensitivity of the diameter growth rate to the plot stocking. Similarly, β_0 represents the recruitment rate for an empty plot and β_1 represents the sensitivity of the recruitment to the plot stocking. A cluster analysis based on (α_0, α_1) (or on (β_0, β_1) would thus favour species groups that behave similarly in large openings and have a similar sensitivity to the stocking. However no empty plot (b = 0) is observed at Paracou, and α_0 and β_0 result from an extrapolation. It may be sounder to use parameters that correspond to situations that are observed at Paracou. In particular the cluster analysis could be based on $(\alpha_0 - \alpha_1, \alpha_1)$ or $(\beta_0 - \beta_1, \beta_1)$, since $\alpha_0 - \alpha_1$ represents the diameter growth rate in the stationary state (b = 1) and $\beta_0 - \beta_1$ represents the recruitment rate in the stationary state. Species groups that are homogeneous with respect to $\alpha_0 - \alpha_1$ or $\beta_0 - \beta_1$ are then more likely to make accurate predictions of the stationary state than species groups based on α_0 or β_0 .

Moreover, expert knowledge of the autecological traits of the Guyanese species should be consulted to validate the species groups that are obtained with the cluster analysis. This is left for future work, the present paper focusing on the methodological aspects of a model with shifting species groups.

Second, the parameter estimation is a more delicate step for the model with shifting species groups than for the classical models based on fix species groups. In the classical approach, a change of a parameter of a given species group only affects this group. The model predictions for a group can then be used to detect anomalous parameter values and correct them. With shifting species groups, the change of a parameter will affect several groups. All the 43 species groups that we obtained at Paracou are interconnected through their parameters: a species group with its parameters cannot be isolated and treated separately from the other groups. As a consequence, the diagnostic of anomalous parameter values from the model predictions is much more difficult.

The interconnection between parameters could be further investigated with an elasticity analysis (de Kroon et al., 1986), by computing quantities such as $\partial \ln P_s / \partial \ln p_{s'}$ where P_s is the predicted number of trees or basal area of species group s and $p_{s'}$ is one of the model parameters relative to group s'.

Eventually, to deal with the different weights of the subplots in regressions (4) and (5), on could replace regressions (4) and (5) by a two-stage weighted least-square regression (Anderson et al., 1985). The first stage would be identical to the longitudinal data regression that is described in this paper and would yield initial estimated $\hat{p}_{sii+1nt}$ and \hat{p}_{siint} . The second stage would be a

longitudinal data regression with the following variance-covariance structure:

$$\begin{array}{lll} \operatorname{Cov}(\varepsilon_{sint},\varepsilon_{si'n't'}) &= 0 & \text{if } n \neq n' \text{ or } i \neq i', \ \forall(t,t') \\ \operatorname{Cov}(\varepsilon_{sint},\varepsilon_{sint'}) &= \hat{\sigma}_{sint}\hat{\sigma}_{sint'}\rho_s^{|t-t'|} \end{array}$$

where $\hat{\sigma}_{sint} = \hat{p}_{sii+1nt}(1-\hat{p}_{sii+1nt})/N_{sint}$ for (4), $\hat{\sigma}_{sint} = \hat{p}_{si\dagger nt}(1-\hat{p}_{si\dagger nt})/N_{sint}$ for (5), and N_{sint} is the observed number of trees of species group s in diameter class i and subplot n at year t. The latter relationships follow from the fact that the numbers of trees of species group s in diameter class i and subplot n the same class, grow up or die follow a multinomial law with parameters $(N_{sint}, p_{siint}, p_{sii+1nt}, p_{si\dagger nt})$.

As a conclusion, the use of shifting species groups in models of forest dynamics offers a higher richness of modelled species behaviours, without an increase of the number of parameters of the model. It however raises specific problems for model correction that would deserve further investigations.

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