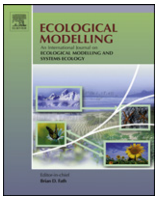
Ecological Modelling xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Clustering species using a model of population dynamics and aggregation theory

Nicolas Picard*, Frédéric Mortier, Vivien Rossi, Sylvie Gourlet-Fleury

CIRAD, Campus international de Baillarguet, TA 10/C, 34398 Montpellier Cedex 5, France

ARTICLE INFO

Article history:
Received 11 March 2009
Received in revised form 6 October 2009
Accepted 8 October 2009
Available online xxx

Keywords:
Aggregation theory
Species grouping
Species richness
Tropical rainforest
Usher model

ABSTRACT

The high species diversity of some ecosystems like tropical rainforests goes in pair with the scarcity of data for most species. This hinders the development of models that require enough data for fitting. The solution commonly adopted by modellers consists in grouping species to form more sizeable data sets. Classical methods for grouping species such as hierarchical cluster analysis do not take account of the variability of the species characteristics used for clustering. In this study a clustering method based on aggregation theory is presented. It takes account of the variability of species characteristics by searching for the grouping that minimizes the quadratic error (square bias plus variance) of some model's prediction. This method allows one to check whether the gain in variance brought by data pooling compensate for the bias that it introduces. This method was applied to a data set on 94 tree species in a tropical rainforest in French Guiana, using a Usher matrix model to predict species dynamics. An optimal trade-off between bias and variance was found when grouping species. Grouping species appeared to decrease the quadratic error, except when the number of groups was very small. This clustering method yielded species groups similar to those of the hierarchical cluster analysis using Ward's method when variance was small, that is when the number of groups was small.

1. Introduction

The high species diversity of some terrestrial or sea ecosystems such as tropical rain forests or coral reefs has raised many questions about their functioning (Hubbell and Foster, 1986; Hubbell, 1997; Whitmore, 1998). Ecologists have tried to simplify this diversity by assigning species to functional groups, i.e. groups of species that have the same functions in the ecosystem (Díaz and Cabido, 1997; Köhler et al., 2000; Fonseca and Ganade, 2001; Baker et al., 2003; Mcgill et al., 2006). Even if marked patterns such as the dichotomy between pioneers and climax species in tropical rain forests have been identified (Swaine and Whitmore, 1988; Baker et al., 2003), the definition of functional groups has remained an inaccessible Holy Grail, the distribution of species along functional gradients always being continuous rather than discrete. To build functional groups, ecologists typically grouped species on the basis of their similarity with respect to ecological characteristic or functional traits (Gourlet-Fleury et al., 2005). The methods used to group species were mainly cluster analysis, when they were not simply an educated guess.

People interested in the modelling of the dynamics of species-rich ecosystem have also paid attention to the grouping of species. The motivation of modellers was basically not to find functional groups, but rather to compensate for the scarcity of data for the less abundant species, that are also the most numerous. The scarcity of data for these rare species prevented from estimating the parameters of the models of population dynamics with enough precision. By pooling species, more sizeable data sets could be formed and reliable parameter estimates could be obtained. Despite this motivation, modellers have mainly stuck to the paradigm of functional groups, i.e. the grouping of species was made on the basis of their similarity with respect to their characteristics (Köhler and Huth, 1998; Köhler et al., 2000). Often the groups of species were built independently from the model of population dynamics (e.g. Favrichon, 1998). Sometimes the building of the groups of species was linked to the model of population dynamics, the grouping being based on the residuals of the model (Vanclay, 1991a, 1992; Gourlet-Fleury and Houllier, 2000).

When pooling species into a group, the number of available observations increases and thus the variance of the estimators of model parameters decreases. But at the same time, an estimation bias is introduced since the values of the parameters for a given species are confounded with those of the group. The wider the group is, the larger the bias is and the smaller the variance is. The bias vanishes when each group is a singleton restricted to a single species, but the variance is then maximum. To assess the interest of a species grouping from the modeller's point of view, it is thus

---

* Corresponding author at: CIRAD, BP 4035, Libreville, Gabon.
Tel.: +241 07 92 12 87.
E-mail addresses: nicolas.picard@cirad.fr (N. Picard), frederic.mortier@cirad.fr (F. Mortier), vivien.rossi@cirad.fr (V. Rossi), sylvie.gourlet-fleury@cirad.fr (S. Gourlet-Fleury).

0304-3800/$ – see front matter © 2009 Published by Elsevier B.V.
doi:10.1016/j.ecolmodel.2009.10.013

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

necessary to compute the quadratic error that results from the groups, where the quadratic error is the square bias plus variance.

This study aims at assessing the interest of groups of species from the modeller's point of view, i.e. on the basis of the quadratic error on model's predictions that it brings. The null grouping is when there are as many groups as species and each group identifies with a species (in other words, no effective grouping is made). A grouping of species will be considered as justified if it brings a lower quadratic error than the null grouping. The quadratic error will be interpreted as a disaggregation error in the context of aggregation theory. Aggregation theory deals with the error implied when shifting the level of description of a system from a detailed level to an aggregated less-detailed level (Iwasa et al., 1987, 1989; Ritchie and Hann, 1997). In the present case, the aggregation consists in replacing s species with g groups of species. Once the disaggregation error is defined, a method for defining groups of species follows by searching, for a given number g of groups, the grouping that minimizes the disaggregation error.

In this study, we presented a general framework useable with any model of population dynamics. We then applied the grouping strategy to 94 well represented tree species of a tropical rain forest in French Guiana. We chose to use a matrix model for size-structured populations to model population dynamics, and we addressed three questions: (i) How to build the disaggregation error? (ii) Is there a statistical interest to build groups, compared to null grouping? (iii) What happens if the groups are built according to a different strategy, either using the same model of population dynamics (groups of Favrichon, 1994, resulting from a cluster analysis), or using a different model (groups of Gourlet-Fleury and Houllier, 2000)?

2. Materials and methods

2.1. Aggregation theory

2.1.1. Aggregation diagram

Let s be the number of species. For each species $k \in \{1, \ldots, s\}$, n_k observations $X_{1k}, \ldots, X_{n_k k}$ are available. Each observation is considered as a random variable drawn from a distribution $F_k(\theta_k)$ that depends on unknown parameters θ_k. These parameters are those of the model of population dynamics. Expectations and variances will refer to the distributions F_k. Parameters θ_k are estimated from observations using an estimator $\hat{\theta}_k$. The model of population dynamics is here considered as an application ξ from $\mathbb{R}^m$ into $\mathbb{R}^p$ that maps a vector of parameters θ with length m onto a prediction $\xi(\theta)$. For aggregation of species to be possible, all species must have the same model of population dynamics. Which makes the difference of predictions between two species is the different values of their parameters. This implies that all species have the same number of parameters: for all k, the length of the vector θ_k is m. As parameters are estimated, the prediction for species k using population dynamics model ξ is a random variable $\xi(\hat{\theta}_k)$ whose distribution follows from F_k (Fig. 1).

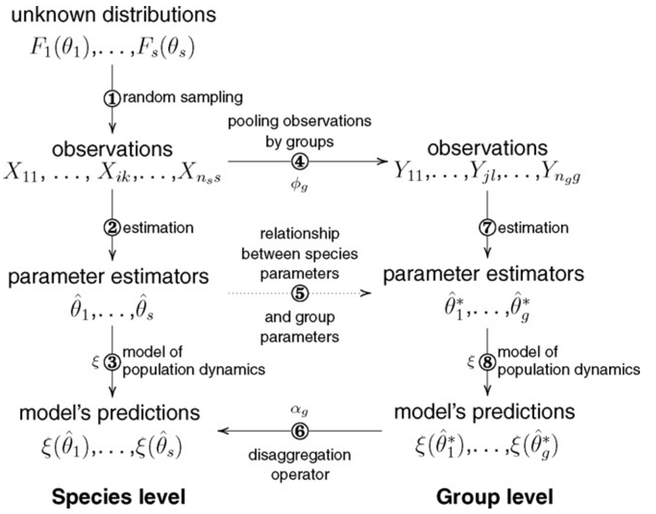


Fig. 1. Aggregation and chain prediction diagram for grouping species according to a model of population dynamics.

Let g be an integer between 1 and s. A grouping into g groups of species is defined as a surjective application ϕ_g from $\{1, \ldots, s\}$ into $\{1, \ldots, g\}$. For a given g, the number of possible groupings is given by Stirling second kind number S_s^g (Sloane, 2004; Abramowitz and Stegun, 1964, p. 824). For a fixed g, $S_s^g \sim g^s/g!$ when $s \to \infty$, which shows that S_s^g grows very quickly. Notice that $S_s^1 = S_s^s = 1$: ϕ_1 groups all species into a single group, whereas ϕ_s is the identity. Basically, the question raised by this study is whether there exists a grouping better than ϕ_s, where "better" refers to the accuracy of the model's predictions. A grouping ϕ_g permits to pool observations by groups. Let $n_l^* = \sum_{k \in \phi_g^{-1}(l)} n_k$ be the number of observations for group l, and $\hat{\theta}_l^*$ be the estimator of the model parameters for group l (where $l = 1, \ldots, g$).

Let α_g be a disaggregation operator from the g groups into the s species. This is an application from $\mathbb{R}^{p\times g}$ into $\mathbb{R}^{p\times s}$ that maps the predictions for the g groups into predictions for the s species. When grouping species, the prediction for a given species is actually confounded with that for the group to which it belongs. It is thus natural to define the disaggregation operator as

$$\alpha_g(\mathbf{y}_1, \ldots, \mathbf{y}_g) = (\mathbf{y}_{\phi_g(1)}, \ldots, \mathbf{y}_{\phi_g(s)})$$

for any prediction $\mathbf{y}_l \in \mathbb{R}^p$. This operator thus duplicates the prediction for a group as many times as there are species in this group.

2.1.2. Disaggregation error

The disaggregation error measures the gap between the predictions at the species level when the aggregation diagram shown in Fig. 1 is browsed clockwise (following arrows 4, 7, 8 and 6) or anticlockwise (following arrows 2 and 3). For a given species k, let Y_{ik} denote the ith component of the prediction for species k following arrows 2 and 3 in Fig. 1; let $l = \phi_g(k)$ denote the group to which this species belongs; and let Y_{il}^* denote the ith component of the prediction for group l following arrows 4, 7 and 8. A natural way of measuring the gap between random variable Y_{ik} and random variable Y_{il}^* is

$$E\left[\left(Y_{il}^* - E(Y_{ik})\right)^2\right] = \mathrm{Var}(Y_{il}^*) + \left[E(Y_{il}^*) - E(Y_{ik})\right]^2 \tag{1}$$

The first term corresponds to the variance for group l whereas the second term corresponds to the square bias for group l with respect to species k. Summing these contributions over all s species and all p components of the prediction gives the following expression for the disaggregation error $\varepsilon : \varepsilon(\phi_g) = E(\mathbf{D}^\top \mathbf{D})$, where $\top$ denotes the transpose and $\mathbf{D}$ is the vector of length $p \times s$ defined by

$$\mathbf{D} = \alpha_g\left(\xi(\hat{\theta}_1^*), \ldots, \xi(\hat{\theta}_g^*)\right) - E\left(\xi(\hat{\theta}_1), \ldots, \xi(\hat{\theta}_s)\right) \tag{2}$$

For a given number of groups g, the optimal grouping is the one that minimizes the disaggregation error:

$$\phi_g^{\mathrm{opt}} = \underset{\phi_g}{\operatorname{argmin}}\, \varepsilon(\phi_g) \tag{3}$$

This optimum is to be found among the S_s^g possible groupings. As this number is very large even for small values of g (for instance

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

S_{94}^2 is close to 10^{28}), it is not possible to compute $\varepsilon(\phi_g)$ for every grouping ϕ_g. The optimization problem was thus solved using a combinatorial optimization algorithm.

2.1.3. Computation of the disaggregation error

As shown by Eq. (1), computation of the disaggregation error involves computing the expectation and variance of the model's prediction. This may be achieved in the most general case using bootstrap, which basically consists in replacing the unknown distributions F_k in Fig. 1 by the empirical distribution of the observations (Efron and Tibshirani, 1993). However, bootstrap is a simulation-based method that can lead to very long computing time when combined with the combinatorial optimization algorithm used to minimize the disaggregation error. An approximate but much quicker method consists in using the δ-method, which permits to compute the first two moments of $\xi(\hat{\theta})$ from the first two moments of $\hat{\theta}$ using a Taylor expansion of ξ (Kendall and Stuart, 1977, pp. 246–247).

A particular but important case is when the estimator $\hat{\theta}$ is proportional to the mean of observations: $\hat{\theta} \propto (\sum_{i=1}^{n} X_i)/n$. Then $\hat{\theta}_l^*$ for group l is the weighted mean of the $\hat{\theta}_k$ for species $k \in \phi_g^{-1}(l)$, using n_k/n_l^* as the weight for species k: $\hat{\theta}_l^* = \sum_{k \in \phi_g^{-1}(l)} w_k \hat{\theta}_k$, where $w_k = n_k/n_l^*$. This implies that:

$$E(\hat{\theta}_l^*) = \sum_{k \in \phi_g^{-1}(l)} w_k \, E(\hat{\theta}_k) \tag{4}$$

$$\mathrm{Var}(\hat{\theta}_l^*) = \sum_{k \in \phi_g^{-1}(l)} w_k^2 \mathrm{Var}(\hat{\theta}_k) + \frac{1}{n_l^*} \sum_{k \in \phi_g^{-1}(l)} w_k [E(\hat{\theta}_k) - E(\hat{\theta}_l^*)]^2 \tag{5}$$

Hence, in the particular case where the estimator is an empirical mean of the observations, the expectation and variance of the parameters for the groups can be directly computed from the expectations and variances of the parameters for the species, without turning back to the observations. This shortcut is shown by arrow 5 in Fig. 1, and permits to considerably speed up computations when applicable.

2.2. Application to Usher matrix models

The method presented in the previous paragraph is general and can be applied to any model of population dynamics. We now apply it to the Usher model, that is a matrix model for size-structured population dynamics (Usher, 1966, 1969; Caswell, 2001). The Usher model relies on a description of the population by a vector $\mathbf{N}(t)$ of length K giving the number of individuals in K size classes at time t. Time is discrete and indexed by integers. Between two successive time steps, an individual may either stay alive in the same size class, move up to the next class, or die. Moving backwards or growing up by more than one class is not allowed. This Usher assumption results in the following recurrence equation on $\mathbf{N}(t)$:

$$\mathbf{N}(t+1) = \mathbf{U}\,\mathbf{N}(t)$$

where $\mathbf{U}$ is the Usher transition matrix, that is a $K \times K$ matrix with non-null elements on its main diagonal, its sub-diagonal and its first row:

$$\mathbf{U} = \begin{pmatrix} q_1 + f_1 & f_2 & \cdots & f_K \\ p_1 & q_2 & & \mathbf{0} \\ & \ddots & \ddots & \\ \mathbf{0} & & p_{K-1} & q_K \end{pmatrix}$$

where f_i is the recruitment rate in class i, q_i is the probability of staying alive in class i, and p_i is the probability of being alive and growing up from class i to $i+1$. These probabilities can be written as $q_i = (1 - p_i^\star)(1 - m_i)$ and $p_i = p_i^\star(1 - m_i)$ for $i = 1, \ldots, K$, where m_i is the mortality rate in class i and $p_i^\star$ is the conditional probability of growing up from class i to $i+1$ knowing that the individual stays alive (where, by convention, $p_K^\star = 0$). For sake of simplicity, we shall assume here that recruitment rates, mortality rates and upgrowth rates are the same in all classes (the extension to varying rates by class is straightforward): $f_1 = \ldots = f_K = f$, $m_1 = \ldots = m_K = m$, and $p_1^\star = \ldots = p_{K-1}^\star = p^\star$. The vector θ of parameters then is $\theta = (f,\ m,\ p^\star)$.

An observation corresponds to the state of a tree at two successive time steps. It can take four values: the tree is recruited between the two time steps (denoted "0"), the tree dies between the two time steps (denoted "†"), the tree stays alive and grows up to the next class (denoted "1"), or the tree stays alive in the same class. The distribution of observations is based on the Bernoulli distribution: for species k, the distribution of observation X_k between the two values 0 and $\neq 0$ is a Bernoulli distribution with parameter f; conditionally on $X_k \neq 0$, the distribution of X_k between the two values † and $\neq$ † is a Bernoulli distribution with parameter m; conditionally on $X_k \notin \{0, \dagger\}$, the distribution of X_k between the two values 1 and $\neq 1$ is a Bernoulli distribution with parameter $p^\star$.

The estimator of θ_k for species k is the proportion estimator (Michie and Buongiorno, 1984):

$$\hat{f}_k = [\textstyle\sum_{i=1}^{n_k} \mathbb{1}(X_{ik} = 0)]/n_k$$

$$\hat{m}_k = [\textstyle\sum_{i=1}^{n_k} \mathbb{1}(X_{ik} = \dagger)]/(n_k - F_{0k})$$

$$\hat{p}_k^\star = [\textstyle\sum_{i=1}^{n_k} \mathbb{1}(X_{ik} = 1)]/(n_k - F_{0k} - F_{\dagger k})$$

where X_{ik} is the ith observation for species k, $\mathbb{1}(p)$ is the indicator function for proposition p (= 1 is proposition p is true and 0 if p is false), $F_{0k} = \sum_{i=1}^{n_k} \mathbb{1}(X_{ik} = 0)$ is the number of recruited trees, and $F_{\dagger k} = \sum_{i=1}^{n_k} \mathbb{1}(X_{ik} = \dagger)$ is the number of dead trees for species k. The proportion estimator is unbiased ($E(\hat{f}_k) = f_k$, $E(\hat{m}_k) = m_k$, $E(\hat{p}_k^\star) = p_k^\star$), and its variance follows from the variance of the Bernoulli distribution:

$$\mathrm{Var}(\hat{f}_k) = \frac{f_k(1 - f_k)}{n_k}$$

$$\mathrm{Var}(\hat{m}_k | F_{0k}) = \frac{m_k(1 - m_k)}{n_k - F_{0k}}$$

$$\mathrm{Var}(\hat{p}_k^\star | F_{0k}, F_{\dagger k}) = \frac{p_k^\star(1 - p_k^\star)}{n_k - F_{0k} - F_{\dagger k}}$$

Two predictions of the model were used to classify species (and thus two distinct classifications were built). The first one was the vector of parameter estimates $\theta = (f,\ m,\ p^\star)$ itself, i.e. ξ was taken as the identity function from $\mathbb{R}^3$ into $\mathbb{R}^3$. The second one was the asymptotic population growth rate, denoted λ, that corresponds to the dominant eigenvalues of $\mathbf{U}$ (Caswell, 2001). Assuming that the vital rates are the same in all classes, it can be shown that

$$\det(\mathbf{U} - \mu\mathbf{I}) = (q - \mu)^{K-1}(1 - \mu + f - m)$$

where $\mathbf{I}$ is the $K \times K$ identity matrix and $\mu \in \mathbb{R}$ (computations are not shown to save space). Then $\lambda = 1 + f - m$.

As the estimator of θ is of the mean type, so is the estimator of λ. Then, both for θ and λ, the disaggregation error could be computed using (4) and (5). In other words, arrow 5 in Fig. 1 was defined, and the disaggregation error was computed from the paths defined by arrows 5, 8, 6 on one hand, and by arrow 3 on the other hand, thus circumventing arrows 2, 4, and 7.

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

2.3. Combinatorial optimization algorithm

The optimization problem (3) was numerically solved for each g using a simulated annealing algorithm (Kirkpatrick, 1984; Press et al., 1992, Section 10.9). At each iteration of the algorithm, a trial grouping is defined by assigning a species taken at random to a group taken at random. This assignment must not deplete a group. Thus the species to assign must be chosen among the groups with at least two species. The disaggregation error $\varepsilon_{\text{trial}}$ for this trial grouping is computed and compared to the current one ε. If $\varepsilon_{\text{trial}} < \varepsilon$, the trial grouping is accepted as the current grouping. Otherwise, the trial grouping is accepted with probability $\exp[(\varepsilon - \varepsilon_{\text{trial}})/T]$, where T is a control parameter of the algorithm. This control parameter is gradually lowered following a stepwise scheme, thus gradually forbidding the transitions that increase the disaggregation error. At each step, the control parameter is multiplied by $\alpha < 1$. Between two steps, q iterations are performed. The initial value T_0 of the control parameter is computed so that 80% of the trial groupings are initially accepted (Kirkpatrick, 1984). The algorithm stops when the control parameter reaches a prescribed value T_f, or when q' iterations have been performed without any change of the disaggregation error. We used: $\alpha = 0.9999$, $T_f = T_0 \times 10^{-7}$, $q = 100$ iterations, and $q' = 20\,000$ iterations. All computations were implemented in C language interfaced with R software (R Development Core Team, 2005). The code is available as supplementary material (see Appendix A).

2.4. Study site

2.4.1. Paracou experimental site

Data for this study comes from the Paracou experimental site (5°18′N, 52°23′W) in French Guiana. The site lies in a terra firme rain forest on the coastal plain with equatorial climate. A dry season occurs from August to mid-November. From March to April, a short drier period interrupts the rainy season. The physiography of the site shows smooth slopes incised by minor streams. Part of the site is covered by permanently waterlogged areas. Species richness and abundance distribution at Paracou is typical of tropical rainforests, with many tree species, few abundant species and many rare species (Fig. 2). The rank-abundance diagram shown in Fig. 2 has a classical S-shape (using logarithm for y-axis) that is consistent with a log-normal distribution for abundances (Hubbell, 2001).

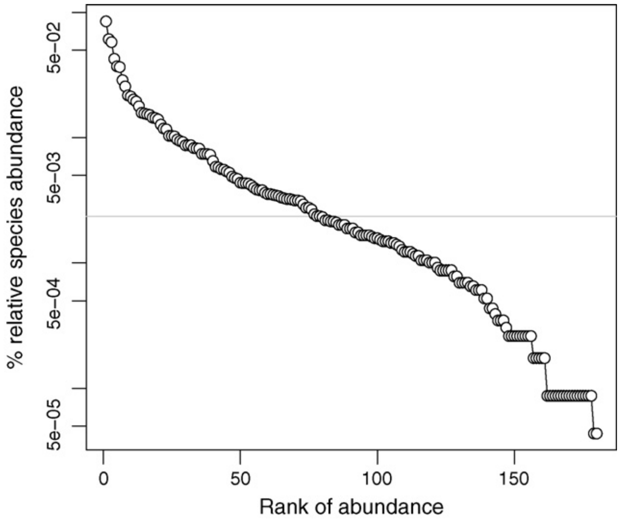


Fig. 2. Rank-abundance diagram for the 180 taxonomic groups found in the control plots of the Paracou experimental site in 1993 and 1995. As some taxonomic groups include more than one species, the number of species is actually greater than 180. Log-transform is used for the y-axis. The horizontal grey line corresponds to the minimum abundance of the species retained for this study.

Paracou is an experimental site dedicated to studying the effects of logging damage on stock recovery. The experimental design was set up in 1984 and consists of three blocks of four 300 m ×300 m permanent sample plots with a 25 m inner buffer zone. Three types of sylvicultural treatments of increasing intensity, combining selective logging and additional thinning, were applied between 1986 and 1988 to nine plots. The three other plots were left as control. In each central 250 m × 250 m square, all trees over 10 cm dbh (diameter at breast height) were identified and georeferenced. Since 1984, girth at breast height, standing deaths, treefalls and newly recruited trees over 10 cm dbh have been monitored annually, and every two years since 1995 (Gourlet-Fleury et al., 2004). Data collected in 1993 and 1995 on control plots were used for this study. Only species with at least 20 individuals were retained for this study. Ninety-four species were thus kept out of the 180 taxonomic groups found in the control plots in 1993 (Fig. 2). For each species, the Usher model was calibrated using $K = 6$ diameter classes with breakpoints 10, 20, 30, 40, 50 and 60 cm.

2.4.2. Comparison with existing species groupings

Previous species groupings have been defined at Paracou by Favrichon (1994) and Gourlet-Fleury and Houllier (2000). Favrichon defined five groups by using a k-means cluster analysis on various structural (mean diameter in control plots) and demographic parameters, including mean diameter increments by diameter class in the control and logged plots, and recruitment rates in the logged and control plots. Gourlet-Fleury and Houllier defined 15 groups, using a single tree distance dependent growth model. They iteratively clustered species such that no species effect remained on the residuals of a regression model including diameter and local competition indices. Thus, while Favrichon's groups encapsulated a general information on dynamics, the groups of Gourlet-Fleury and Houllier were based on growth and reaction to local competition.

Those authors used a larger data set than that used here, including more species. The species grouping defined from the disaggregation error was compared to Favrichon's and Gourlet-Fleury and Houllier's groupings using a Monte Carlo permutation test using the χ^2 statistic as the test statistic. This χ^2 statistic was computed on the contingency table giving the number of species in common to each combination of groups from the two groupings: if s_{ij} is the number of species shared in common between the ith group of the first grouping and the j th group of the second one, then the test statistic is $\sum_{i=1}^{g_1}\sum_{j=1}^{g_2}(s_{ij} - s^\star_{ij})^2/s^\star_{ij}$, where $s^\star_{ij} = (\sum_k s_{ik})(\sum_l s_{lj})/s$, s is the number of species, g_1 is the number of groups in the first grouping, and g_2 is the number of groups in the second one. The p-value was computed by Monte Carlo simulation.

We also compared the species grouping defined from the disaggregation error to the grouping obtained by hierarchical cluster analysis using the Euclidean metrics for computing the distance between species and Ward's method for clustering. Ward's (1963) method computes the distance between two groups of species as the increase in the sum of squared errors (SSE) after merging the two groups into a single one, where the SSE of a set of n values is the sum of squares of the deviations from the mean value. Ward's method seeks to choose the successive clustering steps so as to minimize the increase in SSE at each step, thus providing an approximate minimum of the within-group variance. The hierarchical cluster analysis was based on the table giving the estimates of f, m and $p^\star$ for each species. Each column of this table was centred and scaled prior to the analysis. This table was also analysed

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

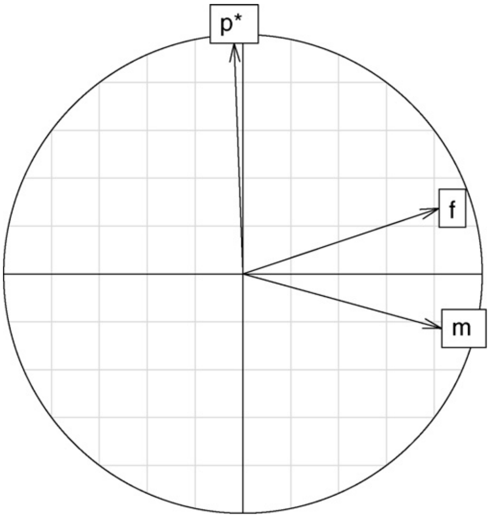


Fig. 3. Correlation circle of the principal component analysis (PCA) of vital rates for 94 tree species in undisturbed forest: f is recruitment rate, m is mortality rate, and $p^\star$ is upgrowth rate.

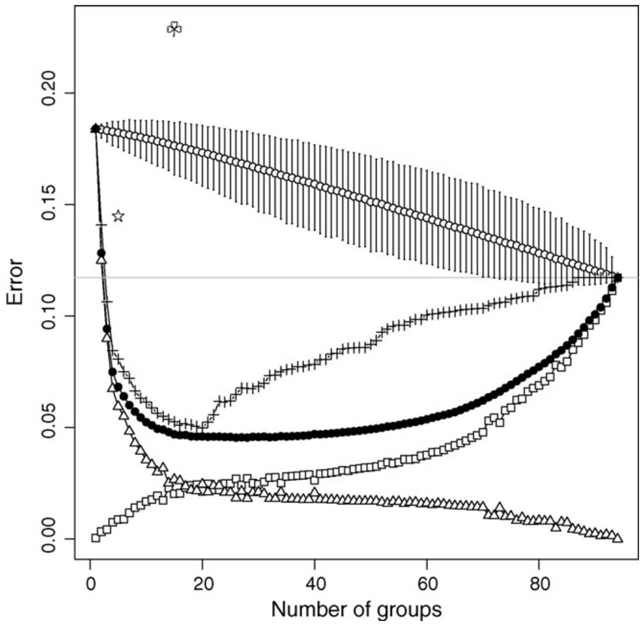


Fig. 5. Disaggregation error as a function of the number of groups g for the 94 species at Paracou, when classifying species on the basis of their vital rates: black dots indicate the minimum disaggregation error $\varepsilon(\phi_g^{\mathrm{opt}})$; triangles indicate the contribution of square bias to $\varepsilon(\phi_g^{\mathrm{opt}})$; squares indicate the contribution of variance to $\varepsilon(\phi_g^{\mathrm{opt}})$; white dots indicate the disaggregation error $\varepsilon(\Phi_g)$ for randomly selected groupings (whiskers correspond to the 95% confidence interval); crosses indicate the disaggregation error for the grouping obtained by hierarchical cluster analysis using Ward's method; the star is the disaggregation error for Favrichon's grouping; and the clover is the disaggregation error for Gourlet-Fleury and Houllier's grouping.

using a principal component analysis (PCA), and the plane formed by the first two axes of the PCA was used to graphically represent the species and their groups.

3. Results

3.1. Species characteristics

Fig. 3 shows the correlation circle of the PCA of the table giving the vital rates ($\hat{f}$, $\hat{m}$, $\hat{p}^\star$) for each species. The recruitment rate is positively correlated with the mortality rate, and together these two rates define the turnover rate. The turnover rate explains the first axis of the PCA. The upgrowth transition rate $\hat{p}^\star$ is almost independent from the turnover rate and explains the second axis of the PCA. The mortality rate is actually close to the recruitment rate for all species, so that the asymptotic population growth rate $\lambda = 1 + f - m$ is close to 1 for all species. Fig. 4a shows the estimates of λ for the 94 species at Paracou together with their 95% confidence interval computed by bootstrap. Only six species have a λ significantly different from one, which is approximately what one would be expected under the null hypothesis that $\lambda = 1$ and a first-order risk of rejection of 5%. However, the precision of estimation of λ for each species is low.

3.2. Clustering based on vital rates

In this section we consider the clustering method based on the vital rates f, m, $p^\star$. The disaggregation error is 0.117 for $g = 94$ (no grouping of species) and 0.184 for $g = 1$ (a single group of species). Thus, on the basis of the disaggregation error, making no groups of species is a better alternative to pooling all species into a single group. The white dots in Fig. 5 show the mean disaggregation error and the dispersion around this mean value that is obtained for each g when the grouping ϕ_g is taken at random among the S_S^g possible

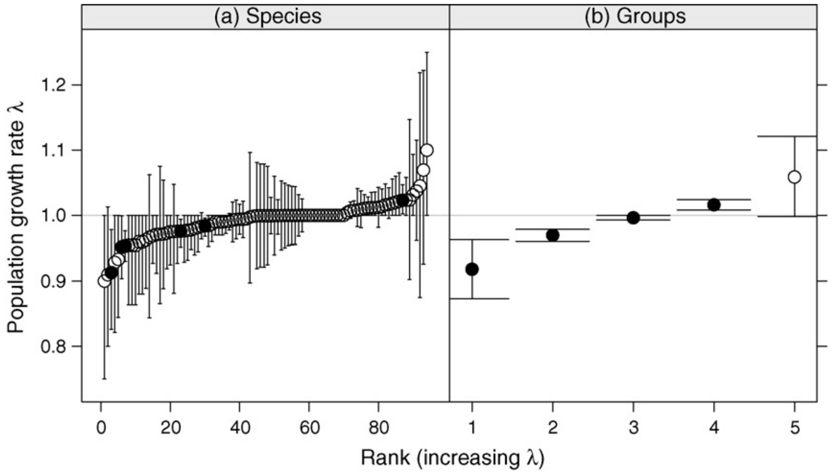


Fig. 4. Asymptotic population growth rate for (a) 94 tree species, and (b) 5 groups of species in undisturbed forest. The dot gives the estimate and the whiskers the 95% confidence interval. Black dots indicate the asymptotic growth rates that are significantly different from one.

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

groupings. This mean disaggregation error for randomly selected groupings monotonically decreases from $\varepsilon(\phi_1)$ to $\varepsilon(\phi_{94})$. Thus, if the grouping of species is to be made at random, the best option on the basis of the disaggregation error is not to make groups of species. The segments shown around the white dots in Fig. 5 indicate the 95% confidence interval for the mean value of $\varepsilon(\Phi_g)$ where Φ_g follows a uniform distribution on $\{\phi_g\}$. The width of the confidence interval increases from $g = 1$ to 55, and then decreases.

The black dots in Fig. 5 show the minimum disaggregation error $\varepsilon(\phi_g^{\mathrm{opt}})$ that is the solution of the optimization problem (3) for each g. For $1 < g < 94$, this minimum disaggregation error is always below the 2.5% quantile of $\varepsilon(\Phi_g)$, which permits to check that the optimal grouping is not like any randomly chosen grouping. For any g greater or equal to 3 and less than 94, $\varepsilon(\phi_g^{\mathrm{opt}}) < \varepsilon(\phi_{94})$. Hence, on the basis of the disaggregation error, it is always possible to find a grouping into g groups with $3 \leq g < 94$ that is a better alternative to making no groups of species. Starting from $g = 1$, the minimal disaggregation error $\varepsilon(\phi_g^{\mathrm{opt}})$ first decreases sharply as g increases, then reaches a plateau, and finally increases until $g = 94$. The minimum value of $\varepsilon(\phi_g^{\mathrm{opt}})$ is obtained for $g = 26$ groups where it equals $\varepsilon(\phi_{26}^{\mathrm{opt}}) = 0.045$, and $\varepsilon(\phi_g^{\mathrm{opt}})$ remains below 0.05 for g in the range 12–52.

Fig. 5 also shows the contributions of square bias and of variance to the disaggregation error. As expected, square bias decreases as g increases, whereas variance increases as g increases. Square bias is very high for $g = 1$ group, whereas variance is close to 0 for $g = 1$. Square bias sharply decreases until $g = 15$. For $g \geq 15$, square bias slowly decreases until $g = s$ where it vanishes. On the contrary, variance increases with g. The domain $12 \leq g \leq 52$ where $\varepsilon(\phi_g^{\mathrm{opt}})$ is almost flat corresponds to a domain where the decrease of square bias and the increase of variance almost cancel out. The value $g = 26$ thus corresponds to the best trade-off in terms of disaggregation error between square bias and variance.

The crosses in Fig. 5 show the disaggregation error $\varepsilon(\phi_g^{\mathrm{W}})$ where ϕ_g^{W} is the grouping that results from hierarchical cluster analysis using Ward's method. For $1 \leq g \leq 20$, $\varepsilon(\phi_g^{\mathrm{W}})$ is close to $\varepsilon(\phi_g^{\mathrm{opt}})$, which suggests that ϕ_g^{W} is similar to ϕ_g^{opt} for $1 \leq g \leq 20$. For $g > 20$, $\varepsilon(\phi_g^{\mathrm{W}})$ diverges from $\varepsilon(\phi_g^{\mathrm{opt}})$, but $\varepsilon(\phi_g^{\mathrm{W}})$ always remain below $\varepsilon(\phi_{94})$. Hence, hierarchical cluster analysis using Ward's method is a good proxy to the optimal grouping ϕ_g^{opt} when the number of groups is small ($g \leq 20$). Moreover, for $3 \leq g \leq 86$ and according to the disaggregation error, making groups using hierarchical cluster analysis and Ward's method is a better alternative to making no groups of species.

Favrichon's and Gourlet-Fleury and Houllier's groupings are shown in Fig. 5 as a star and a clover, respectively. Favrichon's grouping into 5 groups yields a disaggregation error that is significantly lower than $\varepsilon(\Phi_5)$ where Φ_5 is uniformly distributed in $\{\phi_5\}$, but is higher than $\varepsilon(\phi_{94})$. Hence, although Favrichon's grouping is significantly better than a randomly chosen grouping, it is not a better alternative to making no groups of species on the basis of the disaggregation error. Gourlet-Fleury and Houllier's grouping into 15 groups yields a disaggregation error that is significantly higher than $\varepsilon(\Phi_{15})$ where Φ_{15} is uniformly distributed in $\{\phi_{15}\}$. Consequently, it is also higher than $\varepsilon(\phi_{94})$.

3.3. Clustering based on population growth rate

In this section we consider the clustering method based on the asymptotic population growth rate λ, that is related to mortality and recruitment, but not to growth, since $\lambda = 1 + f - m$. The difference $f - m$ basically gives the imbalance in species turnover. Fig. 6 shows the different components of the disaggregation error for this clustering method. The pattern is globally the same as for the clustering based on vital rates, so we shall focus on the details that make a difference. The disaggregation error is 0.0806 for $g = 94$ (no grouping of species) and 0.0812 for $g = 1$ (a single group of species). For any number g of groups, the mean disaggregation error for randomly selected groupings remains close to this value of 0.08.

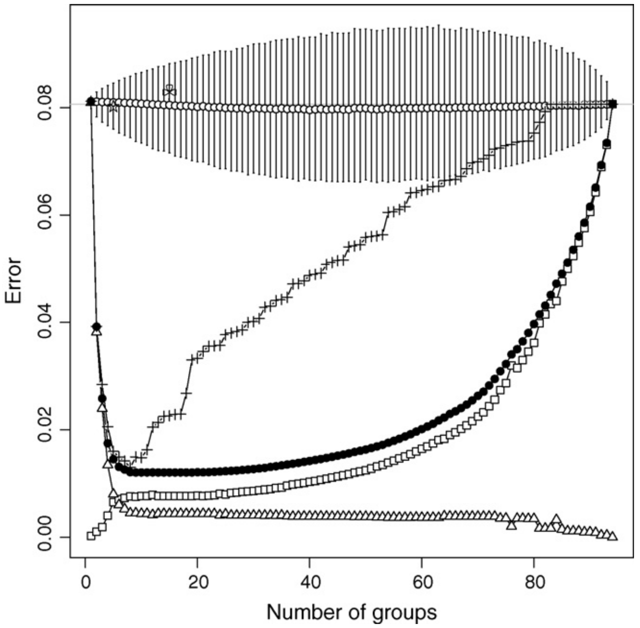


Fig. 6. Disaggregation error as a function of the number of groups g for the 94 species at Paracou, when classifying species on the basis of their asymptotic population growth rate: black dots indicate the minimum disaggregation error $\varepsilon(\phi_g^{\mathrm{opt}})$; triangles indicate the contribution of square bias to $\varepsilon(\phi_g^{\mathrm{opt}})$; squares indicate the contribution of variance to $\varepsilon(\phi_g^{\mathrm{opt}})$; white dots indicate the disaggregation error $\varepsilon(\Phi_g)$ for randomly selected groupings (whiskers correspond to the 95% confidence interval); crosses indicate the disaggregation error for the grouping obtained by hierarchical cluster analysis using Ward's method; the star is the disaggregation error for Favrichon's grouping; and the clover is the disaggregation error for Gourlet-Fleury and Houllier's grouping.

The minimum value of $\varepsilon(\phi_g^{\mathrm{opt}})$ (black dots in Fig. 6) is obtained for $g = 10$ groups where it equals $\varepsilon(\phi_{10}^{\mathrm{opt}}) = 0.012$, and $\varepsilon(\phi_g^{\mathrm{opt}})$ remains below 0.013 for g in the range 7–32. The disaggregation error that results from hierarchical cluster analysis using Ward's method (crosses in Fig. 6) is close to $\varepsilon(\phi_g^{\mathrm{opt}})$ for $1 \leq g \leq 8$. Moreover, for $2 \leq g \leq 67$ and according to the disaggregation error, making groups using hierarchical cluster analysis and Ward's method is a better alternative to making no groups of species. Favrichon's (star in Fig. 6) and Gourlet-Fleury and Houllier's (clover in Fig. 6) groupings both perform as a randomly chosen grouping.

3.4. Comparison of groupings for $g = 5$ groups

Fig. 7 shows the projections of the species together with their group on the plane formed by the first two axes of the PCA, for the optimal grouping that minimizes the disaggregation error $\phi_5^{\mathrm{opt},\theta}$ using vital rates, for the optimal grouping that minimizes the disaggregation error $\phi_5^{\mathrm{opt},\lambda}$ using the asymptotic population growth rate, for the grouping defined by hierarchical cluster analysis $\phi_5^{\mathrm{W},\theta}$ using vital rates, and for Favrichon's grouping. Each species is shown by a dot that is related to the centroid of the group, where the label of the group is displayed. The ellipses indicate the dispersion of species within each group. The locations of the dots in the plots (a)–(d) of Fig. 7 are thus the same. Only line segments and ellipses, that indicate the groups of species, change from one plot to another.

Group 1 of $\phi_5^{\mathrm{opt},\theta}$ is characterized by a low turnover rate. Group 2 is characterized by a high upgrowth rate, contrary to group 3 that is characterized by a low upgrowth rate. Contrary to group 1,

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

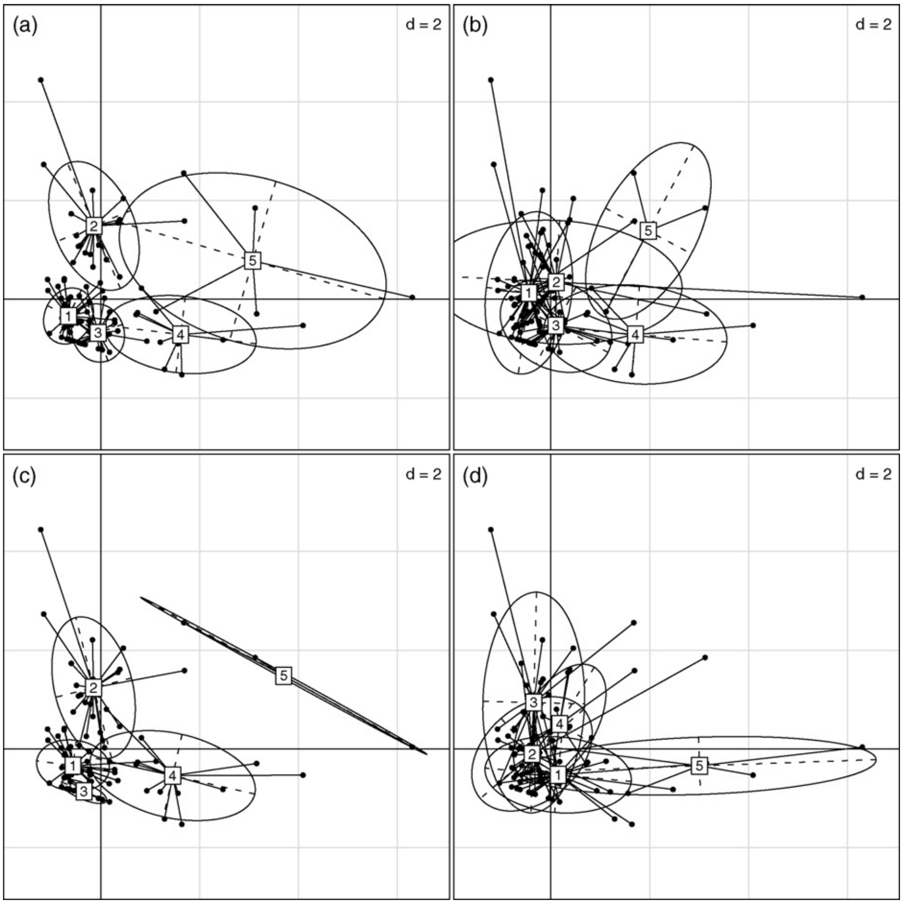


Fig. 7. Projection of the species together with their group on the plane formed by the first two axes of the PCA: (a) Optimal grouping ϕ_5^{opt} that minimizes the disaggregation error on vital rates; the side of the grey grid is 2 in length. (b) Optimal grouping ϕ_5^{opt} that minimizes the disaggregation error on the asymptotic population growth rate. (c) Grouping in 5 groups as defined by the hierarchical cluster analysis using Ward's method on vital rates. (d) Favrichon's grouping in 5 groups.

groups 4 and 5 are characterized by a high turnover rate. These two groups distinguish themselves by the value of their upgrowth transition rate: species in group 5 have a higher growth rate than those in group 4. There is a significant relationship between the grouping $\phi_5^{\mathrm{opt},\theta}$ that minimizes the aggregation error on vital rates and the grouping $\phi_5^{\mathrm{W},\theta}$ defined by the hierarchical cluster analysis using Ward's method ($\chi^2 = 217.7$, p-value $= 0.0005$). All groups contribute to the χ^2 test statistic with a correspondence between group i of $\phi_5^{\mathrm{opt},\theta}$ and group i of $\phi_5^{\mathrm{W},\theta}$ for $i = 1, \ldots, 5$ (Fig. 7a and c). There is also a significant relationship between $\phi_5^{\mathrm{opt},\theta}$ and Favrichon's grouping ($\chi^2 = 46.2$, p-value $= 0.003$). The most important contributions to the χ^2 test statistic come from the groups 1, 2, $4+5$ of $\phi_5^{\mathrm{opt},\theta}$ that correspond respectively to the groups 2, $3+4$, 5 of Favrichon's grouping (Fig. 7a and d).

The groups of $\phi_5^{\mathrm{opt},\lambda}$ (Fig. 7b) are not as well discriminated on the first two axes of the PCA as those of $\phi_5^{\mathrm{opt},\theta}$. However, they do not overlap on the third axis of the PCA (not shown here), that opposes species for which $m > f$ (and thus $\lambda < 1$) to the species for which $m < f$ (and thus $\lambda > 1$). There is no significant relationship between $\phi_5^{\mathrm{opt},\lambda}$ and Favrichon's grouping ($\chi^2 = 15.6$, p-value $= 0.72$). However, there is a significant relationship between $\phi_5^{\mathrm{opt},\lambda}$ and $\phi_5^{\mathrm{opt},\theta}$ ($\chi^2 = 160.7$, p-value $= 0.0005$). The most important contributions to the χ^2 test statistic come from the groups 3, 4, 5 of $\phi_5^{\mathrm{opt},\lambda}$ that correspond respectively to the groups 3, 4, 5 of $\phi_5^{\mathrm{opt},\theta}$ (Fig. 7a and b). Fig. 4b shows the estimate of λ for the five groups defined by $\phi_5^{\mathrm{opt},\lambda}$, together with their 95% confidence interval computed by bootstrap. Four groups out of five have a λ significantly different from one, and the precision of estimation of λ is greater than when considering each species separately.

4. Discussion

4.1. Clustering method

On the basis of the Usher matrix models and for the 94 species studied at Paracou, the choice of modellers to build groups of species is justified: for reasonably well chosen groupings, the gain in variance that results from data pooling over-compensates in terms of quadratic error for the bias that results from the groups. The positive balance in terms of quadratic error is obtained for a large range of number of groups ($3 \leq g < s$ in the present case) and for different grouping methods. Only when grouping species into few groups ($g = 1$ or 2 in the present case) does bias overcomes the gain in variance, with a resulting negative balance in terms of quadratic error. An appropriate grouping method is however required: when assigning species at random into groups, making groups of species is never expected to be a better alternative to making no groups of species.

The disaggregation error formalizes at the species level the quadratic error that results for species grouping. This error was primarily designed to assess if species grouping was justified. However, minimizing the disaggregation error for a targeted number g of groups can also be used as a method for building groups of species. Our study suggests that this method is close to hierarchi-

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

cal cluster analysis using Ward's method for g small enough (here $g \leq 20$ groups on the basis of vital rates and $g \leq 8$ on the basis of the asymptotic population growth rate). The advantage of our clustering method based on the disaggregation error is that it takes account of the variability of species characteristics. Hierarchical cluster analysis using Ward's method considers the estimates of vital rates (or of the asymptotic population growth rate) as fixed. We thus expect our clustering method to bring different results when the variance of species characteristics becomes the dominant component of the disaggregation error. This is precisely what happens: the value of g where our clustering method departs from the hierarchical cluster analysis using Ward's method (that is 20 for vital rates and 8 for the asymptotic population growth rate) coincides with the number of groups such that the variance component of the disaggregation error overcomes its bias component (see Figs. 5 and 6).

Alternate definitions of the disaggregation error could be used. In a previous study (Picard and Franc, 2003), we restrained the disaggregation error to the square bias, disregarding variance. In agreement with the present study, the square bias resulting from the optimal grouping ϕ_g^{opt} was a monotonically decreasing function of g. However, contrary to the present study, no relationship was found between ϕ_g^{opt} and the grouping obtained by hierarchical cluster analysis using Ward's method when the disaggregation error was restrained to the square bias. Including variance in the disaggregation error is actually of primary importance from the modeller's point of view, as defining groups of species aims at reducing the variance of model's predictions. Moreover, the definition of the disaggregation error should be adapted when the model's predictions mix variables with different units. The present definition of the disaggregation error is sensitive to units. For instance, if the model's prediction is a length given in metres, re-expressing this length in millimetres will inflate the disaggregation error by a factor 10^6. Eq. (2) would thus result in different weights for the variables that compose the model's prediction $\xi(\theta)$ whenever these variables are expressed in different units. The most general expression for $\mathbf{D}$ in (2) would be:

$$\mathbf{D} = \mathbf{W}^{-1}\left[\alpha_g\left(\xi(\hat{\theta}_1^*), \ldots, \xi(\hat{\theta}_g^*)\right) - E\left(\xi(\hat{\theta}_1), \ldots, \xi(\hat{\theta}_s)\right)\right]$$

where $\mathbf{W}$ is a $ps \times ps$ diagonal matrix whose main diagonal contains normalizing weights for each variable of the model's prediction and for each species. For instance, when variables are expressed in different units, the normalizing weight for a variable can be taken as its expectation; if the same weight is given to all species, this means that the main diagonal of $\mathbf{W}$ is $E[\alpha_g(\xi(\hat{\theta}_1^*), \ldots, \xi(\hat{\theta}_g^*))]$. This is equivalent with replacing square bias by standardized square bias, and variance by standardized variance.

A question that was left aside is the number of groups of species that should be used. Although the relationship between the number g of groups and the optimal disaggregation error $\varepsilon(\phi_g^{\text{opt}})$ has a minimum for some $g_{\min}$ (here $g_{\min} = 26$ groups), we do not recommend to use $g_{\min}$ as an optimal number of groups. This number of groups corresponds to the best trade-off between bias and variance in terms of quadratic error. It does not take into account of the number of parameters in the model of population dynamics at the group level. On the contrary, the choice of the number of groups to use should penalize groupings depending on the number of parameters of the model of population dynamics, and thus depending on g. Some criterion based on information theory should be used to select the number of groups (Burnham and Anderson, 2002), thus yielding an optimization problem such as

$$\arg \min_{g \in \{1,\ldots,s\}} \text{IC}(\phi_g^{\text{opt}})$$

where IC is an appropriate information criterion and ϕ_g^{opt} is an optimal grouping into g groups of species. This is left for future work.

4.2. Species groups at Paracou

The comparison of the species groups obtained at Paracou using our clustering method with other species groups is symptomatic of the inherent limitations of these statistical approaches for defining functional groups: different results are obtained depending on the variables retained to characterize species and, in the present case, also depending on the model used for forest dynamics. For instance, the comparison of our grouping based on vital rates and Favrichon's grouping (Fig. 7a and d) shows the dependence of the results on the type of forest stands where data were collected, and in particular the degree of disturbance that they experienced. For our grouping, we used only control plots and this is the reason why recruitment rates and mortality rates were highly correlated (Fig. 3). Favrichon (1994) used both control and logged plots, in which growth rates and recruitment rates were correlated (Delcamp et al., 2008), and the variance of all parameters was far higher due to a high environmental heterogeneity created by the logging operations. With this last data set, the behaviour of pioneers was easier to identify and contrasted with the behaviour of shade-tolerant species, because more favourable environments were created for them. This and the fact that Favrichon did not use mortality rates for his work, clearly explains why his groups do not fully correspond to ours, particularly along the first axis of the PCA.

The value of the disaggregation error obtained for the groups of Gourlet-Fleury and Houllier (2000) illustrates the dependence of the results on the model of population dynamics used for predictions. Gourlet-Fleury and Houllier's groups were built by minimizing the residual species effect of a particular growth model. As growth rates are weakly correlated with either the recruitment or the mortality rates (Turner, 2001; Vanclay, 1991b and see also Fig. 3), by grouping species on the basis of their growth only, a high intra-group variability for the f and m parameters (and thus a high ε) can be obtained. This indeed proved to be the case.

Comparisons with other species groups, such as the groups defined by Köhler et al. (2003) at the Piste de Saint-Elie Research Station that is close to Paracou, would be interesting to assess the relevance of our clustering method. Investigating the ecological significance of the various groupings would also shed light on the relevance of functional types.

The present method for clustering species does not solve the issue of very rare species. In the application to Paracou, 86 species or genus with less than 20 individuals were ignored. The appropriate way to deal with such rare species is still an open question. We reckon that, as these species do not bring much information, they should not contribute to the definition of the groups, but should rather be *a posteriori* assigned to existing groups. As the estimates of their parameters are very imprecise, it is likely that this assignment be quite uncertain. On the other hand, as the model of forest dynamics operates at the species level and not at the stand level, disregarding these species is not an issue as long as one is not interested in the dynamics of these specific species.

Finally, the modeller's point of view consisting in minimizing the quadratic error can yield alternate views to considering all species separately. This is illustrated by the variations of the asymptotic population growth rate λ depending on species. The growth rate λ can be taken as a measure of fitness (Caswell, 2001, Section 11.3, p. 295). Testing for equality of fitness between species is an important matter, for instance for the reconciliation between the neutral and

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013

the niche-assembly theories. It has been advocated that differences in life-history traits are consistent with the neutral theory as long as these differences remain confined to a manifold corresponding to a common fitness value (Hubbell, 2001, chapter 10). In the present cases, species have different vital rates. When considering species separately, the null hypothesis that they all have the same fitness (taking λ as a measure of it) cannot be rejected (Fig. 4a), but this may be due to a large intra-specific variability. When considering appropriate species groups that reduce the variability, differences in λ appear to be significant (Fig. 4b).

Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.10.013.

References

Abramowitz, M., Stegun, I.A., 1964. Handbook of Mathematical Functions (with Formulas, Graphs, and Mathematical Tables). No. 55 in Applied Mathematics Series. US Government Printing Office, Washington, DC.

Baker, T.M., Swaine, M.D., Burslem, D.F.R.P., 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspect. Plant. Ecol. Evol. Syst. 6 (1–2), 21–36.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach, 2nd ed. Springer Science+Business Media, Inc., New York.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis and Interpretation, 2nd ed. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Delcamp, M., Gourlet-Fleury, S., Flores, O., Garnier, E., 2008. Can functional classification of tropical trees predict population dynamics after disturbance? J. Veg. Sci. 19 (2), 209–220.

Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. J. Veg. Sci. 8, 463–474.

Efron, B., Tibshirani, R.J., 1993. An Introduction to the Bootstrap. No. 57 in Monographs on Statistics and Applied Probability. Chapman & Hall, New York.

Favrichon, V., 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. Rev. Écol. (Terre et Vie) 49 (4), 379–403.

Favrichon, V., 1998. Modeling the dynamics and species composition of tropical mixed-species uneven-aged natural forest: effects of alternative cutting regimes. For. Sci. 44 (1), 113–124.

Fonseca, C.R., Ganade, G., 2001. Species functional redundancy, random extinctions and the stability of ecosystems. J. Ecol. 89 (1), 118–125.

Gourlet-Fleury, S., Blanc, L., Picard, N., Sist, P., Dick, J., Nasi, R., Swaine, M.D., Forni, E., 2005. Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. Ann. For. Sci. 62 (8), 785–796.

Gourlet-Fleury, S., Guehl, J.M., Laroussinie, O. (Eds.), 2004. Ecology and Management of a Neotropical Rainforest. Lessons Drawn from Paracou, a Long-Term Experimental Research Site in French Guiana. Elsevier, Paris.

Gourlet-Fleury, S., Houllier, F., 2000. Modelling diameter increment in a lowland evergreen rain forest in French Guiana. For. Ecol. Manag. 131 (1–3), 269–289.

Hubbell, S.P., 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs 16 (Suppl.), S9–S21.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography, No. 32 in Monographs in Population Biology. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S.P., Foster, R.B., 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond, J., Case, T. (Eds.), Community Ecology. Harper & Row, New York, pp. 314–329.

Iwasa, Y., Andreasen, V., Levin, S.A., 1987. Aggregation in model ecosystems: I. Perfect aggregation. Ecol. Model. 37 (3–4), 287–302.

Iwasa, Y., Levin, S.A., Andreasen, V., 1989. Aggregation in model ecosystems: II. Approximate aggregation. IMA J. Math. Appl. Med. Biol. 6, 1–23.

Kendall, M., Stuart, A., 1977. The Advanced Theory of Statistics, vol. 1, 4th ed. MacMillan, New York, USA.

Kirkpatrick, S., 1984. Optimization by simulated annealing: quantitative studies. J. Stat. Phys. 34 (5–6), 975–986.

Köhler, P., Chave, J., Riéra, B., Huth, A., 2003. Simulating the long-term response of tropical wet forests to fragmentation. Ecosystems 6 (2), 114–128.

Köhler, P., Ditzer, T., Huth, A., 2000. Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests. J. Trop. Ecol. 16 (4), 591–602.

Köhler, P., Huth, A., 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model Formind. Ecol. Model. 109 (3), 301–321.

Mcgill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21 (4), 178–185.

Michie, B.R., Buongiorno, J., 1984. Estimation of a matrix model of forest growth from re-measured permanent plots. For. Ecol. Manag. 8, 127–135.

Picard, N., Franc, A., 2003. Are ecological groups of species optimal for forest dynamics modelling? Ecol. Model. 163 (3), 175–186.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 1992. Numerical Recipes in C: The Art of Scientific Computing, 2nd ed. Cambridge University Press, Cambridge.

R Development Core Team, 2005. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ritchie, M.W., Hann, D.W., 1997. Implications of disaggregation in forest growth and yield modeling. For. Sci. 43 (2), 223–233.

Sloane, N.J.A., 2004. The online encyclopedia of integer sequences. AT&T Integer Sequences Research. http://www.research.att.com/njas/sequences/.

Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75 (1–2), 81–86.

Turner, I.M., 2001. The Ecology of Trees in the Tropical Rain Forest. Cambridge Tropical Biology Series. Cambridge University Press, Cambridge, UK.

Usher, M.B., 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. J. Appl. Ecol. 3, 355–367.

Usher, M.B., 1969. A matrix model for forest management. Biometrics 25 (2), 309–315.

Vanclay, J.K., 1991a. Aggregating tree species to develop diameter increment equations for tropical rainforests. For. Ecol. Manag. 42 (3–4), 143–168.

Vanclay, J.K., 1991b. Compatible deterministic and stochastic predictions by probabilistic modeling of individual trees. For. Sci. 37 (6), 1656–1663.

Vanclay, J.K., 1992. Modelling regeneration and recruitment in a tropical moist forest. Can. J. For. Res. 22 (9), 1235–1248.

Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. J. Am. Statist. Assoc. 58, 236–244.

Whitmore, T.C., 1998. An introduction to tropical rain forests. Oxford University Press, Oxford.

Please cite this article in press as: Picard, N., et al., Clustering species using a model of population dynamics and aggregation theory. Ecol. Model. (2009), doi:10.1016/j.ecolmodel.2009.10.013