Local disturbance, forest structure and dispersal effects on sapling distribution of light-demanding and shade-tolerant species in a French Guianian forest

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Abstract

The influence of environmental conditions and distance to nearest conspecific adult was determined to explain the distribution of saplings of six tree species in a lowland rain forest of French Guiana. The six focal species were three anemochorous light-demanding non-pioneer species: \textit{Dicorynia guianensis}, \textit{Qualea rosea}, \textit{Tachigali melinonii}, and three zoochorous shade-tolerant species: \textit{Bocoa prouacensis}, \textit{Oxandra asbeckii}, \textit{Pogonophora schomburgkiana}. The study was conducted at the research station of Paracou on forest plots differing in past logging treatments. The description of local environment included a characterization of past disturbance intensity (\(n = 5\) variables), current stand (\(n = 4\)) and canopy structure (\(n = 3\)). Zero Inflated Poisson models were calibrated for each species to explain sapling numbers according to environmental conditions and distance to the nearest conspecific adult. These models extend generalized multiple regression to the case of discrete data with many zero counts. Model predictions were consistent with species temperaments: as expected, saplings of the light-demanding species were found more in disturbed and open local conditions while more saplings of the shade-tolerant species survived in stable and dense places. Predicted establishment curves of saplings around adults showed contrasting behaviour among the species and did not systematically match with \textit{a priori} expectations. These results are discussed in relation with dispersal syndromes and known establishment patterns in forest regeneration. Both differences in species shade-tolerance in early regeneration stages and dispersal limitation proved to account for sapling distribution in the understorey.

\textit{Key words:} canopy openness, dispersal limitation, disturbance, French Guiana, stand structure, sapling distribution, Zero Inflated Poisson models
1 Introduction

In tropical forests, species diversity reaches global maxima at multiple trophic levels despite intense competition for resources including space. Such diversity relates somehow to the level of environmental heterogeneity, suspected to be maximal among terrestrial ecosystems (Ricklefs, 1977). For fixed organisms such as trees, the local occurrence of any species relies on both the suitability of the local environment for survival and the dispersal success of adults. This view refers to the dual scheme of the "niche assembly" perspective and the "dispersal assembly" perspective of community ecology (Hubbell, 2001). In the niche perspective, interspecific competition leading to niche partitioning is the main explanatory mechanism of species coexistence (Grubb, 1977). Alternatively, in the dispersal assembly perspective, coexistence primarily stems from recruitment limitation (Clark et al., 1999).

A major axis along which niche partitioning exists in tropical forests is species sensitivity to disturbance (Whitmore, 1991). Stand disturbance influences the spatial distribution of species according to their respective temperaments. For a given species, the series of development and growth responses to environmental conditions over the life-cycle defines its temperament (Oldeman and Van Dijk, 1991). Species temperaments can be assessed as the average trajectory of trees in the two-dimensional plan of the radiative level of the environment versus the life-stages. For instance, pioneer species whose temperament is well-known, occur in highly radiative environment at all life-stages (Swaine and Whitmore, 1988; Dalling and Wirth, 1998; Kobe, 1999). At a given stage, the realized niche of a species depends on its temperament.

Recruitment limitation at a local scale results mainly from dispersal limitation and chance (Brokaw and Busing, 2000; Dalling et al., 2002). Species dispersal attributes control their ability to colonize new sites. Pioneer species show adaptive traits such as small-sized, well-dispersed and dormant seeds which is common for species where survival depends on unpredictable environmental conditions. The relation is less straightforward for non-pioneer species which account for most of tree species. A trade-off between dispersal ability and early life-stage survival is commonly reported, although sometimes not obvious for tree species (Foster and Janson, 1985; Kelly, 1995; Leishman et al., 1995; Westoby et al., 1996). Dispersal and survival as functions of distance determines the recruitment pattern around seed sources which is critical in population dynamics (Schupp and Fuentes, 1995; Nathan and Casagrandi, 2004).

In tropical forests where catastrophic events are rare as in South America, the natural regime of disturbance is mainly driven by treefalls gaps (Shugart,
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Gap creation temporarily releases between-tree competition and mobilizes resources. Newly recruited trees in early life-stages may take advantage of this change in local conditions to grow and survive according to their temperament and competitiveness. Among all resources, the increase of light availability mostly impacts upon growth and development of trees in the understorey (Whitmore, 1996). Light availability directly interacts with the structure of the canopy which, disturbance apart, relates to the vertical profile of vegetation and to foliage attributes of local species (Montgomery and Chazdon, 2001; Wirth et al., 2001). Light quality and quantity are highly heterogeneous in time and space at various scales (Sterck et al., 1999; Wirth et al., 2001; Poorter and Arets, 2003).

This paper deals with the influence of local environment and dispersal distances on the abundance of saplings of three shade-tolerant and three light-demanding non-pioneer species either anemochorous or zoochorous. We conducted a continuous characterization of local conditions regarding disturbance, stand structure and canopy structure at the experimental research station of Paracou (French Guiana). The study was conducted in a control and a logged area to ensure variation in local conditions was captured. Zero Inflated Poisson (ZIP) models of sapling numbers were calibrated using a regular sampling design. ZIP models extend generalized multiple regression to the special case of count data with many zeros (Ridout et al., 1998).

Light-demanding species were expected to be more frequent in highly radiative environments, i.e. with open/disturbed canopy, and/or low densities of trees, whereas shade-tolerant species were expected to be more present in closed, stable and/or densely populated sites. Differences were expected in the establishment patterns of saplings in relation with dispersal syndromes, especially among anemochorous and zoochorous species. We first describe the level of heterogeneity in local environmental conditions, and then address the following questions: (i) Are sapling distribution explained by local environmental conditions and/or by distance to conspecific adults? (ii) Are the highlighted relations consistent with species temperaments a priori known from adult traits and dispersal syndromes?
2 Material and Methods

2.1 Study Site and census data

The study was conducted at the Paracou Experimental Station (5°18' N, 52°23' W) in the coastal part of French Guiana (figure 1.a). The climate of the region is equatorial with two main seasons: a dry season from August to Mid-November and a rainy season often interrupted by a short drier period form March to April. Annual rainfall in the vicinity of the station is 3041 mm (Gourlet-Fleury et al., 2004). The site is a em terra firma rainforest with tree community dominated by the Caesalpinaceae, Lecythidaceae, Chrysobalanaceae and Sapotaceae families (Sabatier, 1983).

The station experimental design includes twelve 9-ha (300×300 m) permanent sample plots (PSP) established in 1984 in undisturbed forest and assigned to three homogeneous blocks (figure 1.b). Within each plot all trees ≥10 cm DBH (diameter at breast height) are identified and located using geographic coordinates. Since 1984, all trees have been annually censused and DBH measured in a central 250×250 m subplot. Between October 1986 and January 1988, 3 silvicultural treatments of increasing intensity were applied in 9 out of the 12 PSP, according to a random plot design. Treatments consisted of selective logging and additional poison girdling for 6 plots (figure 1). A plot was left undisturbed in each block to serve as a control.

In this study, all data referring to advanced life stages (trees ≥10 cm DBH) derived from Paracou annual plot measurements. Data on the sapling stage derived from a census conducted in 2002 – 2003 on a continuous study area of about 30 ha involving 4 contiguous Paracou PSP (the Southern Block, figure 1). All saplings between 1 and 10 cm DBH of the 6 focal species were extensively surveyed and located using geographic coordinates over this area. Individual DBH were recorded in 1 cm classes.

2.2 Focal Species and life stages

We focused on tree species whose regeneration was abundant in the study area and easy to identify at the sapling stage. We selected 6 species exhibiting contrasting shade tolerance, three endozoochorous shade-tolerant species (Bocoa prouacensis (Aubl., Caesalpiniaceae), Oxandra asbeckii (Pulle, R.E.Fr., Annonaceae), Pogonophora schomburgkiana (Miers ex Benth., Euphorbiaceae)), and three anemochorous light-demanding non-pioneer species (Dicorynia guianaensis (Amshoff, Caesalpiniaceae), Qualea rosea (Aubl., Vochysiaceae), Tachi-
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gali melinonii (Harms, Zarucchi & Herend., Caesalpiniaceae)). Ecological groups, growth, size and dispersal traits are summarized in table I. Species membership to ecological groups is based on (i) previous studies on tree population dynamics conducted at Paracou (Favrichon, 1995; Collinet, 1997; Gourlet-Fleury, 1998; Molino and Sabatier, 2001) (ii) field observations of sapling occurrence. Those studies are essentially based on trees ≥ 10 cm DBH and little information is available for the sapling stage (but see Rankin-de Mérona and Montpied, 2004). Species are further named by their generic name.

Two life stages were defined by DBH thresholds (table I). DBH thresholds accounted for the contrasting temperaments of the focal species. We considered the sapling stage to recruit trees in the DBH class \([1, D_{\text{sap}}]\) where \(D_{\text{sap}}\) was the maximum DBH reached by an average individual of 1cm DBH installed one year after treatment at Paracou (1989). We used the mean growth rate of trees of the DBH class 10-15 cm, at Paracou, as a proxy for sapling growth rate. We then computed \(D_{\text{sap}}\) separately for each focal species (table I). The reproductive adult stage was defined by a seeding or maturity threshold (\(D_{\text{mat}}\), table I), an estimate of the species DBH at first diaspore dispersal. This parameter was set according to available literature on species reproduction (Doligez, 1996). The adult tree population involved all trees above \(D_{\text{mat}}\), including logged or naturally dead trees who were potential parents of saplings of the DBH class \([1, D_{\text{sap}}]\).

2.3 Response, distance and environmental variables

The initial sampling design included 261 sampling points distributed in 3 selected PSP of the Paracou Southern Block differing in past logging history (figure 1.c). Two points were removed from the initial set because of missing data. Within each PSP, we used a regular 12.5×12.5 m grid system at a minimal distance of 12.5 m from plot edges to prevent border effects. The density of saplings on 5 m-radius subplots centered on sampling points served as the response variable for each focal species. Larger 10 m-radius circular subplots centered on sampling points were used to calculate the variables characterizing stands and dynamics. This design allowed us to take into account lateral effects on focal places where saplings were counted.

At each sampling point, distance to the nearest conspecific adult (\(d_{\text{na}}\)) was computed separately for each species. When \(d_{\text{na}}\) was superior to the distance to the edge of the plot for a given species, the sampling point was removed from the analysis to avoid border effects. For each species, \(d_{\text{na}}\) served as an estimation of dispersal distances of saplings around the conspecific adults.
On the 10 m-radius subplots, we described the diameter distribution of all
trees considering 5 DBH classes (10 − 15, 15 − 20, 20 − 30, 30 − 40 and ≥ 40 cm)
and computed the total basal area of trees above 10 cm DBH ($G_{tot}$). In addition,
we calculated the specific basal area of some pioneer taxa ($G_{pioneer}$) as an
indicator of the intensity of past local disturbance (see Molino and Sabatier,
2001). Five pioneer taxa were selected among those of the seed bank to limit
biases in their local occurrence due to dispersal limitation: Cecropia obtusa
(Cecropiaceae), Cecropia sciadophylla (Cecropiaceae), Miconia spp. (Melastomataceae),
Palicourea guianensis (Rubiaceae), Schefflera morototoni (Araliaceae).

Two periods of interest were distinguished to characterize the temporal
dynamics of stands: (i) the period of implementation of the silvicultural treat-
ments extended by one year to account for residual mortality occurring after
logging and thinning (1986 − 1989), (ii) the period of recovery from logging
and thinning disturbances (1989 − 2003). Dynamics variables were calculated
as follows:

- **Damage**: cumulative loss of basal area due to felling, skidding or thinning
  over 1986-1989 ($dG_{damage}$),
- **Mortality**: cumulative loss of basal area due to natural tree death over 1989-
  2003. We distinguished treefalls ($dG_{treefall}$) from standing deaths ($dG_{standing}$)
as they imply different types of disturbance.
- **Recruitment**: cumulative basal area of trees recruited above 10 cm DBH
  between 1989 and 2003 ($dG_{recruit}$),
- **Stand recovery**: change in total basal area between 1989 and 2003 ($dG_{recover}$).

At each sampling point, hemispherical photographs (hemiphots) were taken
to characterize the canopy structure from below. Hemiphots are commonly
used in studies relating forest regeneration to light conditions in the under-
storey (Bebber et al., 2002; Nicotra et al., 1999; Poorter and Arets, 2003). In
the present case, we took hemiphots at 1.5 m above the ground with a digi-
tal camera (Nikon Coolpix 995) and analyzed the images obtained with the
imaging software GLA 2.0 (Frazer et al., 1999). The following variables were
computed:

- **PAI**: Plant Area Index (see Gower et al., 1999),
- **CO$_{20}$ and CO$_{50}$**: canopy openness restricted to solid angles, measured from
  zenith positions, of 20° and 50° respectively.

CO$_{20}$ accounted for gap fraction in a narrow angle above sampling points while
CO$_{50}$ integrated openness in a wider angle. PAI was used as an indicator of
overall space occupied by vegetation.
2.4 Data analysis

Relations among environmental variables. A Correspondence Analysis (CA, Jongman et al., 1995) was conducted on diameter distributions in order to synthesize information. We retained the two first axes (named diam1, diam2) as descriptors of local forest structures. A Principal Component Analysis (PCA) was used with the complete set of variables to inspect relations among environmental variables. Correlations between environmental variables were computed using Spearman’s rho statistic and tested with Spearman’s rank correlation tests. We pooled the two logged areas (figure 1.c) for a comparison of environmental conditions with the control, since they showed weak differences. Differences in mean values were tested with Mann-Whitney tests and differences in variances with Fligner-Killeen tests.

Zero Inflated Poisson Models. Modelling of sapling numbers was done using Zero Inflated Poisson (ZIP) models which extend generalized multiple regression to the special case of count data with an over-represented zero-class (Ridout et al., 1998; Dalrymple et al., 2003). ZIP have been used in ecology to model rare species occurrence (Welsh et al., 1996) for instance. In the ZIP formulation, observations are assumed to proceed from a dual regime process (Zorn, 1996). Zeros proceed either from the transition distribution of the event ”occurrence of a sapling” with a probability ω (structural zeros or supplementary zeros), or from a discrete distribution (classically a Poisson) at a given rate λ (sampling zeros) (Zorn, 1996; Ridout et al., 1998). If \( Y \) is the observed number of saplings, the underlying model is \( Y = BY^* \) where \( Y^* \) is a discrete random variable standing for the observations and \( B \) a dichotomous random variable, with \( B = 0 \) if \( Y \) is non-null and 1 otherwise. Here we used a binomial distribution and a Poisson distribution for \( B \) and \( Y^* \) respectively, so that \( Y \) followed the probability mass function (Johnson et al., 1992):

\[
p(Y = y_i) = \begin{cases} 
\omega_i + (1 - \omega_i)e^{-\lambda_i}, & y_i = 0 \\
(1 - \omega_i) \frac{y_i!}{y_i!} e^{-\lambda_i}, & y_i > 0
\end{cases}
\]

with \( y_i \): the number of saplings of the species observed at sampling point \( i \), \( \omega_i \): the binomial parameter at sampling point \( i \), \( \lambda_i \): the mean of the Poisson distribution. The expected value of \( Y \) is then: \( E(Y) = \mu = (1 - \omega)\lambda \).

The two distribution parameters \( \omega \) and \( \lambda \) were linked to environmental variables using the log and logit functions: \( log(\lambda) = X\beta \) and \( log(\frac{1}{1-\omega}) = Z\gamma \), where \( X \) and \( Z \) were matrices of environmental variables and \((\beta, \gamma)\) two vectors.
Parameters were estimated by Maximum Likelihood Estimation. Environmental variables were centered and scaled before analysis. We restricted \( Z \) to a unique variable, namely the distance to the nearest conspecific adult (\( dna \)) to account for structural zeros. So, we investigated the possibility that zero-inflation was due to dispersal limitation. The effect of \( dna \) on \( \hat{\mu} \) depends on the ratio \( \tau = \frac{\hat{\beta}_{dna}}{\hat{\beta}_{dna} - \hat{\gamma}_{dna}} \), where \( \hat{\beta}_{dna} \) and \( \hat{\gamma}_{dna} \) are the estimated coefficients of \( dna \) in \( X \) and \( Z \). If \( \tau \) is negative, \( \hat{\mu} \) is a strictly decreasing function of \( dna \). If \( \tau \) is positive, \( \hat{\mu} \) shows a maximum at some intermediate distance; the higher \( \tau \), the higher the distance.

For \( X \), we initially retained the whole set of variables. A stepwise method of model selection was then used on \( X \) to identify the most parsimonious model based on the Akaike Information Criterion (AIC) (McCullagh and Nelder, 1989). Major outliers were identified by checking standardized residuals and inconsistent points, and removed from the data after a first fit. A pseudo-\( R^2 \) (\( pR^2 \)) evaluated the goodness of fit: \( pR^2 = \frac{SSR}{SSM} \), where \( SSR \) is the normalized sum of squared residuals and \( SSM \) the normalized sum of squares about the mean. In the case of ZIP models with a logistic link, the null model reduced to a constant term is not nested within the overall model (Jansakul and Hinde, 2002). Hence, the \( pR^2 \) statistics is not used to compare models but indicates how the variability of the data around \( \hat{\mu} \) is reduced compared to the overall variance.

Models fits were interpreted by simulating sapling establishment curves, defined here as the distribution of sapling numbers as a function of the distance form the potential source, in three contrasting types of local environment. This method was used to summarize information contained in the environmental variables. The three types of environment were defined by selecting subplots with high contributions to either of the first two axes of the PCA on all variables, and low contributions to the other axes. We characterized each type of environment by the mean values of environmental variables in the corresponding subplots. For each species, the expected number of saplings \( \hat{\mu} \) was then plotted in the three conditions as a function of the distance to the nearest adult.
3 Results

3.1 Sapling occurrence

Saplings of the focal species occurred on 12 to 41 % of the sampled 5 m-radius subplots (table II). The most common species were Oxandra and Pogonophora, two shade-tolerant species, whereas Tachigali, a light-demanding species, was the less common one. In contrast, Qualea, another light-demanding species, was locally the most abundant species with a maximum of 19 saplings on one subplot. Three species showed a significant difference in mean numbers of saplings between the control area and the logged area: Qualea and Tachigali were more frequent in logged-over forest whereas Oxandra, a shade-tolerant species, was more abundant in undisturbed forest.

3.2 Environmental Conditions

Stand Structure. Total basal area was significantly higher and more variable on subplots in the control area compared to subplots in the logged area (table III). The CA of diameter distributions emphasized the weight of large trees in local forest structures. The first and second axes of the analysis accounted for 33 % and 25 % of total inertia respectively, the first axis being positively driven by the number of trees in the classes 30 – 40 cm, and ≥ 40 cm DBH, and the second axis being positively influenced by the number of trees in the middle classes (15 – 20 and 20 – 30 cm). The control area showed significant higher scores on the first axis and lower scores on the second axis when compared to the logged area (table III). Pioneer basal area was significantly higher in the logged area. Out of 137 subplots occupied by pioneer trees, three occurred in the control area.

Canopy Structure. Thirteen years after logging, canopy structure showed significant differences between the control and the logged area (table III). Measures of canopy openness (CO20 and CO50) were higher in the logged area, while PAI was higher in the control area. Variability was similar for the three variables in both conditions.

Stand history. Mean basal area removal due to logging amounted to 12.7 m².ha⁻¹, while during the same period the loss of basal area was 1.5 m².ha⁻¹ from natural mortality in the control area (table III). Disturbance due to logging implied different pathways during the following 13-year period. The
loss of basal area due to natural mortality was higher in the logged area after logging, both for treefalls and standing trees deaths. Recruitment over 10 cm DBH was four times higher in the logged area. During the recovery period, the control and the logged area showed a gain in basal area indicated by positive mean values of \( dG_{\text{recover}} \). The gain was significantly higher in the logged area. The variability of dynamical variables was also higher in the logged area (table III) indicating high heterogeneity in this area.

3.3 Definitions of three contrasting environments

In the PCA on all environmental variables the first and second axis explained 25 % of the total variance (16 % for the second axis) (figure 3). The first axis was positively driven by \( dG_{\text{damage}} \), \( dG_{\text{recruit}} \), \( G_{\text{pioneer}} \) and negatively by \( \text{diam1} \) and \( G_{\text{tot}} \), thus indicating a gradient of logging disturbance. The second axis was positively driven by \( dG_{\text{standing}} \), \( \text{PAI} \) and negatively by \( dG_{\text{recover}} \) and \( \text{CO}_{50} \).

Pair correlations confirmed the relations shown by the PCA (table IV). Correlations between dynamics variables were significant at \( 10^{-3} \) level (Spearman’s rank tests), except for \( dG_{\text{standing}} \) which was negatively correlated to \( dG_{\text{recover}} \) only (table IV). The highest correlations among variables of structure and dynamics arose between \( dG_{\text{recruit}} \) and \( G_{\text{pioneer}} \) (0.72) and \( dG_{\text{recruit}} \) and \( G_{\text{tot}} \) (-0.63). Variables of canopy structure showed low correlations with the other environmental variables, the higher values being achieved by \( \text{PAI} \). The Plant Area Index was negatively correlated with \( dG_{\text{recruit}} \), \( dG_{\text{recover}} \), and \( G_{\text{pioneer}} \).

Three sets of subplots were isolated to define contrasting environmental conditions (figure 2). The disturbed type \( (n = 13) \) gathered subplots in heavily disturbed conditions, with low basal areas and pioneer trees (figure 3). Above those subplots, canopy showed high openness in both solid angles (with variability for the 20° angle) and low \( \text{PAI} \). In the stable environment \( (n = 11) \), subplots exhibited low values of dynamics variables, in particular \( dG_{\text{treefall}} \), \( dG_{\text{standing}} \), \( dG_{\text{recruit}} \) (low turnover), high total basal area, high \( \text{diam1} \) scores and no occurring pioneer tree. Canopy structure was weakly variable and showed closer mean conditions compared to the disturbed environment.

Subplots in the intermediate environment \( (n = 9) \) were characterized by high values of \( dG_{\text{standing}} \) and \( dG_{\text{treefall}} \), i.e. by important natural mortality during the recovery period. Yet, the mean size of the trees involved in tree falls was lower than in the disturbed environment (not shown). \( \text{PAI} \) were the highest in the intermediate environment, whereas \( dG_{\text{recover}} \), \( \text{diam2} \), \( \text{CO}_{20} \) and \( \text{CO}_{50} \) were the lowest. Overall, those characteristics indicate unstable places with
frequent mortality events involving small trees, leading to small canopy openings favoring the growth of remaining neighbors. Regarding canopy structure, this type of environment showed the most closed and variable conditions.

3.4 ZIP models of sapling numbers

Model selection identified a set of most explanatory variables of sapling numbers and different significant relations according to the focal species (table V). Values of $pR^2$ ranged from 0.12 for Pogonophora to 0.51 for Tachigali.

Sapling numbers in three contrasting environments. The most informative variables differed between species as well as the sign and level of the relations (table V). Variables of stand structure were retained in five cases out of six: sapling numbers of Bocca were insensitive to those variables. The most sensitive species to canopy structure was Tachigali: the three hemiphots variables were retained in the model with significant effects for $CO_{50}$ and PAI. Oppositely, those variables did not explain sapling numbers of Dicorynia. In each of the six models, at least two variables of stand dynamics were retained as informative (two for Oxandra).

Predicted sapling numbers contrasted from one type of environment to another. For the three light-demanding species, the highest numbers of saplings were predicted in the disturbed environmental conditions (figure 4). Among those species, predictions reached intermediate values for Dicorynia and Qualea in the intermediate environment type. Differences between disturbed and other conditions were higher for Dicorynia than for Qualea. Predicted patterns were flat and low for Dicorynia in the stable conditions and for Tachigali in the intermediate conditions. Among shade-tolerant species, predicted sapling numbers were maximal in the stable or intermediate conditions and minimal in the disturbed conditions. Pogonophora and Bocca achieved similar predicted numbers in the stable and intermediate conditions while Oxandra showed slightly higher values in the intermediate compared to the stable conditions.

Sapling numbers and dispersal distances. Our formulation of ZIP models allowed for a twofold influence of distance to the nearest potential adult (dna) on sapling numbers. dna affected the presence/absence of saplings in the binomial part of the models. Such a binomial effect could mimic either strong clumping of saplings around adults or, on the contrary, spacing between occupied cells and adults. In the Poisson part of the model, dna accounted for the decrease of abundances with distance as generally observed in dispersal patterns.
The binomial effect of dna on sapling numbers was significant at the 5 \% level for Qualea and Pogonophora (table V). Among variables selected in the Poisson part, dna was retained as a significant explanatory variable in the six final models. The overall influence of dna on sapling numbers was strictly negative for two species out of six: Dicorynia and Oxandra (figure 4). Establishment patterns showed maxima for the four other species (figure 4), at about 30 m for Tachigali, Pogonophora and Bocoa, and 45 m for Qualea. At further distances, sapling numbers decreased sharply with increasing distance for Qualea and Bocoa, due to a strong binomial effect (table V). Regarding horizontal scales, the highest dispersal distances were achieved for Tachigali and Pogonophora respectively.

As a comparison, actual maximal dispersal distances, approximated by the maximal observed value of dna, were achieved by the three anemochorous light-demanding species (Qualea: 72 m, Tachigali: 65 m, and Dicorynia: 56 m). Pogonophora showed the lowest maximal distance to nearest conspecific adult actually achieved among focal species (26 m).

4 Discussion

Our results bring some support to the hypothesis that in most cases, both niche partitioning and recruitment limitation through dispersal play a part in determining the distribution of particular species. The effect of the environment appeared to be significant in all cases. Dispersal limitation at the studied stage appeared in the influence of the distance to nearest potential adult on sapling numbers. Patterns revealed by the zip models were coherent with expectations based on a priori temperaments.

4.1 Species - environment relations

Differing predicted abundances with local conditions can be interpreted as variations in survival to the sapling stage. In particular, the influence of the most extreme conditions allows to refine temperaments at the studied stage. According to an increasing degree of shade-bearing, species ranked as such: Tachigali < Dicorynia < Qualea << Pogonophora < Bocoa < Oxandra. This ranking is coherent with general knowledge available for the focal species, although it raises questions when examined in detail.

For Tachigali, a light-demanding species, conditions of the intermediate environment proved to be less favorable than in the stable one, whereas it was more favorable for Oxandra, a shade-tolerant species. In this type of environ-
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ment, mortality of small trees generated small canopy gaps which promote rapid closure of the vegetation and are characterized by high PAI values. Although not a pioneer, *Tachigali* is known to be very light-demanding (*Favre-Schon*, 1995; *Gourlet-Fleury*, 1997). In intermediate conditions, canopy gaps seldom provided favorable conditions to the saplings of *Tachigali*, while larger canopy gaps could occur in stable environments. In contrast, *Oxandra* probably benefits from intermediate conditions to settle, being mainly sensitive to the occurrence of small gaps. In a study of the influence of small canopy gaps, *Svenning* (2000) showed that most of the studied shade-tolerant species occurred in the lighter parts of the understorey.

Species temperaments at sapling stage differed from those known through the dynamics of advanced life-stages at Paracou for *Dicorynia* and *Qualea*. *Qualea* is generally thought to be more light-demanding than *Dicorynia* and to react more strongly to stands opening (*Gourlet-Fleury*, 1997; *Gourlet-Fleury* and *Houllier*, 2000). Despite similar ranking for both species among the three studied environments, sapling numbers of *Qualea* appeared less affected by local conditions in the intermediate type. In a study of changes in saplings stocks over the period 1992 – 1995, *Qualea* positively reacted to increasing intensity of disturbance, while *Dicorynia* showed more complicated response patterns (*Rankin-de Mérona* and *Montpied*, 2004). *Baraloto* (2001) showed a lack of influence of continuous light levels or soil conditions on survival of seedlings of *Dicorynia*, while saplings preferred open conditions when characterized by coarse light indices.

Responses of four species out of six differed in contrasting local environments, while *Pogonophora* and *Bocoa* showed similar responses in the stable and intermediate environments. Such decoupling of responses and local conditions suggest plasticity in survival requirements at the studied stage. The relation of CO$_{20}$ with sapling numbers of *Pogonophora* indicates that the species may benefit from vertical light in small gaps for its persistence at the sapling stage. *Kammesheidt* (2000) studied some late-successional and generalist species and showed that establishment of trees of those species could occur in small gaps and under the light canopy of early successional species. Shade-tolerant species may also benefit from lighter conditions due to border effects in logged places. Such effect was evidenced for *Bocoa* for which the most significant relation with an environmental variable was achieved with dG$_{damage}$. Consistent with this finding, *Rankin-de Mérona* and *Montpied* (2004) showed that saplings growth of *Bocoa* benefited from logging in two types of sivicultural treatments out of three.
4.2 Establishment curves of saplings around adults

Dispersal distances measured to the nearest potential adult significantly explained sapling numbers for the six studied species. From model calibration, we could simulate curves of sapling numbers around potential adults. As we considered already settled life-stages, the predicted curves resulted from seed dispersal and subsequent survival to the studied stage. These curves thus reflect sapling establishment as a function of distance from potential adults (Nathan and Casagrandi, 2004). Two types of patterns were detected, either strictly decreasing or leptokurtic with a peak at intermediary distance.

Sapling establishment curves peaked at intermediate distances for four species, two anemochorous and to endozoochorous. Such features are expected in a Janzen-Connell recruitment scheme under local dispersal strictly decreasing with distance and survival increasing with distance through some density-dependence mechanism (Nathan and Casagrandi, 2004). These requirements are not always fulfilled, and such peaks could appear in various conditions here. Sapling numbers of Bocoa were low so that either density-dependence is unlikely for this species, or it occurred in earlier life-stages. Meanwhile, seeds of Bocoa are mostly dispersed by bats dropping seeds on a wide range of distances, from a few meters up to several kilometers from seeds sources (Galindo-Gonzalez, 1998). A strictly decreasing seed dispersal curve might not well describe features of the seed dispersal pattern (Travis and French, 2000).

Regarding Tachigali, occupied subplots were on average located further from adults than vacant subplots. Wind dispersal and sapling survival in suitable conditions rarely close to adults presumably produced this pattern.

Strictly decreasing establishment curves occurred for two of the studied species, Dicorynia and Oxandra. Such curves may arise under local dispersal and various survival distribution, slowly increasing (Hubbell pattern in Nathan and Casagrandi, 2004) or decreasing with distance (McCanny pattern). Although, such cases cannot be discriminated here because we lack data about survival, our results are consistent with local dispersal for these two species. Dispersal of seeds and fruit is limited in Dicorynia despite anemochorous traits (Sabatier, 1983; Loubry, 1993). Maximal dispersal distances vary from 25 to 60 m (Sabatier, 1983; Forget, 1988), a range consistent with observed and predicted dispersal distances of saplings in this study. Such pattern also exists in trees ≥ 10 cm DBH who occur in clusters of radius about 50 m at Paracou (Collinet, 1997; Dessard et al., 2004). Among the three studied shade-tolerant species, Oxandra showed the lowest dispersal with maximal predicted distance of about 50 m. The species is endozoochorous and seeds are mainly bird-dispersed (Sabatier, 1983). Median seed dispersal distances were estimated
below 10 m in disturbed and undisturbed plots of Guyana (Ulft, 2004).

Inference of seed dispersal pattern and recruitment patterns from disper-
sal syndromes is a challenging question in ecology (Wang and Smith, 2002; Howe and Miriti, 2004). Seed shadows of zoochorous species depend on many factors such as foraging and feeding habits of dispersers (Howe, 1989). Further mortality filters modify the patterns across life-stages (Schupp and Fuentes, 1995; Clark et al., 1999). However, while a variable amount of seeds disperse at long distances, regarding the study scale, part of the seed rain is dispersed locally (Howe and Miriti, 2004; Ulft, 2004) and primarily determines establishment chances near parents, as for Oxandra for instance.

Anemophilous species are commonly thought to disperse effectively. In this work, anemophilous species achieved the highest observed as well as pre-
dicted dispersal distances. High variability occurred among those species, with low distances for Dicorynia, intermediate for Qualea, and maximal for Tachigali. Such variability occurred despite similar volumes and dispersal attributes of diaspores for Tachigali and Qualea (seed and fruit respectively) (Roosmalen, 1985; Sabatier, 1983). Theoretically, the efficiency of wind dispersal greatly depends on the forest structure and on the release height of seeds (Nathan et al., 2001), so that this strategy may not be advantageous in dense closed forests, however mostly harboring zoochorous species. Further work could question the impact on wind dispersal of disturbance increasing canopy roughness.

Establishment curves appeared spatially limited for all species, predicted sapling numbers being null at about 50-90 meters. These findings depend on some methodological issues, since nearest neighbors methods tend to under-
estimate actual dispersal distances (Nathan and Muller-Landau, 2000). More realistic stating of dispersal distances could be achieved by taking into account overlapping seed shadows through inverse modeling (Ribbens et al., 1994). Uncertainty in the reproductive sizes of trees also influences the es-
timation of dispersal distances. Ulft (2004) found that minimal and median DBH of 60 fruiting or flowering trees of Oxandra were respectively 5 and 14 cm. The value Dmat of 10 cm used here probably over-estimates the minimal size at maturity for the two sub-canopy species Oxandra and Pogonophora. Considering already settled individuals over 1 cm DBH compensates for such effect since the actual parents should be found in non-firstly fruiting trees.

4.3 Post-logging environment and regeneration

Silvicultural treatments induced an enforced disturbance regime in logged-
over stands which resulted in higher recruitment, natural mortality and recov-
Sapling distribution in a tropical forest understorey

Diameter distributions were shifted towards low DBH classes and basal areas towards low values 18 years after disturbance. Differences in the structure of the canopy also persisted, the forest cover being more open in the logged area than in the control area. In another logged forest of French Guiana, canopy was more open near stumps of cut trees, up to 30% immediately after disturbance, and to a lesser extent twelve years after logging at Paracou (Baraloto and Forget, 2004).

Canopy structure evaluated through hemiphots appeared independent of stand structure and dynamics (see also Ferment et al., 2001). Differences of spatial and temporal scales in the evolution of stand and canopy structures may explain independence. Also, variables of stand structure could not account for plants present in the understorey (trees <10 cm DBH, palms) which contributes to closure in hemiphots. However, measures using different solid angles capture variation in canopy structure more finely than coarse canopy openness alone, and also limit the influence of slope on computation.

Environmental conditions varied among PSP in relation with silvicultural treatments and inside the PSP. Similar site conditions and history occurred in differing levels of disturbance at the PSP scale. Shade-bearing species partly benefited from this local heterogeneity and could persist in areas disturbed on a coarser scale. Among the six species studied, Bocoa, Dicorynia, Tachigali, and Qualea are commercial species logged in French Guiana for their timber. Aggregated species as Dicorynia could suffer heavy damage when larger trees are logged. The light-demanding character of the species could compensate this drawback as saplings would benefit from logging for their survival. RIL techniques should be highly recommended to lower the impact of logging and maintain high heterogeneity in logged stands.

5 Conclusion

This study focused on relations between saplings, adults and the local environment for species of different temperaments. Using ZIP models, we addressed the possibility of simultaneously acting dispersal limitation and niche separation on sapling numbers at our study scale. We conducted a continuous characterization of the local environment regarding past disturbance, stand structure, and canopy structure. The focal species showed coherent relations with environmental conditions according to a priori assessments of their temperaments and showed different sensitivity to local environmental conditions. The conservative estimation of dispersal by distance to nearest adult showed
that dispersal limitation influenced relations between saplings and adults. Patterns were different from one species to another presumably in relation with their dispersal mode. Further improvement of ZIP models of sapling numbers could involve refinement in the characterization of the local environment, including timing from disturbance for instance, and the inclusion of environmental variables in the binomial part of the models. Threshold effects of environmental conditions on the occurrence of saplings of a given species may be detected. This type of model could provide insights into the temperament of poorly known species, and also improve recruitment modelling in spatially explicit models of tropical forest dynamics.

6 Acknowledgements

We thank Sébastien Jésel and Hélène Dessard - CIRAD, Montpellier, France - for providing corrections and useful comments on the manuscript. We also thank Valéry Gond - CIRAD, Cayenne, French Guiana - and Kathelijne Hellemans - Universiteit Antwerpen, Belgium - who collaborated in hemiphotos acquisition, and Lilian Blanc, Jean-Gaël Jourget, Pascal Pétronelli - CIRAD, Kourou, French Guiana - and the field workers at the Paracou station who participated in data collection. We would like to thank the two referees and the associate editor whose comments provided substantial refinement of the manuscript.

References

Sapling distribution in a tropical forest understorey

des spp pb pour la troisième prémisse: plus difficile à prouver: deux études détaillées, ds les 2 cas augmentation de la richS sp. dans les trouées par effet d’augmentation de densiT "the chance occurrence of gaps interact with recruitment limitation to permit species coexistence".


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Leishman, M., Westoby, M., Jurado, E., 1995. Correlates of seed size variation:
a comparison among five temperate floras. Journal of Ecology 83, 517–530,
recherche de syndromes parmi cinq grands ensembles floraux test de la forme
de vie, taille, caractéR perN, mode de dispersion pas de prise en compte de
la phylogénie (contrainte possible ignorée) car phylogénie et écologie non
exclusives.
: dissémination et parasitisme des graines avant dispersion chez un arbre
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determinants and consequences for recruitment. Trends in Ecology and Evo-
of light and woody seedling regeneration in tropical forests. Ecology 80 (6),
1908–1926, mesures de lumière, directes (LAI, quantum sensors) et indi-
rectes (photos) le long de transects (130-160m de long), 3 par sites de nature
diff. (old gr., logged, secondary forest) subdivisé en minitranssects (1*25m).
Inventaire de juvéniles (quadrate 1mš>4mš) entre 20-100cm Résultats : -
plus de sites en conditions sombres en "old" qu’en "second growth" - modèles
de variogrammes : bons fits jusqu’à 40m en "old" , - variations des gammes
de distances de corrélation spatiale : LAI<lumiR transmise<canopyOp, dis-
tance "old" > distance "second" - Juvéniles : - abondants en "second" / "old",
apas de tendance claire entre sites.
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rain forest trees. In: Gomez-Pompa, A., Whitmore, T., Hadley, M. (Eds.),
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Schupp, E., Fuentes, M., 1995. Spatial patterns of seed dispersal and the uni-


Swaine, M., Whitmore, T., 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75, 81–86, "To classify species into groups or guilds imoses a degree of simplification which reduces information content, but reveals general patterns and facilitates prediction about forest processes" définition des notions de "pioneer"/"non-pioneer", subdivision à l’intérieur de ces groupes: arbitraires, car continuum, mais utiles.


Sapling distribution in a tropical forest understorey

la survie des plantules, - temps pdt lequel une plantule peut survivre à des PAR faibles, - quantité de PAR nécessaire pour "quitter la banque des plantules" pb des études sur plantules: étape de l’établissement non appréhendée (ex.: sur BCI, 79 possible de la littérale zonation à l’intérieur des trouées. peu d’étude sur la zone d’influence des trouées (zone limite perturbée jusqu’à 250m) spp pionnière plus plastiques que climax en général Morphologie des plantules: compromis entre ombre interne (diminuée par plagiotropie) et croissance (orthotropie) selon Hallé et Oldeman, trois facteur principaux: Xce apicale/radiale, symétrie radiale/bilatérale, Xce continue/intermittente Réponse aux nutriments: pas de schéma clair, perturbation de sol forestier > pic de nutriments disponibles après perturbation, mais non systématique. réponse variable sols des forêts humides plutôt pauvres, pas de preuve d’interactions entre nutriment et lumière CONCLUSION: il existe une dichotomie de répartition entre pionnière et climax spp, mais entre les deux extrêmes, recouvrement fréquent des spp le long d’un gradient de taille des trouées. pas surprenant compte tenu de l’hétérogénéité des conditions clim. dans les trouées. radiation solaire probablement le paramètre le plus important (PAR, et autre paramètres microclim fortement corrélés à çà. donc spécialisation des spp climax à une taille particulière de trouée peu probable.


Table I

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<tr>
<th>Species</th>
<th>Family</th>
<th>Group</th>
<th>Dispersal mode&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Mean growth&lt;sup&gt;b,c&lt;/sup&gt; (cm.yr&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>H&lt;sub&gt;max&lt;/sub&gt;&lt;sup&gt;b,c&lt;/sup&gt; (m)</th>
<th>D&lt;sub&gt;max&lt;/sub&gt;&lt;sup&gt;d&lt;/sup&gt; (cm)</th>
<th>D&lt;sub&gt;mat&lt;/sub&gt; (cm)</th>
<th>D&lt;sub&gt;sap&lt;/sub&gt; (cm)</th>
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<td>75</td>
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<td><strong>L</strong></td>
<td>A</td>
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<td>45</td>
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<td>Annonaceae</td>
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<td><strong>EZ</strong></td>
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<td>20</td>
<td>29</td>
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Table II
Summary of species distributions. **Max.**: maximal observed number of saplings on a 5 m-radius sampling subplot. **Occurrence**: % of sampling subplots with at least one sapling. **Cont., Log.**: mean number of saplings on subplots in the control area (Cont., \( n = 81 \)) and the logged area (Log., \( n = 178 \)), and number of adult trees per ha in the two areas.

<table>
<thead>
<tr>
<th></th>
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<td>Qualea</td>
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<td>Bocoa</td>
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<td>0.17</td>
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<td>Oxandra</td>
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<td>1.89</td>
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<td>Pogonophora</td>
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<td>0.53</td>
<td>0.87</td>
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Table III
Heterogeneity of local environment. Mean, standard deviation ($\sigma$) and coefficient of variation (C.V) of variables in the control (Con., $n = 81$) and logged areas (Log., $n = 178$), and tests of differences between the two areas. p-values from Mann-Whitney (M.W) tests for means and from Fringel-Killeen tests (F.K) for variances (****: $< 10^{-3}$, **: $< 10^{-2}$, * : $< 5.10^{-2}$, n.s : $>5.10^{-2}$). Units are m$^2$.ha$^{-1}$, except for diam1 and diam2 (scores), CO$_{20}$, CO$_{50}$ (%) and PAI (ratio).

<table>
<thead>
<tr>
<th>Type</th>
<th>Variable</th>
<th>Mean</th>
<th>M.W</th>
<th>$\sigma$</th>
<th>F.K</th>
<th>C.V</th>
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<td>Stand</td>
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<td></td>
<td>diam2</td>
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<td>0.0123n.s</td>
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<td></td>
<td>G$_{tot}$</td>
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<td>15.2</td>
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<td>Canopy</td>
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<td>PAI</td>
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<td>0.2n.s</td>
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</tr>
<tr>
<td>Dynamics</td>
<td>dG$_{damage}$</td>
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<td>dG$_{treefall}$</td>
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<td>2.3</td>
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<td>2.2n.s</td>
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<td>dG$_{recruit}$</td>
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<td>5.8**</td>
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**Table IV**

Correlations among environmental variables. Spearman correlation matrix of environmental variables (p-values from Spearman rank correlation tests: ****: $< 10^{-3}$, ***: $< 10^{-2}$, *: $< 5.10^{-2}$)

<table>
<thead>
<tr>
<th></th>
<th>diam2</th>
<th>Gtot</th>
<th>Gpioneer</th>
<th>CO20</th>
<th>CO50</th>
<th>PAI</th>
<th>dG_damage</th>
<th>dG_treefall</th>
<th>dG_standing</th>
<th>dG_recruit</th>
<th>dG_recover</th>
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<td>-0.16**</td>
<td>-0.12</td>
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<td>diam2</td>
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<td>0.12</td>
<td>-0.06</td>
<td>-0.006</td>
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<td>Gtot</td>
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<td>0.15*</td>
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<td>dG_recruit</td>
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Table V
Summary of calibrated Zero Inflated Poisson Models for the six focal species. For species-variable pair, the first line indicates the value of the estimated coefficient and significance level (***: < 10\(^{-3}\), **: < 10\(^{-2}\), *: < 5.10\(^{-2}\)), and the second line the associated standard error in italics. For intercepts (Int.), and distance to nearest adult (dna), subscripts refer to the binomial (Z) or the Poisson (X) distribution in the models. No value (-) indicates that the corresponding variable was not retained in the stepwise selection procedure. \(pR^2\): value of the pseudo-\(R^2\) statistics. Dg: *Dicorynia*, Qr: *Qualea*, Tm: *Tachigali*, Bp: *Bocoa*, Oa: *Oxandra*, Ps: *Pogonophora*.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Species</th>
<th>(Dg)</th>
<th>(Qr)</th>
<th>(Tm)</th>
<th>(Bp)</th>
<th>(Oa)</th>
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<td>0.23 **</td>
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<tr>
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<td>-</td>
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<td>1.6 **</td>
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<td>-</td>
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<td>3 ***</td>
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<td>-</td>
<td>-0.24 *</td>
<td>0.46 *</td>
<td>0.86</td>
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Legends of figures

**Figure 1:** a) Location of Paracou station in French Guiana, b) Map of the twelve original permanent sample plots PSP of the experimental station. Treatments were applied between 1986 and 1988 with 3 repetitions per treatment in a random block design. T1: selective harvesting of timber from 58 commercial species (diameter cutting limit: 50 or 60 cm DBH according to species). T2: selective harvesting of timber followed by stand thinning involving the poisoning of all non-commercial species ≥ 40 cm DBH. T3: selective harvesting of timber and non-commercial species for fuelwood (diameter cutting limit 40-50 cm DBH) followed by stand thinning of all non-commercial species ≥ 50 cm DBH. T0: undisturbed control plots (Gourlet-Fleury et al., 2004). The present study was conducted in three of the four PSP of the Southern Block. c) Map of the Southern Block and sampling design. Sampling points were located in the control and in two of the logged plots of the block. In the text, we refer to the control area (n = 81 sapling points) and the logged area (n = 178).

**Figure 2:** Relations among environmental variables. Factorial map of the first two axis of the PCA of environmental variables on subplots in the control (black) and logged (gray) areas. Enclosed graph shows the distribution of the eigenvalues. Three sets of points are displayed with special symbols corresponding to the three defined contrasting local environments: disturbed (▽), stable (□) and intermediate (△).

**Figure 3:** Environmental conditions in three types of local environment Box-plots of the environmental variables for the three sets of subplots defining the contrasting environments (disturbed: n = 13, intermediate: n = 9, stable: n = 11). Solid lines in the boxes and stars respectively identify medians and means. Whiskers extend to the lowest and greatest quartile, circles represent extreme data.

**Figure 4:** Predicted dispersal patterns in three contrasting environments. Predicted numbers of saplings calibrated from ZIP models as a function of distance to the nearest conspecific adult in the three defined types of environmental conditions. Horizontal spatial scale is constant on all graphs. Vertical axis scale varies among species, depending on their commonness in the study area.

**Figure 5:** Distances from sampling subplots to nearest conspecific adult for the six focal species. Vacant: sampling subplots with no sapling of the species, Occupied: sampling subplots with at least one sapling of the species. The width of the boxes depends on the number of observations in each group. Solid lines in the boxes and stars respectively identify medians and means. Whiskers extend to the lowest and greatest quartile, circles represent extreme data.
Fig. 1.
Fig. 2.
Fig. 3.
Fig. 4.
Fig. 5.

**D. guianensis**

**B. prouacensis**

**T. melinonii**

**O. asbeckii**

**Q. rosea**

**P. schomburgkiana**