

Shade-tolerance and dispersal of non-pioneer tropical rain forest tree species: is there a competition-colonization tradeoff ?

Abstract

Question: Is there a relationship between competition and colonization abilities of non-pioneer tropical rain forest tree species? If so, is it consistent with the competition-colonization trade-off?

Location: Paracou experimental site, Sinnamary, French Guiana.

Methods: We propose a statistical modeling approach of species performance defined as local sapling density along gradients of past and present environmental heterogeneity. We use Zero Inflated Poisson models to account for zero over-representation in sapling density of fifteen non-pioneer tropical rain forest tree species. We derive proxies of species abilities from the calibrated models: the response of sapling density to a disturbance gradient measures species competition ability, whereas spatial dispersal of saplings measured by distance to adults reflects species ability for colonization. We relate these proxies to species traits commonly used as surrogates of those abilities: wood density and seed volume.

Results: Sapling density showed significant relationships with environmental heterogeneity for fourteen species. Species response to a disturbance gradient consistently varied with shade-tolerance. A significant relationship was found between species response to disturbance and wood density. Regarding dispersal, sapling density varied significantly with distance to adults for seven species. Dispersal limitation was consistent with dispersal modes efficiency. But no relation was found between sapling dispersal and seed volume. For eight species, among which six were animal-dispersed, sapling density was independent of adults position.

Conclusions: Our results challenge the competition-colonization trade-off hypothesis for non-pioneer tropical tree species. The analysis of sapling pattern suggested a decoupling between response to disturbance and dispersal. Meanwhile, the observed differences in competition and colonization abilities were consistent with the *a priori* ranking of species according to shade-tolerance and dispersal mode efficiency. We propose alternative hypotheses to the competition-colonization trade-off.

Key words: coexistence mechanisms, local density, Zero Inflated Poisson models, disturbance gradient, Paracou, French Guiana

1 Introduction

Trade-offs constrain species performance in biological functions (*e.g.* reproduction or nutrition) and promote species coexistence in species-rich communities such as tropical rain forests (Tilman and Pacala, 1993; Kneitel and Chase, 2004). Such constraints appear because living organisms exploit a limited amount of energy at one time, and during their life-time. Regarding plant fecundity, the seed size-number trade-off is a well-known example of such limitation on reproductive outputs (Greene and Johnson, 1994; Westoby *et al.*, 2002). The existence of Trade-offs preclude the emergence, through natural selection, of a "super-species" Tilman (1990) (or "Hutchinsonian demons" Kneitel and Chase, 2004), *i.e.* species that would perform the best across spatial and temporal scales. Tradeoffs are thus key elements in the ecological niche theory because they help explain how and why species differ in their strategies to sustain populations.

The most discussed is probably the Competition-Colonization Trade-off (CCT) according to which competition and colonisation abilities are negatively correlated (Turnbull *et al.*, 1999; Yu and Wilson, 2001; Higgins and Cain, 2002; Clark *et al.*, 2004b). This hypothesis actually address several important components of population dynamics. Competition is the process through which a species causes a decrease in the colonisation rate of another, whereas colonisation is the process of producing adults in new sites (Yu and Wilson, 2001). Competition affects tree growth and development at all life-stages.

This process takes various forms regarding whether nutrients or light are considered (Craine, 2005). Colonisation is basically a sequential process in that colonisation abilities depend on species fecundity which controls the number of dispersed diaspores and dispersal itself which is either spatial, through seed shadows, or temporal, through soil seed banks (Grubb, 1988).

According to the CCT, limited colonization abilities restrain superior competitors to a subset of favorable sites in a community. Such heterogeneity favors less competitive species who colonize sites where competition intensity is low, for instance after a disturbance event. In deterministic community models, the CCT acts as a stabilizing mechanism of species coexistence. Whether this situation could be generalized or not remains unsolved (Levine and Rees, 2002; Clark, 2005). Empirical evidence remains scarce and mostly comes from temperate annual systems (Tilman, 1990; Turnbull *et al.*, 2004).

The degree to which the CCT operates in tropical tree communities has not been tested yet. As regards forests tree species, little is known because temporal and spatial scales challenge population parameters assessment for such perennial organisms (Clark, 2005). The pioneer syndrome matches predictions of the CCT in that pioneer species are good colonizers and poor competitors: they depend on the high light levels of disturbed sites to achieve their life-cycle. Yet, most of tropical trees species are non-pioneer with diverse and poorly known strategies.

A strict ranking of species, as regards competition and colonization abili-

ties, is required for the CCT to operate. But complementary mechanisms may relieve such determinism since trade-offs are multiple and not independent. According to the successional niche hypothesis, species competition capacities depend on resource supplies so that a trade-off exists between species performances at low and high resource levels (Rees *et al.*, 2001; Craine, 2005). Trade-offs may also be at work within the colonisation process, for instance between fecundity and dispersal (Yu and Wilson, 2001; Clark, 2005).

A major issue in assessing the relevance of the CCT is to define pertinent and measurable proxies to characterize species competition ability and colonization ability. Ranking species according to competition ability usually requires experiments in order to compare species performances in controlled conditions (Baraloto *et al.*, 2005). As for trees, such methods are difficult to apply, save on seedlings and *ex situ*. Moreover, ontogenic shifts are likely so that the evaluation of competitive abilities is life-stage-dependent. Colonisation capacities may be evaluated in a *forward* approach, *i.e.* from the pattern of adults to the seed rain and subsequent stages (Wang and Smith, 2002). Alternatively, in a *backward* approach, the relationship between young trees and conspecific adults patterns provide insights into the conditions for effective settlement. The considered stage then needs to be young enough to ensure that the dispersal signal remains in the studied patterns.

Species abilities (*hard* traits, sensu Hodgson *et al.*, 1999) depend on particular soft traits. Wood density relates to competition ability in that it depends

on species strategies for resource allocation and conservation: light-wooded species tend to have high growth rates and low resistance to damage and pathogens, whereas heavy-wooded species are slow-growing and less vulnerable species. In grasslands, large-seeded species tend to win in competition with smaller-seeded species (Turnbull *et al.*, 1999, 2004). Seed mass then serves as a relative criterion to rank species colonisation abilities, or even as a surrogate for the CCT (Turnbull *et al.*, 1999; Levine and Rees, 2002). But this shortcut may miss critical aspects of the colonization process. In tropical forests, species are mostly animal-dispersed, often over 80% (Sabatier, 1983; Hammond *et al.*, 1996). Furthermore, the output of such a mutualism, that is the seed shadow, depends on various dispersers traits: body mass, home range, social organization or territoriality induce high variability.

Here, we address the evidence of a trade-off between competitive and colonization abilities of tropical tree species. The proposed approach deals with competition for light and spatial dispersal. We focused on a set of non-pioneer species that *a priori* differ in their shade-tolerance at adult stage and in their dispersal modes. Following Austin (2002), we inferred species abilities from the analysis of patterns of settled saplings. Species performance was measured as the local density of the sapling stage which is an instantaneous measure of the installation success. For each species, we calibrated a statistical model of sapling density based on explicative variables measuring past and present environmental heterogeneity. Zero-Inflated Poisson models were used

to account for zero over-representation in sapling density (Lambert, 1992; Welsh *et al.*, 1996; Ridout *et al.*, 1998; Flores *et al.*, 2006)

Using the calibrated models, we inspected the influence of disturbance and distance to conspecific adults on sapling density and derived proxies of species abilities. The response of sapling local density along a disturbance gradient measured species competition ability. Our hypothesis was that the less competitive species should be favored in the most disturbed sites. Regarding the colonization aspect, spatial dispersal of saplings measured by distance to adults reflected species ability for colonization. Dispersal distance was approximated as the distance to the nearest adult (Nathan and Muller-Landau, 2000). This approximation likely results in underestimated but conservative dispersal distances. We assumed that the more species are limited by dispersal, the more sapling density decrease with dispersal distance.

We ask the following questions:

- (1) Is there a species-specific link between response to disturbance and dispersal around adults along the shade-tolerance continuum?
- (2) If this link exists, is it consistent with the competition-colonization trade-off?
- (3) Are soft traits such as seed volume and wood density good proxies for species competition and colonisation abilities?

Finally, we discuss the separate aspects of competition and colonisation abilities regarding the relevance of our proxies and related mechanism such as

the successional niche trade-off and dispersal limitation.

2 Material and Methods

2.1 Study site

We studied sapling patterns at the Paracou experimental site (5°18' N, 52°23'W) in French Guiana. The site lies in a *terra firme* rain forest of the coastal plain, between 10 and 42 m above sea-level (Gourlet-Fleury *et al.*, 2004). The climate is equatorial, with a main dry season from August to mid-November, and a shorter one from March to April. Annual rainfall in the vicinity of the site is 3041 mm (Gourlet-Fleury *et al.*, 2004). The physiography of the site shows smooth slopes incised by minor streams. Soils are mainly shallow ferralitic soils. Part of the site is covered by permanently waterlogged areas.

The design of the site consists in three blocks of four 300 × 300 m permanent sample plots with a 25 m inner buffer zone. In each central 250 × 250 m square, all trees ≥ 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. In each block, stands experienced three treatments during the 1986-1988 period combining selective logging of increasing intensity and additional poison-girdling. One plot per block was left as control.

The present work focused on the four plots of the Paracou Southern Block (PBS) gathering an undisturbed control plot and three treated plots. We defined two periods in order to describe past disturbance and dynamics: the *logging period* (1986–1989) and the *recovery period* (1989–2003).

2.2 Focal species, life-stages and response variable

Species attributes regarding shade-tolerance and dispersal Fifteen non-pioneer species were chosen along two different axes regarding shade-tolerance in advanced stages (≥ 10 cm DBH) and dispersal mode. We evaluated shade-tolerance from previous classifications based on species status, dynamics and growth pattern at Paracou and botanists expertise (Molino and Sabatier, 2001). Secondary criteria of species choice were commonness in the study site and the possibility of identify saplings easily in the field. Focal species occupied different layers in the vegetation profile from understory for shade-loving species to upper canopy for hemi-tolerant and light-demanding species. Our *a priori* ranking of species shade-tolerance was paralleled, although not strictly, by wood density and maximal size which respectively increased and decreased with increasing shade-tolerance (Table 1).

We classified species according to their dispersal mode, derived from literature, as unassisted, wind-dispersed or animal-dispersed. The *animal-dispersed* group gathers species with several dispersal agents among which bats, birds, rodents and monkeys which imply different dispersal patterns. Seed volume

was retained as a measure of seed size and evaluated from the literature (Table 1). Among the focal species, *V.michelii* is dioecious, while all others are hermaphrodites.

Species	Family	Tol	Dis	H _{max} (m)	D _{mat} (cm)	D _{sap} (cm)	V _{seed} (cm ³)	d _{wood} –
<i>Oxandra asbeckii</i> (Pulle)R.E.Fr.	ANNO	S	A	20	10	2	0.6	0.90
<i>Pogonophora schomburgkiana</i> Miers ex Benth.	EUPH	S	U	20	10	2	0.8	0.95
<i>Gustavia hexapetala</i> (Aubl.)J.E.Sm.	LECY	S	A	17	10	2	1.3	0.85
<i>Bocoa prouacensis</i> Aubl.	CAES	S	A	34	25	2	1.1	1.22
<i>Lecythis persistens</i> Sagot	LECY	S	A	28	15	2	2.1	0.86
<i>Licania alba</i> (Bern.)Cuatrec.	CHRY	T	A	35	25	3	5.9	1.06
<i>Sextonia rubra</i> (Mez)van der Werff	LAUR	T	A	35	35	3	1.5	0.65
<i>Pradosia cochlearia</i> (Lecomte)T.D.Penn.	SAPO	T	A	43	35	4	0.6	0.93
<i>Dicorynia guianensis</i> Amshoff	CAES	M	W	40	25	5	0.4	0.78
<i>Eperua falcata</i> Aubl.	CAES	M	U	33	35	4	5.4	0.87
<i>Eperua grandiflora</i> (Aubl.)Benth.	CAES	M	U	35	35	3	49.1	0.94
<i>Qualea rosea</i> Aubl.	VOCH	M	W	45	35	4	1.2	0.71
<i>Carapa procera</i> DC.	MELI	L	A	32	25	5	48.3	0.70
<i>Virola michelii</i> Heckel	MYRI	L	A	27	25	6	2.5	0.49
<i>Tachigali melinonii</i> (Harms)Zarucchi & Herend.	CAES	L	W	35	35	9	1.3	0.60

Table 1

Attributes of the focal species. *Family*: Anno: Annonaceae, Caes: Caesalpinaceae, Chry: Chrysobalanaceae, Euph: Euphorbiaceae, Laura: Lauraceae, Lecy: Lecythidaceae, Meli: Melilaceae, Myri: Myristicaceae, Sapo: Sapotaceae, Vochy: Vochysiaceae. *Tol*: shade-tolerance group, S: sciaphilous, T: tolerant, M: mid-tolerant, L: light-demanding. *Disp*: dispersal mode: W: wind-dispersal, U: unassisted, A: animal-dispersal, H_{max}: species maximal height, D_{mat}: DBH at maturity, D_{sap}: upper DBH limit for sapling stage, V_{seed}: seed volume, d_{wood}: wood density.

Life-stages In 2002-2003, all plants with $1 \text{ cm} \leq dbh \leq 10 \text{ cm}$ were sampled in $10 \times 10 \text{ m}$ cells over a complete grid within the four plots. DBH were recorded in 1 cm classes. For each species, we defined saplings as plants which most likely settled during the post-logging period. We limited the sapling stage by a specific upper DBH limit (D_{sap}, Table 1) accounting for differences in average growth among species (Gourlet-Fleury, unpublished data). Sapling local density in the $10 \times 10 \text{ m}$ sampling cells served as the response variable

in statistical models (n=2500 observations).

The adult stage gathered potential mother-trees larger than a given DBH at maturity. We defined specific DBH at maturity from literature or with regards to the status of the species in the canopy (Table 1). In order to account for the death of potential mother-trees, adult sets included logged and naturally dead trees as they could have set saplings measured in 2002-2003. For *V.michelii*, field surveys helped to distinguished male and female trees (I. Scotii, unpublished data). Only female positions were used to calculate dispersal distance for this species.

2.3 Ecological descriptors and gradients

Explicative variables described three aspects of environmental heterogeneity inside the plots (Table 2): topography (elevation and slope) was derived from a Digital Elevation Model (DEM), stand heterogeneity and population heterogeneity. Stand and population variables were either static or dynamic and calculated from basal area on 20 m-radius circular subplots centered on sampling cells. This design allowed to take into account lateral effects on the focal cells where saplings were counted. Dynamic variables concerned either the logging period or the recovery period.

Stand variables described the local forest structure in 2002: total basal area, basal area of pioneer taxa and the first two axes of a CA (Correspondence Analysis) on diameter distributions (see Table 2). Disturbance variables

separately quantified the loss of basal area due to either treefalls or standing deaths (Table 2). Two variables quantified tree recruitment over 10 cm DBH and the gross change in basal area during the recovery period. Mean and standard deviation of treefalls ages characterized the temporal pattern of local disturbance during the recovery period.

Finally, three population variables characterized intraspecific relationships experienced by saplings (Table 2): the distance from cells center to the nearest adult estimated dispersal distance of saplings around adults, the basal area of conspecific trees (≥ 10 cm DBH) in 2002 and its variation over the recovery period accounted for possible intraspecific competitive effects.

2.4 Models of sapling density

We studied sapling patterns with Zero Inflated Poisson (ZIP) models in order to account for the over-representation of zero observations (sapling absence) (Lambert, 1992; Barry and Welsh, 2002). In ZIP models, the response variable \mathcal{Z} follows a mixture of two Poisson distributions: $\mathcal{Z} \sim \omega\mathcal{P}(0) + (1 - \omega)\mathcal{P}(\lambda)$, where $\mathcal{P}(0)$ is the zero-point probability mass function and ω the unknown proportion of mixture between the two distributions. The mean and variance are then:

$$E(\mathcal{Z}) = \mu = (1 - \omega)\lambda, V(\mathcal{Z}) = \mu + \left(\frac{\omega}{1 + \omega}\right)\mu^2 \quad (1)$$

Table 2

Explicative variables used to calibrate specific models of sapling density (*units* in brackets). *Topography* derived from a DEM (Digitalized Elevation Model). *Stand* and *population* variables derived from census data of trees ≥ 10 cm DBH. The period indicates calculus years: *logging* (1986–1988) or *recovery* (1989–2002). Statical variables were calculated in 2002. *diam1* and *diam2* derived from a Canonical Analysis of the numbers of trees in 11 DBH classes from 10-15 cm to 55-60 cm and >60 cm DBH (16 and 14 % of total inertia explained).

Type	Label	Description	Period
<i>Topography</i>	Ele	Elevation (<i>m</i>)	-
	Slo	Slope ($^{\circ}$)	
<i>Stand</i>	G _{pio}	Basal area of pioneer taxa (m^2)	2002
	diam1	Axis1 of CA on diameter distribution	
	diam2	Axis2 of CA on diameter distribution	
	G _{tot}	Total basal area (m^2)	
<i>Stand</i>	M _{tfL}	Basal area lost in treefalls (m^2)	Logging
	M _{sdL}	Basal area lost in standing deaths (m^2)	
	M _{tfR}	Basal area lost in treefalls (m^2)	Recovery
	A _{tf}	Mean age of treefalls (<i>yr</i>)	
	SD _{tfR}	Standard deviation of treefall ages (<i>yr</i>)	
	M _{sdR}	Basal area lost in standing deaths (m^2)	
	Recru	Basal area of recruits ≥ 10 cm DBH (m^2)	
dG	Change in basal area (m^2)		
<i>Population</i>	dna	Distance to nearest adult (<i>m</i>)	2002
	G _{con}	Basal area of conspecific trees ≥ 10 cm dbh (m^2)	Recovery
	dG _{con}	Loss of basal area from conspecific trees death (m^2)	

and the likelihood (Jansakul and Hinde, 2002) :

$$\ell = \ell(\mathcal{Z}|\omega, \lambda) = \sum_{z_k=0} \log [\omega_k + (1 - \omega_k)e^{-\lambda_k}] + \sum_{z_k>0} \log(1 - \omega_k) - \lambda_k + z_k \log \lambda_k - \log(z_k!), \quad k = 1 \dots n, \quad (2)$$

where n is the number of observations and z_k the density in cell k .

ZIP models present two major interests with regards to the study of species spatial patterns:

- response curves to a given explicative variable allow two main shapes: monotonous

(increasing or decreasing) or unimodal ,

- a given variable influences either the presence–absence pattern of saplings only (through parameter ω) or sapling counts (through parameter λ), or both (dual variable, Zorn, 1996; Flores *et al.*, 2006).

For each species separately, we selected explicative variables in a two-stage procedure (see also Barry and Welsh, 2002). In a logistic GLM, we first selected the set of variables explaining sapling presence–absence only (**B**). Given **B**, we then selected variables explaining sapling counts in a complete ZIP model (**P**). At each step, a stepwise selection procedure retained the most informative variable through Maximum Likelihood Estimation (MLE) and Akaike Information Criterion (AIC) (McCullagh and Nelder, 1989): $AIC = D + 2p$ where D is the model deviance and p is the number of parameters. As a rule of thumb, we retained variables that improve the model deviance at least by 2.

In order to simplify model interpretation and species comparison, we characterized species response, *i.e.* the predicted sapling density, along a major disturbance gradient. We defined this gradient from the Principal Component Analysis (PCA) of the explicative variables, population variables excepted. The first axis of the analysis indicated a gradient of disturbance initiated during the logging period. It was positively supported by variables M_{tFL} , $Recru$ and G_{pio} , and negatively by $diam1$ (24% of initial inertia explained). Our disturbance gradient sampled cells according to their score and high inertia on the axis ($n = 37$ cells). The score criterion ensured high variability of distur-

bance intensity in retained cells while the inertia criterion ensured low variability along the other axes of the analysis (especially regarding topographic position). The resulting gradient is thus defined independently from species patterns. It allows species responses to be compared in similar conditions while isolating the effect of disturbance only.

3 Results

3.1 Sensibility to explicative variables

Species	n_p	D_{exp}	ρ_s	ρ_p
<i>D.guianensis</i>	11	11.8	0.21	0.28
<i>B.prouacensis</i>	11	5.1	0.19	0.17
<i>C.procera</i>	4	2.4	0.08	0.08
<i>T.melinonii</i>	14	9.2	0.19	0.22
<i>S.rubra</i>	3	1.3	0.06	0.05
<i>E.falcata</i>	13	36.9	0.51	0.52
<i>P.cochlearia</i>	8	2.8	0.15	0.14
<i>L.persistens</i>	11	4.0	0.20	0.20
<i>G.hexapetala</i>	5	4.2	0.15	0.12
<i>Q.rosea</i>	21	25.3	0.36	0.34
<i>O.asbeckii</i>	21	17.9	0.46	0.45
<i>V.michelii</i>	17	12.5	0.36	0.37
<i>E.grandiflora</i>	17	25.6	0.47	0.43
<i>P.schomburgkiana</i>	14	5.9	0.23	0.25
<i>L.alba</i>	12	3.9	0.21	0.20

Table 3

Summary of calibrated ZIP models on sapling densities. n_p : number of parameters in models, D_{exp} : percentage of explained deviance, ρ_s, ρ_p : Spearman and Pearson correlation coefficients between observed and adjusted densities.

All species were sensible to explicative variables, although at largely different levels. Calibrated models explained from about 37% of explained deviance for *E.falcata* to 1% for *S.rubra* (Table 3). Correlation coefficients between ob-

served and fitted densities ranged from 0.51 for *E.falcata* to 0.06 for *S.rubra* for Spearman's ρ , and from 0.52 to 0.05 for Pearson's ρ . The explicative power related to model complexity regarding the number of retained variables: a single variable was retained in models for *C.procera* and *S.rubra*, according to the selection rule of thumb, whereas up to fourteen variables were explicative in the model for *Q.rosea* (Table 4). Significant effects were detected in all models at 5%-level, except for *S.rubra* (Table 4).

	Dg	Bp	Cp	Tm	Sr	Ef	Pc	Lp	Gh	Qr	Oa	Vm	Eg	Ps	La
Intercept	D***	D***	D***	D***	D***	D***	D***	D***	D***	D***	D***	D***	D***	D***	D***
Ele	B***	D***	-	-	-	-	B***	D***	-	D***	B***	D***	D***	D***	D***
Slo	-	-	-	P*	-	-	-	D+*	-	B***	D+***	B**	-	D***	D+*
M _{tfL}	-	-	-	B+	-	P*	-	-	-	-	B*	B***	B*	-	P*
M _{sdl}	-	-	-	P**	-	P**	D+***	B**	B***	D***	B***	D***	-	-	B***
M _{tfR}	-	-	-	-	-	-	P**	-	-	-	-	B+	P***	-	P**
M _{sdlR}	P***	-	-	-	-	-	-	-	-	P***	P***	-	P*	B***	-
A _{tf}	-	-	-	B**	-	-	P*	-	-	P*	D***	P***	-	B**	-
SD _{tf}	B*	-	-	-	B+	-	-	P**	-	P**	-	-	-	-	-
Recru	B***	-	D+***	D+***	-	D***	-	-	-	-	D***	-	D+***	-	P*
dG	B***	-	-	-	-	-	-	-	-	P*	-	P**	-	-	-
diam1	-	B***	-	-	-	-	-	-	-	P***	D+***	-	D+***	B*	-
diam2	-	B*	-	D* *	-	D+***	-	P*	-	D*+	B*	B*	-	D***	P*
G _{tot}	D* *	B***	-	B*	-	-	-	B***	-	P***	D***	B**	D+***	-	-
G _{pio}	-	B***	-	D+***	-	D***	-	-	-	P***	-	-	B**	D***	P***
dna	D***	D***	-	-	-	B***	-	-	D+**	D***	D+***	-	D***	-	-
G _{cons}	-	B**	-	P**	-	D***	B**	B***	-	P*	D***	D+***	P*	P**	B***
dG _{cons}	-	-	-	-	-	-	-	-	-	D+*	-	D***	-	-	-

Table 4

Summary of ZIP models indicating selected variables for each species with associated distribution and p-values (**<10⁻³, **<10⁻², * <0.05, + ≥ 0.05. **B**: influential variable on saplings presence-absence (binomial distribution), **P**: influential variable on sapling counts (Poisson distribution), **D**: dual variable present in both distributions (Binomial and Poisson). For dual variable, symbols figure p-values for the Binomial and the Poisson distributions. Symbol - indicate variables not retained in the models.

3.2 Species response to disturbance and shade-tolerance

The calibrated models allowed us to calculate species response to environmental conditions in the thirty-seven cells of the disturbance gradient (Fig.1). Variability in local conditions implied variability in species responses along the gradient (dotted lines, Fig.1); still, tendencies appeared in the mean responses (dashed lines, Fig.1). In order to characterize species response along the gradient, we calculated the regression coefficient (α_{dis}) of the linear relationship between predicted values and cell positions on the disturbance gradient (*i.e.* cell scores in the PCA of explicative variables, solid lines, Fig.1).

In the shade-loving group, three species showed the most negative responses (*B.prouacensis*, *O.asbeckii*, *P.schomburgkiana*, Fig.2.a). Two others showed weak positive responses (*G.hexapetala* and *L.persistens*, Fig.2.a), although for *L.persistens*, the response peaked in the middle of the gradient (bell-shape, Fig.1). In the tolerant and mid-tolerant group, responses were also variable, from negative for four species (*D.guianensis*, *E.grandiflora*, *L.alba*, *P.cochlearia*) to positive for *E.falcata* and null or weak for *Q.rosea* and *S.rubra*. In the light-demanding group, responses were positive for the three species (*C.procera*, *V.michelii*, *T.melinonii*), as predicted densities increased at the high disturbance levels (Fig.1).

More generally, response to disturbance was significantly related to species wood density (Spearman's ρ and correlation test: $\rho_s = -0.74$, $p = 2.10^{-3}$, $n = 15$, Fig.2.b): species with light wood tended to respond positively whereas

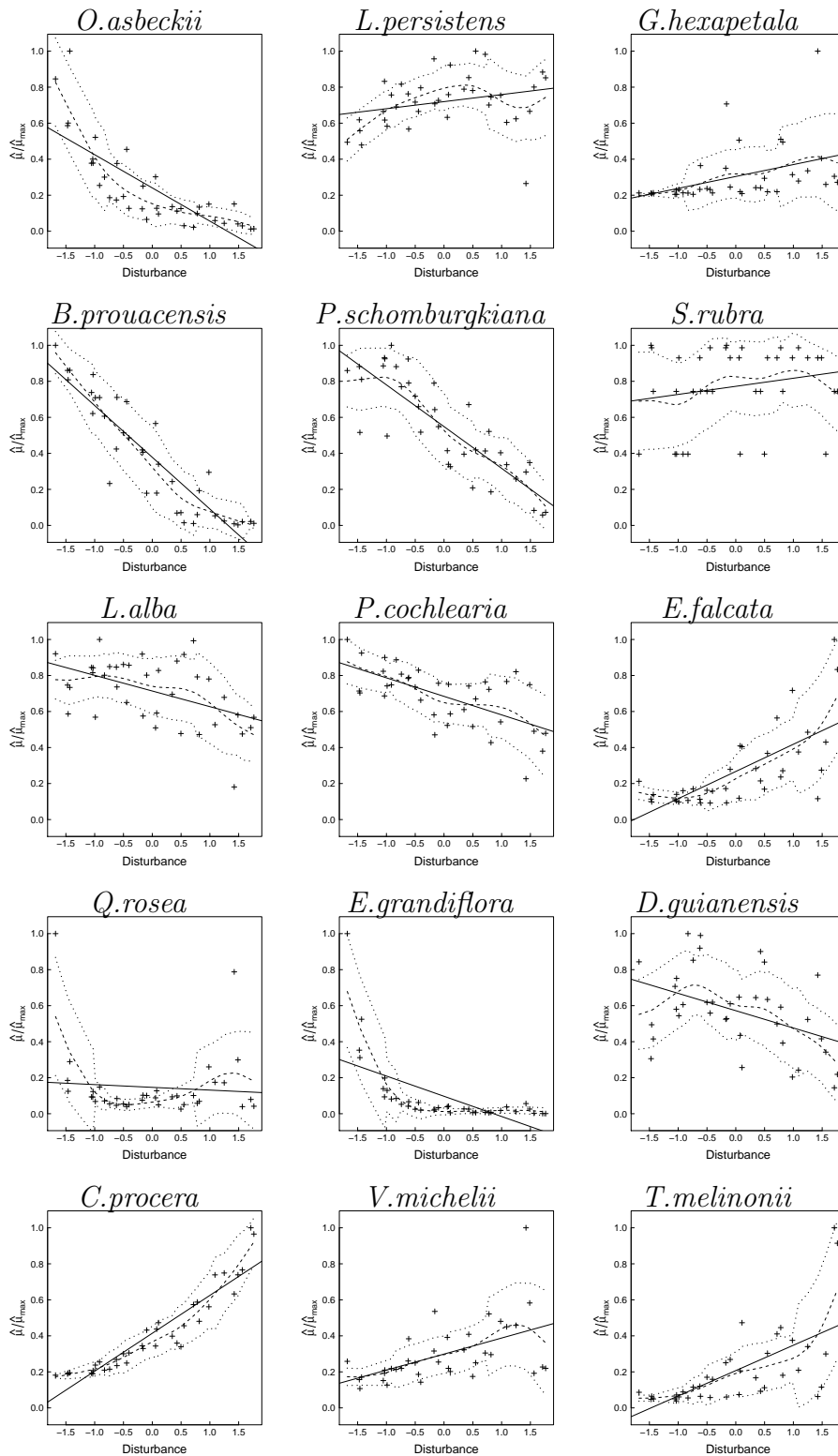


Fig. 1. Normalized predicted sapling density for the fifteen species along the disturbance gradient (normalized cell scores, $n = 37$). Smooth dashed lines represent the mean density. Dotted lines show the variability of predictions along the gradient (calculated variance on a moving window). Solid lines show the regression line between cell scores and predictions.

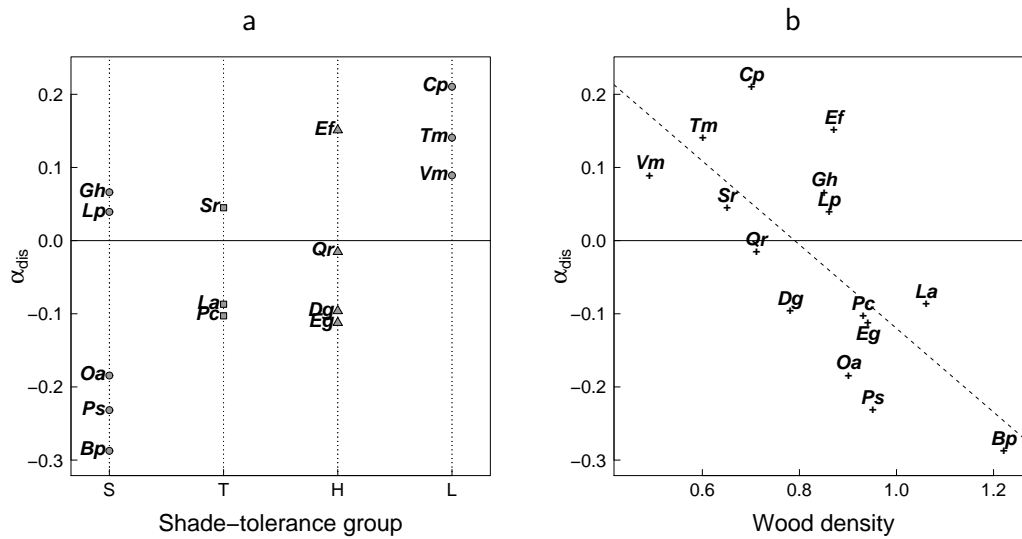


Fig. 2. Shade-tolerance and response to disturbance. Species are labeled by the initials of their botanical name. (a) Slope of species response along the disturbance gradient against shade-tolerance groups: S: shade-loving, T: tolerant, M: mid-tolerant, L: light-demanding. (b) Relation between wood density and response to disturbance. Dashes show the regression line between the two variables (Spearman's ρ and correlation test: $\rho_s = -0.74$, $p = 2.10^{-3}$).

species with dense wood showed negative responses.

3.3 Sapling installation pattern and dispersal traits

Among focal species, the distance to the nearest adult had a significant effect on the local density of saplings for seven of them (Table 4). For the others, sapling density was independent of dna . Among these, five were animal-dispersed (*C.procera*, *L.alba*, *L.persistens*, *P.cochlearia*, *S.rubra*), one was wind-dispersed (*T.melinonii*) and one had unassisted dispersal (*P.schomburgkiana*, Table 4). For these species, sapling density was not independent of intraspecific processes since the basal area of conspecific trees (G_{cons}) had explicative power, except for *C.procera* and *S.rubra* (Table 4).

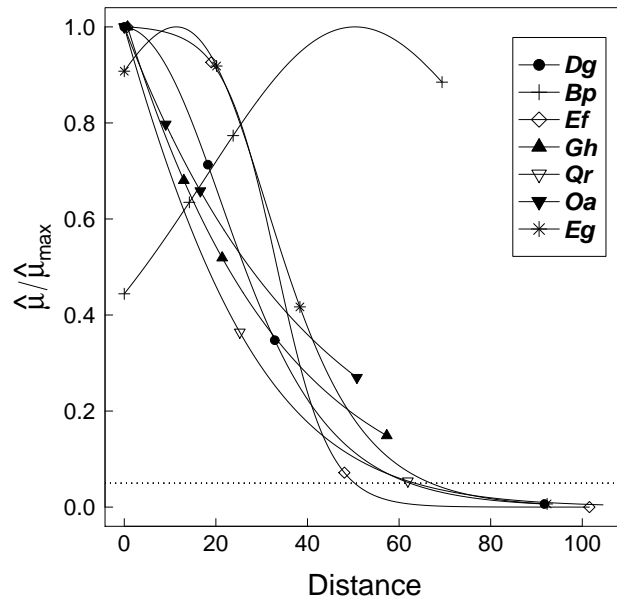


Fig. 3. Normalized predicted sapling density ($\hat{\mu}/\hat{\mu}_{\max}$) against distance to the nearest adult. For each species, the curve is figured on the range of distance to nearest adult that was sampled in the field. Dots show the threshold of 5% of the maximum predicted density.

Response curves to distance to the nearest adult. We focus here on sapling density predicted by calibrated models as a function of the distance to the nearest adult while setting the other variables to zero. This method allowed to isolate the effect of the distance alone for the seven species whose sapling density depended on the distance to the nearest adult (Fig.3). Five species had maximal predicted density at the origin, among which three showed convex curves (*G.hexapetala*, *O.asbeckii*, *Q.rosea*) and two showed concave curves (*D.guianensis*, *E.falcata*) indicating some spacing of saplings around adults (Fig.3). This feature appeared clearly for two species which showed maximal predicted density at intermediary distances (*B.prouacensis*, *E.grandiflora*, Fig.3). For *B.prouacensis*, the curve had a particular shape and reached maximal density at about 55 m.

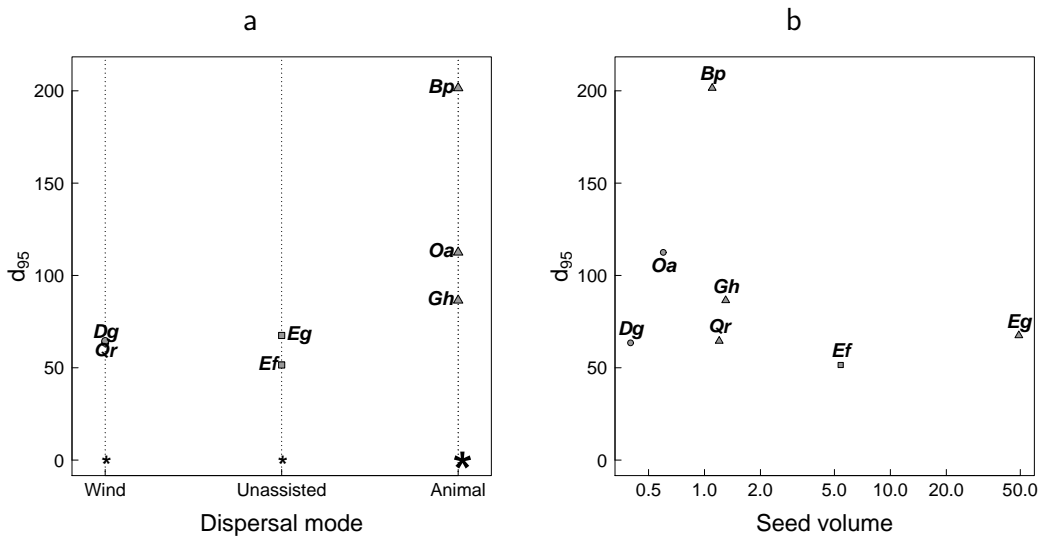


Fig. 4. Dispersal traits and dispersal distance (d_{95}). (a) Dispersal mode: asterisks indicate species for which sapling density was independent of dna (1 in *wind*, 1 in *unassisted*, 6 in *animal*). (b) Seed volume (cm^3 , logarithmic scale): only species for which dna was an explicative variable are shown.

Relationships with dispersal traits As for the response to disturbance, we used two simple indices to characterize sapling dispersal. For each species, we calculated distance at which the predicted density decreased below 5% of the maximum in Fig.3 (d_{95}), and the integral of the curve, from zero to infinity, which is a more accurate characterization ($I_{\hat{\mu}}$, not shown). No significant relationship was detected between seed volume and d_{95} (Fig.4.b) or $I_{\hat{\mu}}$. The wind-dispersed species had similar values of d_{95} (*D.guianensis*: 64 m, *Q.rosea*: 65 m, Fig.4.a). The unassisted species had values of 52 m for *E.falcata* and 68 m for *E.grandiflora*. The three animal-dispersed species showed higher distances: 202 m for *B.prouacensis*, 87 m for *G.hexapetala* and 113 m for *O.asbeckii*.

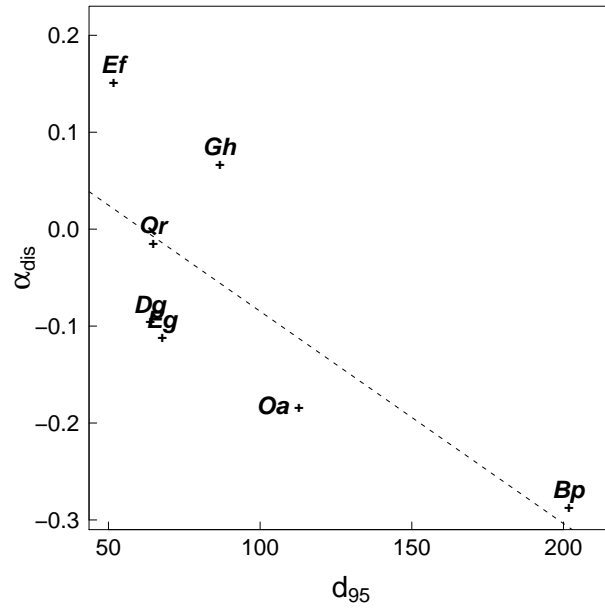


Fig. 5. Relation between dispersal distance and response to disturbance. Only species for which the distance to nearest adult (d_{na}) was selected as an explicative variable are shown.

3.4 Relation between species response to disturbance and dispersal pattern

At last, we looked for possible relationships between response to disturbance and dispersal pattern among the seven species for which d_{95} could be calculated. When α_{dis} (characterizing species response to disturbance) was plotted against d_{95} or $l_{\hat{\mu}}$ (species dispersal characteristics), a negative tendency appeared: the species that responded positively to disturbance also showed the lowest dispersal parameters. However, this should be taken cautiously because the correlations were not significant. Negative but non-significant relationships linked response to disturbance and dispersal characteristics (Spearman's ρ and correlation tests, α_{dis} vs d_{95} : $\rho_s = -0.75$, $p = 0.07$, $n = 7$ Fig.5.b, α_{dis} vs $l_{\hat{\mu}}$: $\rho_s = -0.71$, $p = 0.08$, $n = 7$, not shown).

4 Discussion

4.1 Evidence in favor of the CCT?

The calibrated models allowed us to relate the distribution of sapling density to ecological conditions including abiotic, stand (interspecific) and population effects. With these models, we analyzed sapling densities through parameters that characterized both the species response along a disturbance gradient and the spatial dispersion of saplings around conspecific adults. Although the amount of explained deviance varied widely among the fifteen species, all, except *S.rubra*, were significantly influenced by abiotic and stand conditions. For seven of them, sapling density varied significantly with distance to the nearest adult. When a significant relationship was detected, we could characterize sapling pattern through a quantitative measure of dispersal and relate it to species response to disturbance.

Regarding the seven species sub-sample, no clear evidence in favor of CCT was found, although one must carefully interpret the independence between sapling local density and dispersal for the eight other species. On the contrary, we found a negative but not significant trend between the two components. Such a relationship, if confirmed, would be in opposition with the CCT, but we reckon that the low number of species (7) and a sampling effect due to their particular identities may induce such trend. Among the seven species, the most reactive to disturbance was *E.falcata* whose dispersal is unassisted.

Meanwhile, the less reactive was *B.prouacensis*, which is animal-dispersed and whose main dispersers are frugivorous bats.

What would favor local dispersal for poor competitors, or in our view disturbance-favored species? We suspect two situations. First, early settlement could be facilitated for instance if the species appears in clumps where conspecific trees die at higher rate than the overall stand. Although we investigated this hypothesis, we found no evidence of relationship between dispersal and mortality rates (not shown). Second, local dispersal can be favored for species occurring in stressful conditions that maintain competition to low levels (Snyder and Chesson, 2003). For instance, *E.falcata* occurs mainly in bottomlands where water saturation constrain root anchorage and respiration and maintain low stand densities. No such constraint is known for the other species.

For eight species, the distribution of adults, as accounted for by the distance to nearest adult, had no influence on the distribution of sapling density. Hence, they were not considered to quantify the relationship between response to disturbance and sapling dispersal.

Whereas the most reactive to disturbance and light-demanding species showed uncoupling between sapling density and adult distribution, species at the other end of the shade-tolerance gradient exhibited more variability. Although a stabilizing mechanism such as the CCT may operate at the community level between contrasted ecological groups such as pioneers and shade-loving species, we found little support for such mechanism among the studied non-

pioneer species.

4.2 Response to disturbance, competition ability and successional niche

The multivariate analysis of explicative variables highlighted a major disturbance gradient among sampled cells, although they were separate in space. Sapling density of all species, except *S.rubra*, varied significantly along the disturbance gradient. As a proxy for competition ability, we used the slope of the regression line, as a single parameter characterizing species sensitivity to disturbance. This method reduced the response to a simple linear relationship which induces a loss of information, especially for bell-shaped responses. Yet, it was then possible to compare species responses apart from intraspecific effects.

The retained definition of species competition ability was based on a classical relationship between competition and disturbance. Competition for light seemingly appears as the most structuring process in tropical forest communities (Whitmore, 1996). The process varies following two gradients that determine the level of light level (Falster and Westoby, 2005): vertical from the upper canopy to the understorey and spatio-temporal because of disturbance. Disturbed sites are thus favorable to light-demanding species. In the CCT perspective, pioneer species for instance are poor competitors since they rely on high resource supply to achieve their life-cycle and are finally overwhelmed by later successional species. Some authors propose an other view of the com-

petition ability depending on the level of resource supply (Rees *et al.*, 2001; Craine, 2005). Species success during succession would depend on a trade-off between their competition ability at high and at low resource supply.

Species response to disturbance was significantly related to wood density. Among tree species, wood density stands as a proxy for resource allocation strategy (Enquist *et al.*, 1999; Falster and Westoby, 2005). Light-wood species tend to grow faster, have shorter life-spans and show higher susceptibility to pathogen attacks than heavy-wood species. Among the non-pioneer species studied here, light-wood species showed stronger reaction to disturbance, *i.e.* higher sapling density in disturbed places than in non-disturbed places. Hence, species differ in their strategy of resource allocation coherently with the way they cope with disturbance.

The presented conclusions depend on a number of hypotheses and methodological choices. Life-stages (sapling and adult) were defined through size-classes in order to account for differences in species growth and size at maturity. These choices may not be the most appropriate for some species. But uniform sizes among species would lead to misestimate the density of the sapling stage and dispersal distances. Also the modeling approach retained here did not account for spatial autocorrelation among observations. In a comparative study of models with and without autocorrelation, it appeared that autocorrelation leads to overestimate the effects of explicative variables (Flores *et al.*, submitted). Yet, conclusions regarding the nature and sense of the relation-

ships held as well as species ranking.

4.3 Evidence of dispersal limitation from sapling pattern

A dispersal limitation appeared for seven of the fifteen studied species, whose sapling density decreased with dispersal distance. The lack of such pattern for the other eight species, however, does not necessarily imply an absence of dispersal limitation.

We propose two compatible reasons for this uncoupling of sapling density and distance to adults. Either those species are not limited by dispersal at the study scale, or the dispersal signal was lost at the studied life-stage. The first reason may concern species with effective dispersal mode, mostly among animal-dispersed species. The second reason more likely concerns species settling in specific conditions which are randomly-distributed regarding adults, such as canopy gaps. Among those eight species showing uncoupling, six species are animal-dispersed (*C.procera*, *L.persistens*, *L.alba*, *P.cochlearia*, *S.rubra*, *V.michelii*) among which two are light-demanding (*C.procera* and *V.michelii*). Hence, for *V.michelii*, both reasons could be at stake. Regarding *C.procera*, the heavy seeds are dispersed at short distances by Rodents after falling under tree crowns (Forget, 1988). Specific requirement at sapling-stage more likely led to uncoupling. The same effect also probably affected sapling pattern of *T.melinonii*, the most light-demanding species of the study. The lack of relationship with the dispersal distance was more surprising for the

unassisted species *P.schomburgkiana*. Because of morphological fruits traits, some authors suggested that some ant species could achieve secondary dispersal (Skatulla *et al.*, 2000, Sabatier, pers.comm.), but we found no reference of this mechanism being observed. Dispersal distances by ants are reputedly short but may vary depending on disperser species (Yu *et al.*, 2001).

Dispersal modes implied differences in dispersal abilities. Coherently with general knowledge as well as recent evidence (Clark *et al.*, 2005), our results suggest that unassisted and wind-dispersed species show stronger dispersal limitation than animal-dispersed species. The present ranking of wind-dispersed species relates to physical features of the ecosystem such as vegetation height and canopy roughness which limit air-circulation in and above the canopy Nathan *et al.* (2001). Among animal-dispersed species, sapling density often showed independency with dispersal distance. Trees generally act as dispersal foci and concentrate seeds and fruits around them (Clark *et al.*, 2004a). Yet, compared to other dispersal modes, animal-generated seed rains probably show higher roughness and more local density peaks unrelated with parent trees. For this dispersal mode, the hypothesis of the nearest adult is probably too simplistic to describe relationships between the local density of early life-stages and adults position.

The relationship between seed size and seed number has been used as a proxy for the CCT (Levine and Rees, 2002). Among the studied species, we found no link between seed volume and dispersal distance. Seed mass is

likely to influence dispersal distances of species with a common dispersal mode, especially for physical dispersal agents (wind, water). Yet, for animal-dispersed species, dispersers behavior implies additional variability: for instance, two species with comparable seed mass might be dispersed by birds having different behaviors and home ranges.

Characterizing dispersal in a *forward* approach, *i.e.* from the pattern of seeders to the seed rain (Wang and Smith, 2002), implies multiple spatial and temporal scales and requires intensive measurement (Clark *et al.*, 1999, 2004b, 2005). Alternatively, in a *backward* approach as presented here, one can study saplings and relate their position to the conspecific adult pattern to infer the consequences of seed dispersal. These saplings need to be young enough to ensure that the dispersal signal, *i.e.* traces of the initial seed rain, remains in their position relative to conspecific adults. As mortality thinning filters occur, this signal is likely to evolve and might totally vanish at older stages.

Biotic mortality filters are likely to induce systematic survival patterns relative to adults. For instance, increasing survival with distance is suggested in the Janzen-Connell model. The generality of such effects is still controversial (Hyatt *et al.*, 2003): variability in biotic conditions might be the rule in any predator(pathogen)-plant dynamics and prevent such deterministic pattern to occur (Sheil and Burslem, 2003). Yet, when dealing with settled life-stages, one cannot exclude that density- or distance- dependent processes shaped the observed patterns.

5 Conclusion

Trade-offs are major determinants of community assemblage since they relate to species strategies to sustain populations. Although often discussed in theoretical and empirical literature, the generality of the Competition-Colonization Trade-off is not clearly established. In the present work, intensive survey of early-settled life-stages and numerous data regarding abiotic conditions and stand monitoring helped characterize species patterns as well as past and present environmental heterogeneity. The statistical modeling approach allowed us to relate species local performance to various components. Species showed different abilities in competition and colonization which were consistent with an *a priori* ranking of species shade-tolerance and dispersal modes efficiency. Meanwhile, our results provide little support to the CCT among the studied the non-pioneer species. Additional work is required to address wider spatial scales at which dispersal limitation is more likely to occur. A better comprehension of tropical communities assemblage should also arise from further studies on the widespread plant-animal mutualism, and particularly on its role in trees dispersal and colonization.

6 Acknowledgements

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