

Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest

NATALIA NORDEN, JÉRÔME CHAVE, ADELINÉ CAUBÈRE*,
PATRICK CHÂTELET†, NICOLE FERRONI, PIERRE-MICHEL FORGET*
and CHRISTOPHE THÉBAUD

*Laboratoire Evolution et Diversité Biologique, UMR 5174 Université Paul Sabatier/CNRS, F-31062 Toulouse, France, *Département Ecologie et Gestion de la Biodiversité, UMR 5176 CNRS-MNHN, 4 av. du Petit Château, F-91800 Brunoy, France, and †Station d'Etudes des Nouragues, CNRS UPS 656, French Guiana*

Summary

1 Both spatial and temporal processes are assumed to play an important role in driving seedling dynamics. We assessed the magnitude of these two processes in a neotropical forest in French Guiana. We first quantified temporal changes in seedling community structure, then evaluated the relative importance of environmental heterogeneity and temporal fluctuations in seed arrival in determining seedling dynamics.

2 We monitored the seedling dynamics of 6244 seedlings by censusing 370 1-m² seedling plots in 160 stations over 20 months. At each station, we quantified environmental variability (light availability, soil resources, litter depth, topography), and measured temporal fluctuations in seed input by sampling seed arrival into seed traps located in each station.

3 Temporal changes in seedling density and diversity between four consecutive censuses were compared with those predicted by a neutral model assuming random recruitment and mortality. Seedling density fluctuations were considerably more variable over time than expected under the neutral assumption. Diversity changes showed less consistent results. For the two first census intervals, seedling diversity was more constant than under the neutral expectations. For the last census interval, seedling diversity was more variable than expected under neutrality.

4 Seedling recruitment, mortality and diversity of recruits were modelled against environmental variables and seed arrival. Sites with higher light availability and soil fertility had more diverse recruits ($P < 0.01$) but lower seedling survival ($P < 0.05$). Both density and diversity of local seed arrival had a positive effect, respectively, on density and diversity of recruited seedlings ($P < 0.05$).

5 Our results show that temporal pulses in seedling community are mainly driven by large temporal fluctuations in seedling recruitment. Annual variation in seedfall and environmental filtering both contribute to explaining spatio-temporal variation in seedling dynamics to a large degree. Irrespective of species identity, tropical seedling communities are both seed- and establishment-limited. The temporal component of seed-limitation appears to be of critical relevance in the structuring of tropical seedling communities.

Key-words: environmental heterogeneity, French Guiana, recruitment fluctuations, seed arrival, seedling diversity, seedling dynamics, temporal fluctuations

Journal of Ecology (2007) **95**, 507–516
doi: 10.1111/j.1365-2745.2007.01221.x

Introduction

Spatio-temporal heterogeneity in plant distribution remains a challenge to an integrated understanding of natural plant regeneration in species-rich communities. Most theories seeking to explain observed patterns of plant species distribution have focused on either spatial or temporal processes, rarely on both. Spatial niche theory assumes habitat specialization of coexisting species (Levene 1953; Ashton 1977; Tilman 1982). This view provides an intuitive framework for explaining the spatial distribution of tree species in relation to physical habitat variables (Harms *et al.* 2001; Potts *et al.* 2002; Phillips *et al.* 2003). Although habitat specialization is predicted to operate throughout plant ontogeny, it is likely to be more intense at the seedling stage (Grubb 1977). Consequently, much attention has focused on testing the predictions of the niche theory in order to understand the regeneration patterns of tropical plants. Yet it remains unclear whether such patterns hold for the seedling stage. For instance, Webb & Peart (2000) and Baraloto & Goldberg (2004) both failed to find strong environmental determinism in tropical seedling communities, suggesting that habitat filtering may not be the only process structuring such communities.

Temporal niche theory (or ‘storage effect’) assumes that temporal rather than spatial partitioning of species will slow competitive exclusion and facilitate species coexistence. This can be achieved if long-lived species fluctuate in their recruitment success (Chesson & Warner 1981). Temporal partitioning should lead to non-equilibrium species distribution patterns that differ sharply with those predicted by spatial niche theory (Hurtt & Pacala 1995). In temperate forests, large temporal fluctuations in recruitment have a much greater effect on population dynamics than spatial environmental heterogeneity, suggesting that the stor-

age effect plays an important role in species coexistence in these species-poor communities (Beckage *et al.* 2005). In tropical forests, the importance of this temporal variability has rarely been quantified, in spite of ample evidence of important interannual fluctuations in recruitment success (Forget 1997; Connell & Green 2000; Curran & Webb 2000). For example, a study in Mexico (Kelly & Bowler 2002) provided indirect evidence for a role of temporal niches in fostering the coexistence of pairs of closely related species (but see Lusk 2003).

By examining the seedling stage one should be able to quantify better the relative roles of spatial and temporal variation, as plants at this stage suffer the most from both environmental constraints and competition (Harper 1977). Recently, Wright *et al.* (2005) carried out the first detailed study of the spatial and temporal variation in seedfall and seedling recruitment in a seasonal tropical forest in Panama. They showed that recruitment success depends on seedfall through differential strengths of density-dependent processes during the seed-to-seedling transition. Their result underlines the fact that mechanisms driving seedling dynamics may vary over time, and that both spatial and temporal variation should be assessed simultaneously.

In this study we combine data on seedfall and habitat quality to predict the dynamics of a tropical seedling community. Our conceptual framework encompasses the combined influences of spatial and temporal environmental variation on seedling communities across microsites, as illustrated in Fig. 1. The first scenario (Fig. 1a, a’) assumes that abiotic filtering is the main force shaping the seedling community. Different environmental conditions may thus support different seedling densities and diversities. Under this scenario, a favourable microsite should support greater seedling density than an unfavourable one because of a higher resource supply. Also, seedling diversity should depend

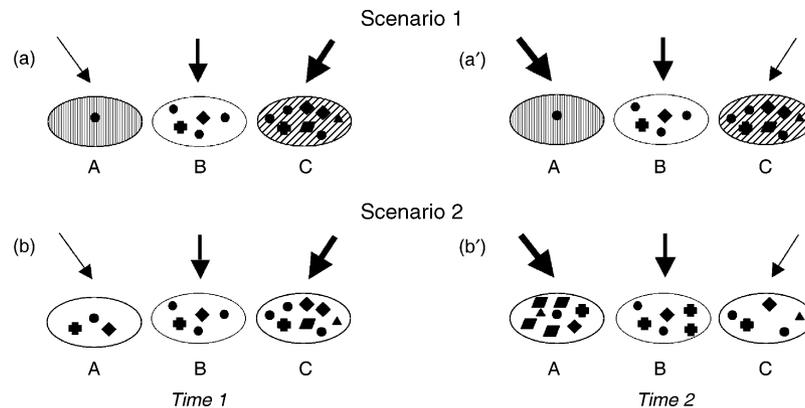


Fig. 1 Conceptual framework of the possible mechanisms that drive seedling dynamics assuming that environmental conditions do not undergo important changes over time. In all panels, different forms illustrate different species, while different patterns illustrate different abiotic conditions. The arrow widths illustrate the intensity of the seed input. (a) Differential seedling density and diversity are the result of differential filtering by abiotic conditions. (a’) Stability in habitat quality results in temporal stability in seedling density and diversity. (b) Differential seedling density and diversity are the result of differential seed input driven by species-specific fluctuations in seed production. (b’) Species-specific fluctuations in seed production result in temporal variation in both seedling density and diversity.

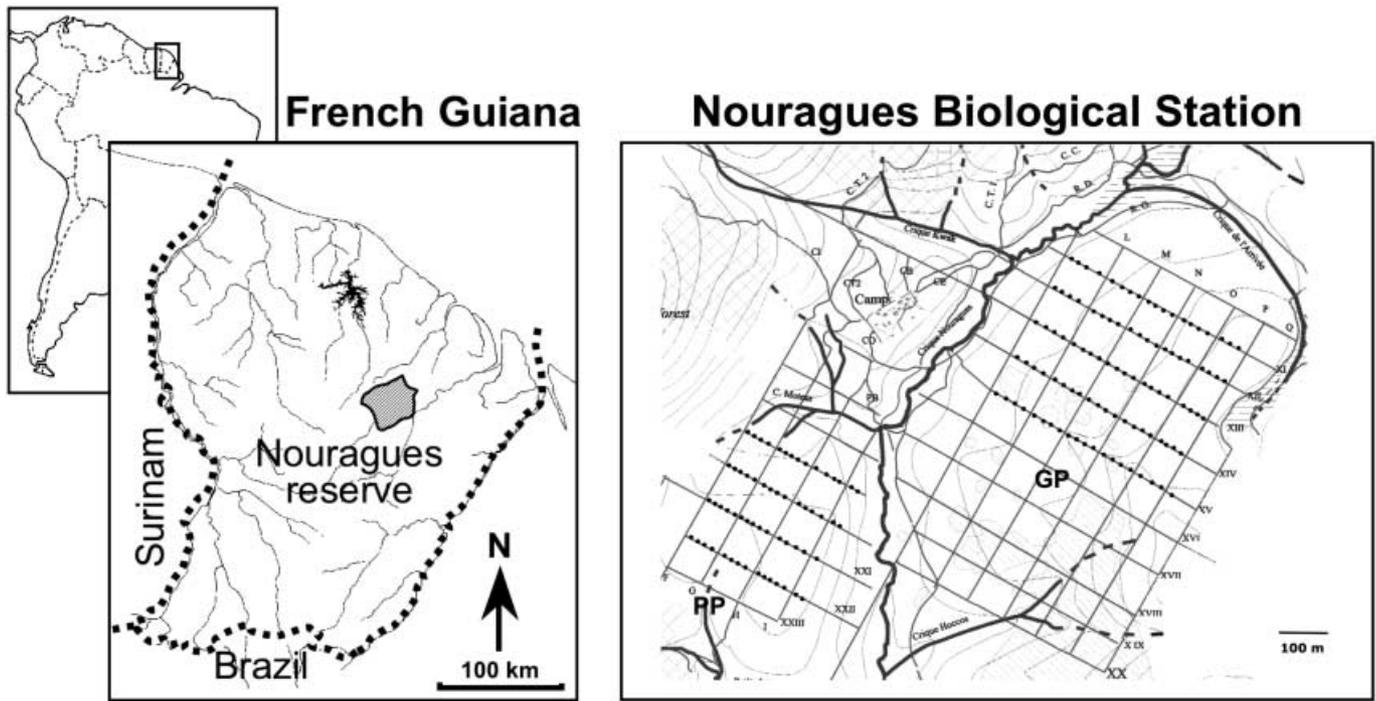


Fig. 2 Geographical location of the Nouragues station, French Guiana. The dots represent the location of the stations within the study area.

on the level of habitat specialization of seedling species and interspecific competition. Thus, if the abiotic environment does not fluctuate over time, seedling density and diversity should be constant, irrespective of the variability in seed input. Under the second scenario (Fig. 1b, b'), patterns of seedling density and diversity are caused by differential seed input. If one site has higher or more diverse seed input, it will also have higher seedling density or diversity. In this case, seedling density and diversity should fluctuate over time, following temporal fluctuations in seed arrival. Here, we address two issues. First, we investigate whether seedling density and diversity are constant over time, reflecting environmental determinism in the structure of the seedling community. We then explore the possible mechanisms leading to these temporal patterns. Specifically, we evaluate the relative importance of local abiotic environment and seed arrival on the dynamics of the seedling community.

Materials and methods

STUDY SITE

This study was conducted in a pristine tropical rainforest of Central French Guiana, at the Nouragues Biological Station (4°05' N, 52°40' W; Fig. 2; Bongers *et al.* 2001a). Average annual rainfall is 2990 mm with a 2–3-month dry season, from September to November. The study area consists of two plateaus dominated by high mature forest in which a grid network of permanent forest plots covering *c.* 85 ha has been established (Fig. 2).

One of the plateaus, Grand Plateau (GP), is on clay soil with a metamorphosed volcanic substrate (*c.* 70% clay and 8% sand, Grimaldi & Riéra 2001) and the other, Petit Plateau (PP), is on granitic-derived sandy soil (*c.* 36% clay and 49% sand). Fruiting phenology in the area shows marked seasonal patterns. Overall, the species richness and biomass of ripe fruits, especially of animal-dispersed species, peaks in April–May and is minimal in August–September (Sabatier 1985; P.-M. Forget, N. Norden & P. Châtelet, unpublished data).

SEED AND SEEDLING CENSUSES

The Nouragues Plant Regeneration Monitoring System parallels the protocol initiated in 1994 in the 50-ha Barro Colorado Island forest dynamics plot, Panama (Wright *et al.* 1999; Harms *et al.* 2000), and subsequently extended to other tropical forests through the Center for Tropical Forest Science (M. Metz *et al.*, unpublished data). A network of 160 0.5-m² seed-traps was set up, with 100 traps in the GP along five parallel trails (20 per trail) separated by 100 m, and 60 in the PP along four parallel trails (15 per trail) also separated by 100 m. Traps were installed at random locations close to the trail at nearest-neighbouring trap distances ranging from 15 m to 50 m. Seeds and fruits were collected twice a month since the establishment of the experiment, and viable seeds (with undamaged endosperm) counted and identified to species or morpho-species. Two to three 1-m² seedling plots were established around each trap in February 2004, at 1.5 m from the edge of the trap and located away from the trail, for a total of 370

plots (250 plots in the GP and 120 plots in the PP). We henceforth term a 'station' the seed-trap plus the seedling plots around the trap. In February–March 2004, all woody seedlings in the seedling plots, including self-supporting lianas, were tagged with a unique number, mapped and their height measured. Individual seedlings were identified to morpho-species by comparing them against digital photographs of a reference collection of seedling specimens growing in the vicinity of the plots. Vouchers were matched to specimens at the Herbarium de Guyane (Cayenne, CAY). When vouchers could not be matched reliably, they were given a morpho-species name. Subsequent censuses took place in October 2004, March 2005 and October 2005. During each census, newly recruited seedlings were tagged, mapped and measured, and missing seedlings were recorded as 'dead'. Surviving seedlings were measured once a year. Here we focus our analyses on plants < 100 cm in height, which we will refer to as 'seedlings'.

We report data on seedling dynamics and on seedling diversity per station. We define seedling dynamics as seedling recruitment, the number of recruited seedlings per station at each census; and seedling mortality, the proportion of dead seedlings per station at each census. We estimated seedling diversity in each station using the Simpson index. This index represents the probability that two randomly selected individuals belong to different species (Magurran 2004). We also carried out analyses using the Shannon index and Fisher's alpha. Because the results were similar, we only report the results obtained with the Simpson index.

ENVIRONMENTAL MEASUREMENTS

We characterized the local habitat of each station using several environmental variables measured at the plot or the station level. Environmental measures were taken as follows.

Light availability

In October 2004, we took hemispherical photographs of each seedling plot using a Nikon Coolpix 2300 camera with a Nikon FC-8 fisheye lens. Photographs were taken at 1.30 m above the ground, early in the morning (06:30–08:00 h) or late in the afternoon (16:40–18:30 h) to avoid over-exposure by direct sunlight. Because light intensity varies considerably during sunset and sunrise, the pictures were taken at different exposure times (1/60, 1/125 and 1/250) to ensure the same level of contrast between canopy openings and the surrounding vegetation. The photograph with the best contrast and the least over-exposure was chosen for analysis so that all had approximately the same level of contrast. Digital photographs were analysed using the Gap Light Analyser (GLA Version 2.0; Frazer *et al.* 1999). This provided estimates of the percentage of transmitted diffuse and direct radiation. These instantaneous measures have been shown to provide an appropriate measure of light

availability in the tropical forest understorey (Nicotra *et al.* 1999; Montgomery & Chazdon 2002).

Soil sampling and chemical analyses

In October 2004, we measured pH and carbon and nitrogen concentrations at the 160 stations. Soil pH is expected to give valuable information about soil fertility as low pH leads to an increased concentration of toxins in the soil (such as Al^{3+}), and a reduced concentration of base metal cations (Sollins 1998). Likewise, nitrogen availability may constrain productivity (Sollins 1998), and is therefore a good measure of soil fertility. For each station, 1 kg of soil was collected, by bulking four soil samples from the topsoil (0–10 cm depth) to yield a single sample. Superficial leaf litter and the humus layer were removed before soil sampling. Soils were dried in the field at *c.* 60 °C for 24 h and then stored dry until laboratory analysis. In the laboratory, the samples were re-dried at 50 °C for 3 days and then filtered with a 2-mm mesh sieve. Carbon and nitrogen concentrations were measured using a CHN analyser (NA 2100 Protein, CE Instruments®). We used the C : N ratio as a predictive variable, rather than carbon and nitrogen independently, because these two variables were strongly correlated. Soil pH was measured in a standard solution made up of one volume of soil diluted in three volumes of water.

Leaf litter depth

We measured leaf litter depth in each plot to the nearest 0.5 cm in five random points using a ruler. Because leaf litter fall is strongly seasonal, we measured litter depth at each census. Mean values over time were calculated per station.

Topography

We defined the local topography of the station as a categorical variable with three levels (flat, low slope and steep slope).

STATISTICAL ANALYSES

Temporal fluctuations in seedling density and diversity

To assess whether seedling density and diversity were constant over time, we calculated the observed net change in seedling density and diversity at the station level between consecutive censuses. We predicted that constancy in seedling density and diversity would result in low interstation variance of net change. We compared the observed variances with those obtained from a simulated neutral seedling dynamic model, in which all the individuals had the same prospects of birth and death. One thousand random replications were generated using the observed number of recruited and dead seedlings at each census. For each replication,

we calculated the interstation variance in the change of both seedling density and diversity. This was used to generate a frequency distribution of the expected variances for seedling density and diversity, which were compared with the observed variances. Constancy or variability in seedling density and diversity between consecutive censuses should result in observed variances differing significantly from the values expected under neutral seedling dynamics. We repeated this analysis on recruited and dead seedlings independently to determine whether the patterns were primarily driven by recruitment or by mortality.

Relating seedling dynamics to environment and fluctuations in seed supply

In a second set of analyses, we evaluated whether seedling dynamics and seedling diversity could be predicted by biotic and abiotic environmental factors using linear mixed models for repeated measures (Pinheiro & Bates 2000). Mixed effects models are useful in cases where temporal pseudo-replication in the seedling variables measured at each station violates the crucial assumption of independence of errors (Crawley 2002). The response variables were: (i) seedling recruitment m^{-2} , the mean number of recruited seedlings per station at each census; (ii) seedling mortality rate, defined as the proportion of dead seedlings per station between censuses; and (iii) diversity of recruits, the diversity of recruited seedlings per station at each census measured with the Simpson index.

We regressed seedling recruitment m^{-2} and seedling mortality rate against seed arrival (number of intact seeds fallen in the intercensus period), physico-chemical environmental factors and seedling density. Because seedling–seedling interactions are potentially important processes at local scales (Coomes & Grubb 2000), we included seedling density as a predictive variable in our analyses. The diversity of recruits was regressed against the diversity of seed input (also measured with the Simpson index) and physico-chemical environmental factors. Because the response variables were spatially autocorrelated among 1- m^2 plots within stations, we performed all regression analyses at the station level by averaging these response variables across plots at each station. The census period was considered as a random factor. This allowed us to estimate the amount of variance explained by the temporal variability without including it as a predictor (Crawley 2002). In order to respect normality, all seedling and seed variables were log-transformed.

In preliminary explorations of our data set, we found significant collinearity among the environmental predictors. Therefore, we used a stepwise procedure to select the best submodel for these environmental factors. The model selection procedure was based on a penalized likelihood measure of the goodness of fit, the Akaike Information Criterion (AIC). As the goodness of fit statistic R^2 is not an appropriate measure for

Table 1 Summary of environmental characteristics of the 160 stations. Shown for each variable is the mean (standard deviation) and the range

	Mean (SD)	Range
Trans. direct radiation (%)	4.99 (2.67)	0.35–16.19
Trans. diffuse radiation (%)	3.88 (1.50)	1.32–9.60
C (% of dry soil)	29.83 (9.84)	13.21–62.42
N (% of dry soil)	2.57 (0.82)	1.16–5.56
C : N	12.04 (1.48)	8.53–16.72
pH (1 : 3 in H ₂ O)	4.81 (0.34)	3.96–6.09
Litter depth (cm)	2.56 (1.35)	1–7

mixed models, we assessed *a posteriori* the quality of the model by calculating the squared correlation between fitted and observed values (Pinheiro & Bates 2000). To assess the relative contribution of each factor in the selected model by the stepwise procedure we eliminated terms sequentially, and we compared the AIC among these models (Burnham & Anderson 1998). For each model where the i^{th} factor was removed, we calculated Δ_i where $\Delta_i = AIC_i - AIC_{\text{min}}$ and AIC_{min} is the AIC of the model selected by the stepwise procedure. High values of Δ_i reflect a high contribution of the removed term in explaining the variance of the model.

Statistical analyses were performed using the R statistical package (R Development Core Team 2005, version 2.1.1). We used the packages ‘nlme’ for linear mixed models (Pinheiro *et al.* 2005), and ‘vegan’ (Oksanen *et al.* 2005) for the calculation of the Simpson diversity index.

Results

During this survey we censused a total of 6244 seedlings. We marked 4705 seedlings during the initial census and 1539 recruits in the three subsequent censuses (Table 1). Among the 4705 seedlings censused initially, 1199 (25.5%) had died by the final census. Recruited seedlings suffered a higher mortality rate, with 469 (43.2%) seedlings out of the 1084 recruited from the second and the third censuses dead by the final census. Simpson diversity index was locally high at the station level (range 0.51–0.97, median = 0.93), with most species being represented by one or very few seedlings.

TEMPORAL STABILITY IN SEEDLING DENSITY AND DIVERSITY

Observed interstation variances in net change of seedling density were significantly higher than under neutral expectations between all consecutive censuses (Table 2). This was mostly due to high variance in the number of recruited seedlings. The observed variance in changes in seedling diversity was significantly lower than the neutral expectation for the two first census intervals but was significantly higher for the last interval.

Table 2 Observed interstation variance in the net change of seedling density, in the number of recruited and dead seedlings, and in the net change of seedling diversity (Simpson index) between consecutive censuses. Confidence intervals of the variances (obtained from 1000 randomizations) are given in parentheses

	Variance in the net change in density	Variance in recruitment	Variance in mortality	Variance in the net change in diversity
Interval 1	24.41 (6.42–10.54)	22.01 (7.44–11.52)	7.43 (4.77–7.53)	9×10^{-4} (11×10^{-4} – 14×10^{-4})
Interval 2	8.63 (4.40–7.17)	4.74 (2.53–4.12)	6.54 (4.51–7.17)	3×10^{-4} (5×10^{-4} – 7×10^{-4})
Interval 3	20.78 (5.0–7.84)	19.06 (3.69–5.93)	7.14 (4.75–7.34)	12×10^{-4} (7×10^{-4} – 10×10^{-4})

Table 3 Results from the linear mixed model predicting the number of seedlings recruited m^{-2} , the proportion of dead seedlings per station and the diversity of recruits m^{-2} . If the predictor was not selected in the stepwise procedure or is not used in the model the cell is empty. Significant effects are indicated with asterisks ($***P \leq 0.001$, $**P \leq 0.01$, $*P \leq 0.05$). Δ is the difference between AIC_{\min} (obtained for the best model) and the AIC of the model lacking the independent variable

	ln(number of recruits + 1)		ln(percentage mortality + 1)		ln(diversity of recruits + 1)	
	Estimate	Δ	Estimate	Δ	Estimate	Δ
ln(seed density + 1)	0.05*	3.15	–	–	–	–
ln(seed diversity + 1)	–	–	–	–	0.11**	6.75
ln(seedling density + 1)	0.16***	8.62	–0.03***	16.14	–	–
direct radiation	–	–	0.01*	2.01	0.01***	10.13
diffuse radiation	0.05***	8.34	–	–	–	–
pH	–	–	0.03**	6.33	–	–
C : N	–	–	–	–	–0.11*	2.7
leaf litter depth	–	–	–	–	–	–
slope	–	–	–	–	–	–

RELATING SEEDLING DYNAMICS TO ENVIRONMENT AND SEED SUPPLY

The relationships between seedling dynamics and environment and seed arrival are summarized in Table 3. Seedling recruitment significantly increased with transmitted diffuse radiation, seedling density and seed arrival. Seedling density had the strongest effect on seedling recruitment, followed by transmitted diffuse radiation and seed arrival. The proportion of dead seedlings significantly increased with transmitted direct radiation and pH, but decreased with seedling density. Seedling density had the strongest effect on seedling mortality, followed by pH and transmitted direct radiation. Finally, the diversity of recruits increased with transmitted direct radiation and seed diversity but decreased with C : N ratio. Transmitted direct radiation had the strongest effect on the diversity of recruits, followed by seed diversity and C : N ratio. Neither litter depth nor slope had a significant effect on any of the response variables studied. The squared correlation coefficient between fitted and observed response variables was generally small ($R^2 = 0.14$, 0.06 and 0.14 for recruitment, mortality and diversity models, respectively). The census period had a weak effect, but this effect was considerably higher in the recruitment and diversity models (ratio of the variance attributed to the census over residual variance, henceforth VCR = 0.08 for both models) than in the mortality model (VCR < 10^{-9}). Hence, the total number of recruits and their diversity varied much more among censuses than the proportion of dead seedlings.

Discussion

TEMPORAL FLUCTUATIONS IN SEEDLING DENSITY AND DIVERSITY

Net changes in seedling density between consecutive censuses were always significantly higher than under the neutral expectation. At a given site, seedling density was thus very variable over small time scales (c. 6 months). Such variation in local seedling density was mostly related to large recruitment events experienced at some stations. Many studies have shown that seedling populations undergo long-term changes in abundance over time (Forget 1997; Connell & Green 2000; DeSteven & Wright 2002), resulting from episodes of very high seedling recruitment rather than from intermittent mortality events (DeSteven 1994; Connell & Green 2000; Delissio *et al.* 2002). Our findings show that temporal pulses in seedling recruitment are a major cause of the large variation in seedling density across the forest understorey. These fluctuations in local seedling density seem to be independent of seasonality. The largest departures from randomness for both variation in seedling density and seedling recruitment were observed between the March and October censuses for both years, which coincides with the germination peak at Nouragues (June–July; N. Norden, personal observation). However, we also found that net changes in seedling density were larger than expected under neutral dynamics between the October and March censuses, when seed-fall is minimal. Because these short time scale fluctuations of seedling density were consistently observed

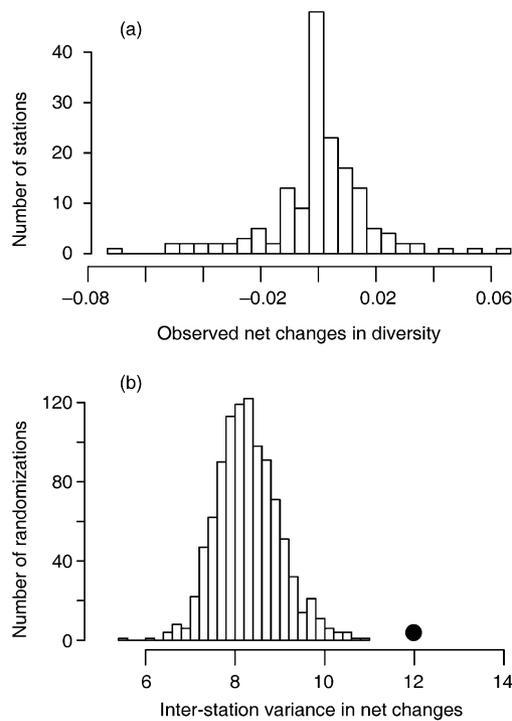


Fig. 3 (a) Histogram of the observed seedling diversity changes between the March 2005 and the October 2005 censuses. (b) Frequency distribution of the expected interstation variance in the seedling diversity changes between the March 2005 and the October 2005 censuses resulting from 1000 randomizations of neutral seedling dynamics. The dot represents the observed interstation variance of net change in seedling diversity.

between four consecutive censuses, we believe that this is a robust result, and that these fluctuations will persist over longer time periods.

Changes in seedling diversity between consecutive censuses were less consistent than seedling density changes. For the two first census intervals, seedling diversity was less variable than under the neutral expectation, whereas it was more variable than expected under neutrality for the last census interval. This finding suggests that local seedling diversity may remain constant in spite of important changes in the number of individuals. However, constancy was only observed over short time periods, as revealed by the large interstation variance in the last census interval (Fig. 3). Because the Simpson index gives more weight to the more abundant species, this measure is little affected by addition or loss of rare species. However, our results were unchanged using other diversity indices (Fisher's alpha and Shannon) that have greater sensitivity to rare species. This suggests that the bias towards common species was not significant. It is difficult to compare our results with published studies addressing temporal changes in diversity as such studies are scarce. A disproportionate seedfall from a single species may result in reduced seedling diversity (Hubbell 1980), and intense conspecific density-dependent mortality may

increase diversity by benefiting rare species (Janzen 1970; Connell 1971). Because recruitment appeared to be far more variable over time than mortality, changes in seedling diversity are likely to be driven by temporal variation in the diversity of recruited seedlings.

IMPORTANCE OF ENVIRONMENT AND SEED ARRIVAL IN DETERMINING SEEDLING DYNAMICS

Temporal variation in the seedling community structure appeared to be largely driven by pulses in seedling recruitment. Successful recruitment reflects the combined effects of spatio-temporal variability in seed arrival and habitat filtering. Below, we discuss the importance of each of these factors in driving seedling dynamics.

Environmental filtering

We found that light availability had important effects on seedling recruitment and mortality. Tropical plant species display a broad array of responses to variable light environments (Lee *et al.* 1996; Montgomery & Chazdon 2002; Dalling *et al.* 2004). For instance, Montgomery & Chazdon (2002) found that, despite a strong light gradient partitioning by tropical tree seedlings at low light conditions, all species showed a positive relationship between light availability and seedling growth. This suggests that in tropical forests light availability is a limiting resource for most tree species at the seedling stage. In their study of a tropical forest seedling community in Costa Rica, Nicotra *et al.* (1999) showed that the observed spatial pattern of seedling density depends on the past influence of light availability on recruitment. Our result is consistent with that of Nicotra *et al.* (1999), and suggests that spatial variation in light availability affects the recruitment process at both the species and the community level.

Soil acidity had a positive effect on seedling mortality rates, but no effect on recruitment. As pH and C : N ratio were negatively correlated ($P < 0.001$), it is possible that high seedling mortality was associated with high N availability. The relationship between pH and soil fertility is at best weak, although several studies suggest that high pH is usually associated with richer soils (Sollins 1998; Phillips *et al.* 2003; Tuomisto *et al.* 2003). Several fertilization experiments in tropical forests have shown that both seedling recruitment and growth show a positive response to nutrient availability (Gunatilleke *et al.* 1997; Lawrence 2003; Ceccon *et al.* 2004; Baraloto *et al.* 2006). One possible explanation for our result is that, because seedlings grow faster in fertile sites, spatial competition becomes more intense, leading to an increased mortality among seedlings. Fertile soils may thus enhance seedling turnover, a pattern also observed across neotropical plots for trees ≥ 10 cm d.b.h. (Phillips *et al.* 2004).

The diversity of recruited seedlings increased with both light availability and soil fertility. Models seeking

to explain species coexistence in heterogeneous environments predict that plant diversity should be a unimodal function of measures of habitat productivity (Ashton 1977; Tilman & Pacala 1993). At low fertility levels, increases in fertility are correlated with increases in diversity and the reverse pattern is observed at high fertility levels. In a recent meta-analysis compiling 15 tropical studies, Lawrence (2003) suggests that, because seedlings of most tree species respond positively to increased nutrient availability, competitive exclusion may be more intense in fertile sites, resulting in a decline of diversity with fertility. Likewise, Ceccon *et al.* (2004) found that the addition of fertilizers to study plots in a tropical dry forest in Mexico diminished seedling diversity. The Guianan shield has poor soils (ter Steege *et al.* 2006), and the Nouragues station is characterized by closed canopy forest leading to low light levels (Bongers *et al.* 2001b). Hence, the positive relationship between diversity of seedling recruits and both soil fertility and light availability may be simply interpreted by the existence of limiting resources.

Seedling density had a strong positive effect on both seedling recruitment and seedling survival rates. The relationships between seedling density and either seedling survival or recruitment have often served as tests of density-dependent effects on plant populations (Hubbell 1980; Augspurger 1984; Webb & Peart 1999; Blundell & Peart 2004). In this study, we focused on a community-level response, and it is therefore difficult to interpret our result within this framework. The positive relationship between seedling recruitment and seedling density may be due to seed sources, which may largely control seedling density and recruitment at local stations (Muller-Landau *et al.* 2002).

Seed arrival

Seed arrival also played an important role in the recruitment process. We found a significant positive effect of seed density on the density of recruits. Sites receiving fewer seeds thus had lower recruitment, which suggests a community-level seed-limitation. In a seed addition experiment performed at BCI (Panama), Svenning & Wright (2005) also found that the whole plant community was seed-limited in terms of both seedling recruitment and overall seedling density. Taken together, these results suggest that seed arrival plays a major role in seedling community dynamics.

Manipulation experiments have shown that seed arrival from the species pool may largely determine the diversity in local sites (Houle & Phillips 1989; Eriksson 1993; Zobel *et al.* 2000). In our empirical study, the species pool can be identified as those trees found next to each station, and their species diversity is reflected in the diversity of incoming seeds. We found that the diversity of recruited seedlings was positively related to seed diversity, which suggests that seed limitation influences local diversity by limiting the diversity of recruited seedlings. We were unable to find reports of

similar studies addressing this relationship in a tropical community (but see Harms *et al.* 2000), so we cannot infer that this pattern is general.

Conclusions and perspectives

Overall, our results do not support the view that habitats have fixed attributes favouring temporal constancy in seedling spatial structure. We have shown that, because of large temporal fluctuations in seedling recruitment, recruitment and mortality events do not compensate for each other in the short term. This causes important changes in seedling density and diversity over time. Scenario 2 of Fig. 1 appears to provide a better description of the processes underlying the observed structure in this seedling community. However, the role of the environment cannot be neglected. The environmental filtering appears to be controlled by both biotic and abiotic factors. Our whole community was both seed- and establishment-limited. Linking seed limitation processes to annual variation in seedfall provides useful insights into the storage dynamics of tropical seedling communities. Further studies on the temporal variation in seed production at both the population and the community levels throughout a number of tropical forests will be required to clarify the role of temporal partitioning on species coexistence.

Acknowledgements

We thank Emilie Morin, Flore Moser, Thomas Samel, Jean-Phillippe Orts and Diego Navarrete for their help in the field. Bernard Riéra provided invaluable help for seedling identification in the field, and Françoise Crozier at the Herbarium de Guyane. We are grateful to Pierre and Mireille Charles-Dominique for their hospitality and logistic support in French Guiana. Sergine Ponsard, David Laloï, Christophe Andalo and Emmanuel Paradis provided useful comments on earlier versions of this manuscript. Cam Webb, Christopher Baraloto and one anonymous referee provided helpful comments that contributed substantially to the final version of this manuscript. This work has been funded through a grant Action Concertée Incitative Jeunes Chercheurs of the French research Ministry to J.C., by the CNRS and by the MNHN (Plan pluri-formation 'Ecologie Fonctionnelle et Développement Durable') to P.M.F.

References

- Ashton, P.S. (1977) Contribution of rain forest research to evolutionary theory. *Annals of the Missouri Botanical Garden*, **64**, 694–705.
- Augspurger, C.K. (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps and pathogens. *Ecology*, **65**, 1705–1712.
- Baraloto, C., Bonal, D. & Goldberg, D.E. (2006) Differential seedling growth response to soil resource availability among nine neotropical tree species. *Journal of Tropical Ecology*, **22**, 487–497.

- Baraloto, C. & Goldberg, D.E. (2004) Microhabitat associations and seedling bank dynamics in a neotropical forest. *Oecologia*, **141**, 701–712.
- Beckage, B., Lavine, M. & Clark, J.S. (2005) Survival of tree seedlings across space and time: estimates from long-term count data. *Journal of Ecology*, **93**, 1177–1184.
- Blundell, A.G. & Peart, D.R. (2004) Density-dependent population dynamics of a dominant rain forest canopy tree. *Ecology*, **84**, 704–715.
- Bongers, F., Charles-Dominique, P., Forget, P.-M. & Théry, M. (eds) (2001a) *Nouragues: Dynamics and Plant Animal Interactions in a Neotropical Rainforest*. Kluwer Academic Publishers, Dordrecht.
- Bongers, F., van der Meer, P.J. & Théry, M. (2001b) Scales of ambient variation. *Nouragues: Dynamics and Plant Animal Interactions in a Neotropical Rainforest* (eds F. Bongers, P. Charles-Dominique, P.-M. Forget & M. Théry), pp. 19–29. Kluwer Academic Publishers, Dordrecht.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. Springer, New York.
- Ceccon, E., Sanchez, S. & Campo, J. (2004) Tree seedling dynamics in two abandoned tropical dry forests of differing successional status in Yucatan, Mexico: a field experiment with N and P fertilization. *Plant Ecology*, **170**, 277–285.
- Chesson, P.L. & Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive-systems. *American Naturalist*, **117**, 923–943.
- Connell, J.H. (1971) On the role of enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (eds P.J. den Boer & G.R. Gradwell), pp. 298–312. Centre for Agricultural Publication and Documentation, Wageningen, The Netherlands.
- Connell, J.H. & Green, P.T. (2000) Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology*, **81**, 568–584.
- Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs*, **70**, 171–207.
- Crawley, M.J. (2002) *Statistical Computing – an Introduction to Data Analysis Using S-Plus*. Wiley and Sons, Chichester.
- Curran, L.M. & Webb, C.O. (2000) Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**, 129–148.
- Dalling, J.W., Winter, K. & Hubbell, S.P. (2004) Variation in growth responses of neotropical pioneers to simulated forest gaps. *Functional Ecology*, **18**, 725–736.
- Delissio, L.J., Primack, R.B., Hall, P. & Lee, H.S. (2002) A decade of canopy-tree seedling survival and growth in two Bornean rain forests: persistence and recovery from suppression. *Journal of Ecology*, **18**, 645–658.
- DeSteven, D. (1994) Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. *Journal of Tropical Ecology*, **10**, 369–383.
- DeSteven, D. & Wright, S.J. (2002) Consequences of variable reproduction of seedling recruitment in three neotropical tree species. *Ecology*, **83**, 2315–2327.
- Eriksson, O. (1993) The species-pool hypothesis and plant community diversity. *Oikos*, **68**, 371–374.
- Forget, P.-M. (1997) Ten-year seedling dynamics in *Vouacapoua americana* in French Guiana: a hypothesis. *Biotropica*, **29**, 124–126.
- Frazer, G.W., Canham, C.D. & Lertzman, K.P. (1999) *Gap Light Analyzer (GLA)*, Version 2.0. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Grimaldi, M. & Riéra, B. (2001) Geography and climate. *Nouragues: Dynamics and Plant Animal Interactions in a Neotropical Rainforest* (eds F. Bongers, P. Charles-Dominique, P.-M. Forget & M. Théry), pp. 9–18. Kluwer Academic Publishers, Dordrecht.
- Grubb, P.J. (1977) Maintenance of species-richness in plant communities: importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, **52**, 107–145.
- Gunatilleke, C.V.S., Gunatilleke, A.U.N., Perera, G.A.D., Burslem, D.F.R.P., Ashton, P.M.S. & Ashton, P.S. (1997) Responses to nutrient addition among seedlings of eight closely related species of *Shorea* in Sri Lanka. *Journal of Ecology*, **85**, 301–311.
- Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, **89**, 947–959.
- Harms, K.E., Wright, S.J., Calderón, O., Hernández, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Houle, G. & Phillips, D.L. (1989) Seed availability and biotic interactions in granite outcrop plant communities. *Ecology*, **70**, 1307–1316.
- Hubbell, S.P. (1980) Seed predation and the coexistence of tree species in tropical forests. *Oikos*, **35**, 214–229.
- Hurt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation – Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Kelly, C.K. & Bowler, M.G. (2002) Coexistence and relative abundance in forests trees. *Nature*, **417**, 437–440.
- Lawrence, D. (2003) The responses of tropical tree seedlings to nutrient supply: meta-analysis for understanding a changing tropical landscape. *Journal of Tropical Ecology*, **19**, 239–250.
- Lee, D.W., Baskaran, K., Mansor, M., Mohamad, H. & Yap, S.K. (1996) Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. *Ecology*, **77**, 568–580.
- Levene, H. (1953) Genetic equilibrium when more than one ecological niche is available. *American Naturalist*, **87**, 331–333.
- Lusk, C. (2003) Tree-species competition and coexistence. *Nature*, **422**, 580–581.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Oxford.
- Montgomery, R.A. & Chazdon, R.L. (2002) Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, **131**, 165–174.
- Muller-Landau, H.C., Wright, S.J., Calderón, O., Hubbell, S.P. & Foster, R.B. (2002) Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. *Seed Dispersal and Frugivory* (eds D.J. Levey, W.R. Silva, M. Galetti), pp. 35–53. CAB International, Wallingford.
- Nicotra, A.B., Chazdon, R.L. & Iriarte, S.V.B. (1999) Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, **80**, 1908–1926.
- Oksanen, J., Kindt, R. & O'Hara, R.B. (2005) *Vegan: Community Ecology Package*. R package version 1.6–10.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Vargas, P.N., Silva, J.N.M., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patino, S., Pitman, N.C.A., Quesada, C.A., Salidas, M., Lezama, A.T. & Vinceti, B. (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **359**, 381–407.

- Phillips, O.L., Vargas, P.N., Monteagudo, A.L., Cruz, A.P., Zans, M.E.C., Sanchez, W.G., Yli-Halla, M. & Rose, S. (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*, **91**, 757–775.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed Effects Models in S-PLUS*. Springer, New York.
- Pinheiro, J.C., Bates, D., DebRoy, S. & Sarkar, D. (2005) *nlme: Linear and nonlinear mixed effects models*. R package version 3.1–66.
- Potts, M.D., Ashton, P.S., Kaufman, L.S. & Plotkin, J.B. (2002) Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology*, **83**, 2782–2797.
- R Development Core Team (2005) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Sabatier, D. (1985) Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Ecologie la Terre et la Vie*, **40**, 289–320.
- Sollins, P. (1998) Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology*, **79**, 23–30.
- ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vásquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–447.
- Svenning, J.C. & Wright, S.J. (2005) Seed limitation in a Panamanian forest. *Journal of Ecology*, **93**, 853–862.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Tilman, D. & Pacala, S.W. (1993) The maintenance of species richness in plant communities. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R.E. Ricklefs & D. Schuler), pp. 13–25. University of Chicago Press, Chicago.
- Tuomisto, H., Poulsen, A.D., Ruokolainen, K., Moran, R.C., Quintana, C., Celi, J. & Cañas, G. (2003) Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications*, **13**, 352–371.
- Webb, C.O. & Peart, D.R. (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology*, **80**, 2006–2017.
- Webb, C.O. & Peart, D.R. (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, **88**, 464–478.
- Wright, S.J., Carrasco, C., Calderón, O. & Paton, S. (1999) The El Niño Southern Oscillation variable fruit production, and famine in a tropical forest. *Ecology*, **80**, 1632–1647.
- Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. (2005) Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology*, **86**, 848–860.
- Zobel, M., Otsus, M., Liir, J., Moora, M. & Möls, T. (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, **81**, 3274–3282.

Received 2 November 2006
 revision accepted 11 January 2006
 Handling Editor: Kyle Harms