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

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ABSTRACT

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

1. Introduction

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

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

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

In tropical forests where catastrophic events are rare as in South America, the natural regime of disturbance is mainly driven by treefalls gaps (Shugart, 1984; Brokaw and Busing, 2000; Shnitzer and Carson, 2001). Gap creation temporarily releases between-trees competition and mobilizes resources. Newly recruited trees in early life-stages may take advantage of this change in local conditions to grow and survive according to their temperament and competitiveness. Among all resources, the increase of light availability mostly impacts upon growth and development of trees in the understorey (Whitmore, 1996). Light availability directly interacts with the structure of the canopy that, disturbance apart, relates to the vertical profile of vegetation and to foliage attributes of local species (Montgomery and Chazdon, 2001; Wirth et al., 2001). Light quality and quantity are highly heterogeneous in time and space at various scales (Sterck et al., 1999; Wirth et al., 2001; Poorter and Arets, 2003).

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

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

2. Material and methods

2.1. Study site and census data

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

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

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

2.2. Focal species and life stages

We focused on tree species whose regeneration was abundant in the study area and easy to identify at the sapling stage. We selected six species exhibiting contrasting shade tolerance, three endozoochorous shade-tolerant species (*B. prouacensis* (Aubl., *Caesalpiniaceae*), *O. asbeckii* (Pulle, R.E.