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Spatial patterns of tree community dynamics are detectable in a small (4 ha) and disturbed fragment of the Brazilian Atlantic forest

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RESUMO – (Padrões espaciais de dinâmicas da comunidade de arbórea num fragmento pequeno (4 ha) e perturbado podem ser detectados). A dinâmica da comunidade arbórea e de doze populações foi investigada em um fragmento de Floresta Semidecídua, com base em inventários conduzidos em 2000 e 2005 em 29 parcelas de 20 × 20 m. O objetivo principal foi verificar se seria possível detectar padrões de dinâmica relacionados à heterogeneidade ambiental de um fragmento florestal de área pequena (4,0 ha). Foram obtidas taxas de mortalidade e recrutamento de árvores e taxas de ganho e perda de área basal para a amostra total, quatro habitats de solo previamente definidos, classes de diâmetro e populações. A comunidade arbórea mostrou-se instável no período, uma vez que as taxas de mortalidade superaram as de recrutamento e as taxas de perda superaram as de ganho em área basal tanto na amostra total como nos habitats de solo. Tais mudanças gerais se relacionaram, possivelmente, a uma fase de degradação do ciclo silvigenético provavelmente desencadeada por um severo episódio de distúrbio ocorrido no passado. A dinâmica da comunidade não foi homogênea em todo o fragmento, diferiu significativamente entre os habitats de solo. As variáveis ambientais que se correlacionaram mais fortemente com a variação das taxas de dinâmica foram aquelas vinculadas à disponibilidade de água, luz e nutrientes minerais. Em contraste com a tendência global, as espécies de subdossel expandiram em densidade no período, provavelmente em resposta ao mesmo evento de distúrbio.

Palavras chave: dinâmica de comunidades arbóreas, dinâmica florestal, dinâmica de populações arbóreas, floresta tropical semidecídua

Abstract – (Spatial patterns of tree community dynamics are detectable in a small (4 ha) and disturbed fragment of the Brazilian Atlantic forest) The dynamics of the tree community of a fragment of tropical semideciduous forest was investigated in south-eastern Brazil. Surveys were carried out in 2000 and 2005 in 29 20 × 20 m plots. The main purpose was to assess the possibility of detecting spatial patterns of dynamics that could be related to the heterogeneity of both the environment and disturbance history in a small forest area (4.0 ha). Rates of mortality and recruitment of trees and gain and loss of basal area were obtained for the whole sample, four pre-defined soil habitats, diameter classes and twelve tree populations. The tree community was rather unstable in the period, once mortality rates surpassed recruitment rates and loss rates of basal area surpassed gain rates all-over the area denoting the prevalence of a degradation process, possibly triggered by a clear felling in 1985 that reduced the area of the fragment in 26%. The tree community dynamics showed no spatial autocorrelation but was not evenly distributed throughout the fragment. This spatial heterogeneity was chiefly determined by the disturbance history of each site while environmental heterogeneity played a secondary but significant role. The main causes of disturbance heterogeneity were the extension of the adjacent felled area, cattle trampling and selective logging. The environmental variables that most strongly correlated with the variations of the dynamics rates were those related to the availability of light, water and mineral nutrients. In contrast with the overall trends, three understory species expanded in the period, possibly at the expense of the steeply declining density of mid-sized trees.

Key words: Forest disturbance, Forest fragments, Forest regeneration, Tropical semideciduous forest

Introduction

Processes of tree community dynamics in tropical forests frequently show a striking variation over small distances that produces spatial heterogeneity of both physiognomic structures and floristic composition (Whitmore 1989; Lieberman & Lieberman 1989; 1994; Felfili 1995; Guilherme *et al.* 2004; Appolinário *et al.* 2005). This heterogeneity results from a combination or interaction of several factors, among which variations of the physical environment and disturbance regimes are prominent (Martinez-Ramos 1985; Denslow 1987). A background source of variation is the substrate, which produces spatial and temporal heterogeneity of ground water and mineral nutrients availabilities (Pinto & Hay 2005). Disturbances cause an additional heterogeneity, modifying various aspects of the physical environment, notably the intensity and quality of light, temperature and humidity (Caswell & Cohen 1991; Burslem & Whitmore 1999). In fact, local disturbance history has been reported as one of the main forces driving the dynamics of tropical tree communities, and disturbances caused by tree falls, in particular, were postulated by some authors as a leading factor in maintaining the high species diversity of tropical forests (Hubbell 2001; Bell *et al.* 2006). Regeneration cycles triggered by tree-falls would result in a picture of tropical forests as ever-changing mosaics composed of patches at different successional stages and variable in both size and species composition (Richards 1979; Oldeman 1983; 1989).

The approach to tree species distribution and diversity in tropical forests in articulation with environmental heterogeneity, in both space and time, is ultimately based on the classic view of plant community organization mediated by ecological niches. This perception has been seriously challenged since Hubbell (2001) proposed his Unified Neutral Theory of Biodiversity and Biogeography (UNTB) and the chain of stochastic events has gained increasing relevance in 'explaining' species distribution, dynamics and diversity in tropical forests leaving a minor role for species differentiation with respect to the physical environment.

At this critical historical age when human kind is seeking ways to conserve the vanishing biological diversity of the

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remaining tropical forests, it is of utmost importance to understand the mechanisms driving dynamics processes of tree communities and populations, particularly those confined in forest fragments. Large scale and long-term monitoring of permanent plots has been shown to yield promising results in the study of dynamic processes and related factors (Whitmore 1988; Condit 1995; Condit *et al.* 1996; Tomás 1996). The ongoing theoretical discussion, in particular, gives relevance to the assessment of the relative role played by both stochastic events and environmental variables as factors determining tree species distribution in space and time. In the present paper we analyze the short-term (5 yr) dynamics of the tree community of a small (4 ha) and disturbed forest fragment in south-eastern Brazil with the purpose of seeking for spatial patterns related to environmental variables. The hypothesis was that, despite its small area and severe disturbance history, the spatial variation of tree community dynamics is affected by both substrate heterogeneity and disturbance distribution.

Materials and methods

Study area and habitat classification – The study was carried out in a forest fragment known as Mata da Lagoa situated in Lavras, Minas Gerais state, south-eastern Brazil (21°13’11”S, 44°58’15”W) at 884 m of altitude. The fragment area was 4.0 ha during the study period (2000–2005), but was approximately 5.4 ha in 1986 when a clear felling took place at its edges causing a 26% reduction of the area (Fig. 1).

Mata da Lagoa is a fragment of montane semi-deciduous seasonal forest according to the IBGE classification of Brazilian vegetation (Veloso *et al.* 1991) and is also included in the wide-sense definition of Atlantic Forest (Oliveira-Filho & Fontes 2000). The fragment is surrounded by pastures and isolated from its nearest neighbor fragment by ca. 1 km. The drainage duct of a nearby reservoir flows close to southern edge of the fragment. Evident current impacts to the forest were those caused by selective logging and cattle trampling in the search for shade and shelter.

The climate of the region is classified as Köppen’s Cwb type (mesothermic with wet summers and dry winters). The mean annual temperature and precipitation are 19.3 °C and 1493.2 mm respectively, with 66% of the annual rainfall concentrated between November and February (Vilela & Ramalho 1979). Following the Brazilian system of soil classification (Embrapa 2000) the two occurring soil types are Red-Yellow Dystrophic Argisols (PVAd) and Red Eutroferric Nitosols (NVef).

As described in Machado *et al.* (2004), we classified the 29 sample plots into four soil habitats based on the two soil types, Argisols and Nitosols, and three drainage classes: ‘moderately drained’, ‘well drained’ and ‘highly drained’, which were assigned to plots following the criteria proposed by Embrapa (2000). The resulting soil habitats (Fig. 1) were: Upper Argisols (well drained), *n* = 5; Lower Argisols (moderately drained), *n* = 9; Upper Nitosols (highly drained), *n* = 5; e Lower Nitosols (well drained), *n* = 10 plots. Because Machado *et al.* (2008) demonstrated that several tree community features differed significantly among these soil habitats without spatial dependence, we used them to investigate whether dynamics rates differed accordingly.

Tree community surveys – In the years 2000 and 2005 we carried out two tree surveys in 29 permanent plots with 20 × 20 m of dimensions totaling an area of 1.16 ha (29.1% of the fragment area). We distributed the plots

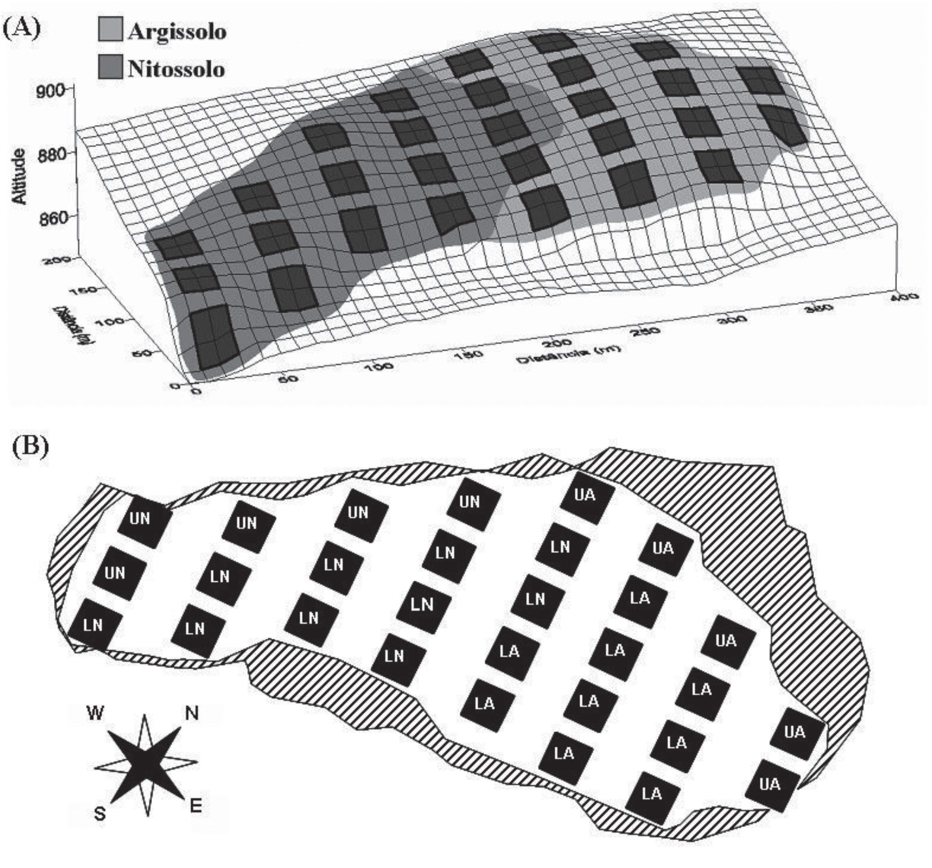

Figure 1. (A) Surface diagram showing the topography of Mata da Lagoa and the distribution of the 29 sample plots (20 × 20 m) and two soil types. (B) Map showing the area of Mata da Lagoa in 2000–2005 (inner polygon), the area cleared in the 1980’s (dashed) and the classification of sample plots according to four soil habitats: UA = Upper Argisols; LA = Lower Argisols; UN = Upper Nitosols; LN = Lower Nitosols.

systematically in eight parallel transects crossing the fragment from border to border up the main slope (Fig. 1). Transects were placed 30 m apart and plots along transects were spaced 10 m apart. As described in Machado *et al.* (2004), between April and May 2000 we carried out the first survey of all live individual trees with a diameter at breast height (dbh) $\geq$ 5 cm, labeled them with numbered aluminum tags, identified them to species, measured their circumference at breast height (cbh) and estimated their total height. Five years later, between April and May 2005, we accomplished the second tree survey during which we registered the dead, re-measured the survivors, and labeled, measured and identified the recruits (trees that surpassed dbh $\geq$ 5 cm in the period). The following death categories were registered for dead trees: fallen, standing, felled and broken.

Dynamics rates – In order to detect changes in species richness, we contrasted species gains and losses in the total sample and its four soil habitats by means of comparisons of Poisson counts (Zar 1996). We also compared the species richness of the two surveys in each soil habitat by means of species rarefaction curves with increasing sample size produced by the means and 95% confidence limits of the number of species of all possible combinations of sample plots necessary to produce each sample size (Arrhenius 1921; McCune & Mefford 1999). Differences among species richness curves were assessed through their confidence limits.

We calculated dynamics rates for tree assemblages (total sample, soil habitats, individual plots, diameter classes and tree populations) in the five-year interval (2000–2005) for two aspects of tree dynamics: demography (tree counts) and basal area represented by the sum of sectional areas of individual trees at breast height. Based on Sheil *et al.* (1995, 2000), we assumed that changes in population size per unit time were a constant proportion to the initial population size and calculated the mean annual rates of tree mortality (M) and recruitment (R), and loss (L) and gain (G) of tree basal area as follows:

$$M = \{1 - [(N_0 - N_m)/N_0]1/t\} \text{ x } 100,$$
$$R = [1 - (1 - N_r/N_t)1/t\ ] \text{ x } 100,$$
$$L = \{1 - [(AB_0 - AB_m - AB_d)/AB_0]1/t\} \text{ x } 100, \text{ and}$$
$$G = \{1 - [1 - (AB_r + AB_g)/\ AB_t]1/t\} \text{ x } 100,$$

where t is the time interval between surveys (5 yr), N_0 and N_t are the initial and final counts of individual trees, N_m and N_r are the number of dead and recruited trees, AB_0 and AB_t are the initial and final basal areas, AB_m and AB_d are the basal areas lost by tree death and decrement (tree decay and partial stem loss), and AB_r and AB_g are the basal areas gained by recruited trees and increment (growth) of surviving trees.

Additionally, in order to represent global dynamics, we obtained turnover rates from averaging mortality and recruitment rates as well as gain and loss rates (Oliveira-Filho *et al.* 1997; Werneck & Franceschinelli 2004). Following Korning and Balslev (1994), we also obtained net rates of change for both tree counts (Ch_N) and basal area (Ch_{AB}) using the expressions:

$$Ch_N = [(N_t/N_0)1/t - 1] \text{ x } 100, \text{ and}$$
$$Ch_{AB} = [(AB_t/AB_0)1/t - 1] \text{ x } 100.$$

In the analysis of tree dynamics per size class, we adopted the diameter classes of increasing amplitude proposed by Appolinário *et al.* (2005) to make up for the strong decrease in density in the larger size classes typical of the negative exponential distribution known as J-reverse. We then counted up the number of trees that experienced the following events between the two surveys: (a) remained in the class, (b) death, (c) recruitment, (d) ingrowth and (e) outgrowth. The latter two are inter-class migration events and can be either progressive or regressive (Lieberman *et al.* 1985). Based on the distribution of diameters in 2000, we used chi-squared tests to assess whether the frequencies of both live trees in 2005 and dead trees were independent of the diameter classes. We used comparison of Poisson counts (Zar 1996) to assess the balance between the number of tree admissions (recruits + ingrowth) and exclusions (dead + emigrants) in each diameter class.

In order to seek for changing trends in the species abundance distribution we also obtained dynamics rates for the 12 species with 20 or more individuals in the two surveys, including the dead and recruited ones. We assessed changing trends in population demography through comparison of Poisson counts (Zar 1996) of recruited and dead trees. We classified the species into the five regeneration guilds proposed by Lieberman and Lieberman (1987) to help interpretation of community changes through the trends observed for particular populations (Gentry & Terborgh 1990).

Environmental variables – Five environmental variables were chosen to investigate their correlation to dynamics rates: (a) drainage classes converted into an ordinal scale to express water availability; (b) soil pH, to express mineral nutrients availability; (c) leaf area index (LAI), to express light availability in the understory; (d) total tree basal area in 2000, to express saturation of standing biomass; and (e) edge factor, to express edge effects.

We calculated the 'edge factor' for each plot following Oliveira-Filho *et al.* (1997) to evaluate the influence of the proximity of the forest edge. The edge factor of a plot is the total length of one or more segments of the fragment perimeter enclosed by a circle of radius *R* whose origin is at the plot center. *R* should represent the maximum reach of edge effects on the trees of a forest fragment. We chose *R* = 100 m because it has proven effective in detecting edge effects in the tree community structure of six other fragments in the region (see Carvalho *et al.* 2007).

Following the procedures described by Pezzopane *et al.* (2002), we estimated the canopy cover of each plot through measures of LAI (leaf area index) obtained with the help of two LI-2050 sensors connected to LI-2000 data-loggers from LI-COR. We installed one sensor in a nearby open area and the other within the forest. We made all readings at 1.30 m from the ground and in overcast days, preferentially early in the morning or late in the afternoon, due to the diffuse light condition. We obtained a mean LAI value for each plot from readings made at four different positions. All readings took place in September 2004 coinciding with the peak of the leaf-fall season, *i.e.* maximum canopy openness.

Geostatistical treatment and correlation analyses – Because sampled events were not spatially randomized in the plots and, perhaps, not independently distributed, we applied a geostatistical analysis to incorporate an eventual dependence residual between plots. Spatial variables corresponding to coordinates x and y of the plot centers were used to define a network of points. We then performed a preliminary exploratory analysis to observe the general spatial pattern of environmental variables and dynamics rates. The spatial dependency was analyzed by means of semivariogram adjustment using isotropic models to test the functions (Burrough and McKonnell, 1998). We found no structural function with a semivariance capable of being modeled in all variographic analyses indicating that there was no spatial dependency for all variables of both sets, dynamics and environmental.

Given the results of geostatistical treatments, we then analyzed all variables through classical methods of least squares parametric statistics, but only after performing Bartlett normality tests and applying the arc-sin $\sqrt{x}$ transformation to variables expressed by proportions (Zar 1996). We performed comparisons among the four soil habitats using analyses of variance coupled with Tukey-Kramer tests and assessed the relationship between dynamics rates and the five environmental variables using Pearson's correlation for soil pH, leaf area index, tree basal area and edge factor, and Spearman's (non-parametric) correlation for drainage classes because of its ordinal nature (Zar 1996). We adopted the significance threshold of $\alpha < 0.05/5$ (*i.e.* $\alpha < 0.001$) to account for the Bonferroni correction (Miller 1991) for five independent variables. Due to evident contrasting patterns related to size classes we split dynamics variables of tree demography into two pre-defined diameter classes: $5 \leq \text{dbh} < 10$ cm and dbh $\geq$ 10 cm.

Results

Changes in species richness were generally small in the whole sample as were in its four soil habitats (Tab. 1). The balance between the numbers of lost and gained species was not significant in all cases (total sample: $Z = 1.41$, Upper Argisols: $Z = 0.0$, Upper Nitosols: $Z = 0.33$, Lower Nitosols: $Z = 1.13$) but the Lower Argisols, where the number of species lost was significantly greater than the number gained (13 : 1; $Z = 3.21$, $p = 0.002$). The same trends were

Table 1. Tree community dynamics in the Mata da Lagoa, between 2000 e 2005, given for the Whole sample and its four soil habitats. Values within parentheses are expected frequencies and those within brackets are the means of the *N* sample plots (20 × 20 m) of each soil habitat. *p* is the significance of statistical tests (see text). Means followed by the same lower-case letters do not differ significantly in Tukey-Kramer tests.

	Whole sample ($N = 29$)	Upper Argisols ($N = 5$)	Lower Argisols ($N = 9$)	Upper Nitosols ($N = 5$)	Lower Nitosols ($N = 10$)	*p*
No. of species:						
Initial (2000)	145	68	88	64	90	
Final (2005)	141	68	76	65	93	
Lost	6	8	13	4	2	
Gained	2	8	1	5	5	
No. of trees:						
Initial (2000)	1307	201	442	225	439	
Final (2005)	1250	188	416	215	431	
Survivors	1114	159 (177.6)	391 (360.5)	184 (197.6)	380 (378.3)	
Dead	193	42 (30.8)	51 (62.5)	41 (34.2)	59 (65.5)	
Recruits	136	29 (21.7)	25 (44.0)	31 (24.1)	51 (46.2)	
Mortality rate (% yr^{-1})	3.15	4.6 [4.8]	2.4 [2.6]	3.9 [3.9]	2.8 [2.8]	ns
Recruitment rate (% yr^{-1})	2.28	3.3 a [3.4]	1.2 b [1.1]	3.1 ab [3.2]	2.5 ab [2.4]	*
Turnover rate (% yr^{-1})	2.71	3.9 a [4.1]	1.8 b [1.8]	3.5 ab [3.5]	2.7 ab [2.6]	*
Change rate (% yr^{-1})	-0.89	-1.3 [-1.4]	-1.2 [-1.4]	-0.9 [-0.8]	-0.4 [-0.3]	ns
Basal area (m^2):						
Initial (2000)	34.242	4.608	13.972	4.037	11.625	
Final (2005)	32.703	4.266	13.254	3.919	11.265	
Dead (m^2)	3.727	0.644	1.456	0.582	1.045	
Decrement (m^2)	0.552	0.069	0.163	0.077	0.244	
Recruits (m^2)	0.400	0.077	0.073	0.101	0.148	
Increment (m^2)	2.341	0.294	0.828	0.440	0.780	
Loss rate (% yr^{-1})	2.63	3.3 [3.9]	2.4 [3.1]	3.5 [3.5]	2.3 [2.3]	ns
Gain rate (% yr^{-1})	1.74	1.8 ab [2.0]	1.4 b [1.4]	2.9 a [3.1]	1.7 b [1.7]	*
Turnover rate (% yr^{-1})	2.18	2.6 [2.9]	1.9 [2.2]	3.2 [3.3]	2 [2.0]	ns
Change rate (% yr^{-1})	-0.92	-1.5 [-2.0]	-1.0 [-1.7]	-0.6 [-0.4]	-0.6 [-0.6]	ns

* p <0,01; ns = non significant

confirmed by the species accumulation curves (Fig. 2), which indicate a significant species loss in the Lower Argisols and no significant change in the other habitats.

There was a net decline of both tree density and biomass (expressed as basal area) in all soil habitats (Tab. 1). Despite the overall decline in the number of trees due to a higher number of dead over recruited trees, this was significantly unbalanced only for the whole sample ($Z = 3.14$; $p < 0.002$) and Lower Argisols ($Z = 2.98$; $p < 0.005$). The number of dead and recruited trees did not differ significantly in the Upper Argisols ($Z = 1.54$; $p > 0.1$), Upper Nitosols ($Z = 1.18$; $p > 0.1$) and Lower Nitosols ($Z = 0.76$; $p > 0.1$). Thus the Lower Argisols habitat was probably the main responsible for the predominance of dead over recruited trees. In addition, the frequencies of surviving, dead and recruited trees were not independent of the four soils habitats (3 × 4 contingency

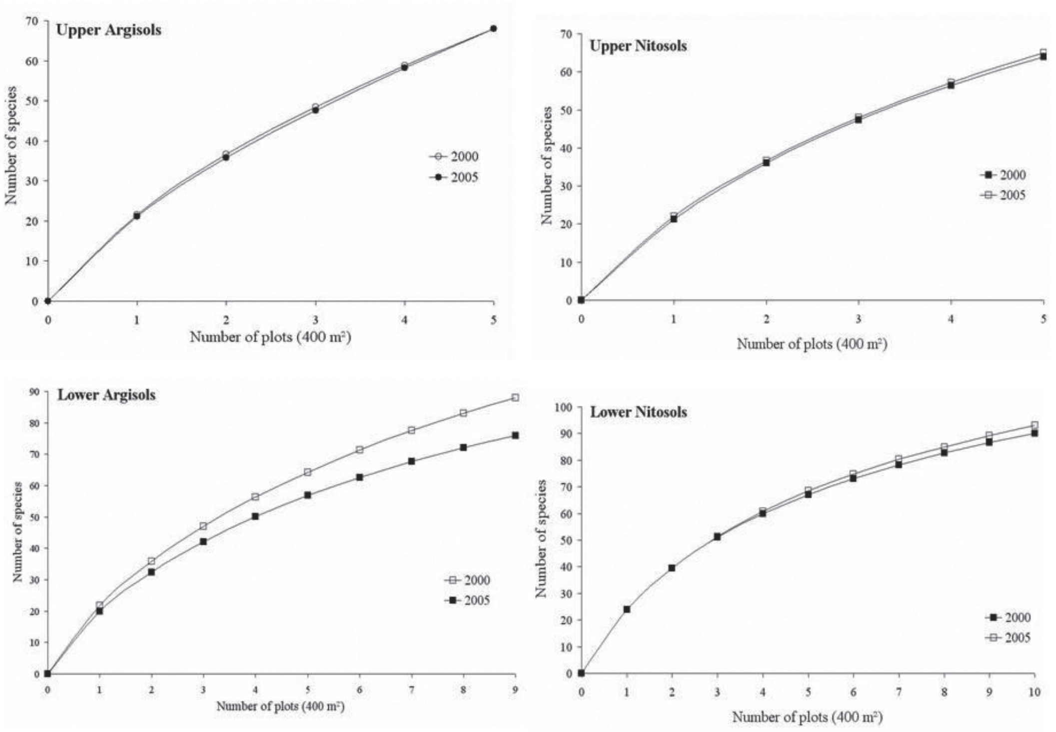

Figure 2. Species accumulation curves with increasing number of 20 × 20 m sample plots in the four soil habitats and two surveys (2000 e 2005) carried out in Mata da Lagoa. Curves representing 95% confidence limits are given only for the Lower Argisols, for clarity.

table: $\chi^2 = 26.81$, $p < 0.001$). Nevertheless, the frequencies of surviving trees in all soil habitats and of surviving, dead and recruited trees in the two Nitosols habitats did not differ significantly from the total sample. Contrasts were therefore restricted to the frequencies of recruited and dead trees in the two Argisols habitats. The frequencies of recruited and dead trees were both higher than expected in the Upper Argisols ($\chi^2 = 8.52$, $p < 0.01$) and lower than expected in the Lower Argisols ($\chi^2 = 12.89$, $p < 0.001$). This suggests that tree community dynamics was more accelerated in the Upper Argisols and less in the Lower Argisols, with respect to the other habitats, as confirmed by the comparison of dynamics rates. No significant difference was found among soil habitats in their rates of tree mortality ($F = 2.79$, $p > 0.06$) and net decline in tree density ($F = 0.60$, $p > 0.6$), but significant differences were found for recruitment ($F = 4.64$, $p < 0.01$) and turnover rates ($F = 5.95$, $p < 0.003$), with higher values in the Upper than in the Lower Argisols, but no contrast with respect to the Nitosols habitats.

Different patterns emerged in tree community dynamics expressed as tree basal area (Tab. 1). No significant difference was found among soil habitats in their rates of net decline ($F = 0.70$, $p > 0.5$) and loss of basal area ($F = 0.55$, $p > 0.6$). Nevertheless, the habitats differed in their rates of gain in tree basal area ($F = 0.70$, $p > 0.5$), which were higher in the Upper Nitosols than in the Lower Nitosols and Lower Argisols, with Upper Argisols in an intermediate position and no significant differences with the other three habitats.

Tree density distributions per diameter (dbh) classes did not change markedly between the two surveys in the four soil habitats except for the declining density of trees of the $10 \leq$ dbh < 20 cm class in all habitats but the Upper Nitosols (Fig. 3). Diameter distributions in 2005 did not differ significantly from expected frequencies based on 2000 (Tab. 2) for the whole sample ($\chi^2 = 7.19$, $p > 0.06$) as well as for its soil habitats (Upper Argisols: $\chi^2 = 4.73$, $p > 0.10$; Lower Argisols: $\chi^2 = 2.56$, $p > 0.10$; Upper Nitosols: $\chi^2 = 0.30$, $p > 0.10$; Lower Nitosols: $\chi^2 = 2.18$, $p > 0.10$). Despite this, the concentration of tree density reduction in the $10 \leq$ dbh < 20 cm class was confirmed by the imbalance between the number of inter-class immigrants (ingrowth and recruits) and emigrants (dead and outgrowth), which was significant only for this dbh class in all soil habitats but the Upper Nitosols.

The proportion of dead trees differed significantly among dbh classes in the Lower Argisols ($\chi^2 = 6.65$, p < 0.05) and Lower Nitosols ($\chi^2 = 5.74$, $p < 0.10$) but not in the Upper Argisols ($\chi^2 = 2.81$, $p > 0.10$), Upper Nitosols ($\chi^2 = 0.28$, $p > 0.10$) and the whole sample ($\chi^2 = 5.18$, $p > 0.10$). Dead trees in the Lower Argisols were in smaller number than expected in the $5 \leq$ dbh < 10 cm class and larger than expected in the $10 \leq$ dbh < 20 cm class. In the Lower Nitosols dead trees were in larger number than expected in the $5 \leq$ dbh < 10 cm class. Differences were not significant for the other dbh classes of either habitat. Death mortality categories were not independent of soil habitats (Tab. 3). Significant differences were found for felled and broken trees, which occurred at higher numbers than expected in the Lower Nitosols.

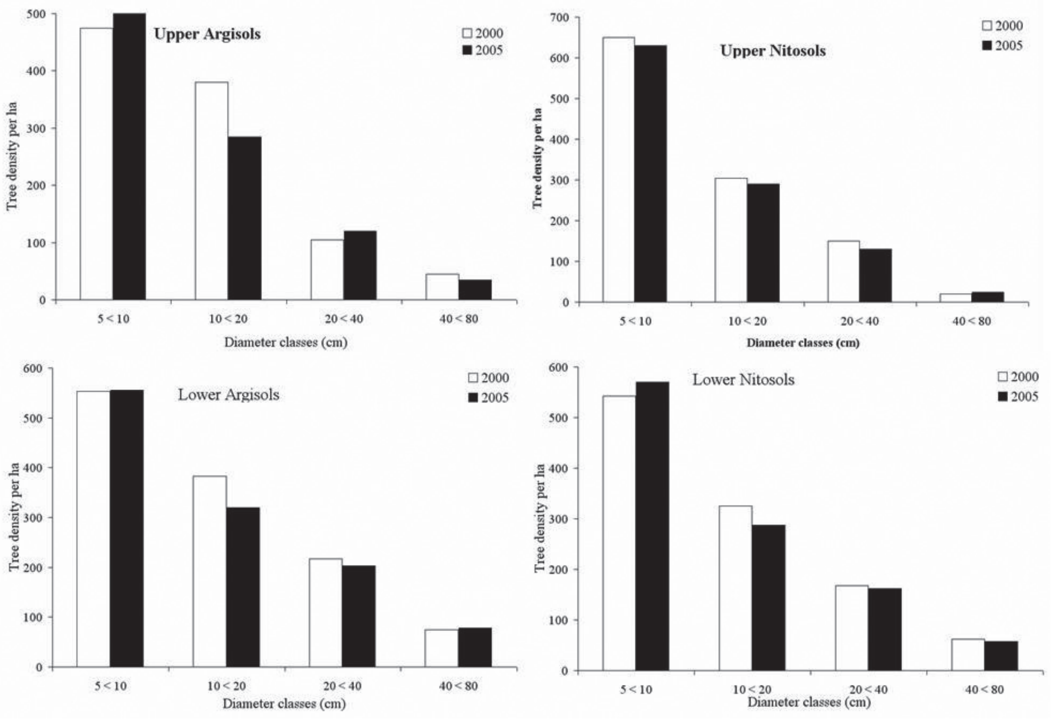

Figure 3. Distribution of tree density per diameter class in the four soil habitats and two surveys (2000 e 2005) carried out in Mata da Lagoa.

Four out of five environmental variables were significantly correlated with at least one of the six dynamics rates (Tab. 4); the edge factor yielded no significant correlation. Tree mortality rates in the 5 ≤ dbh < 10 cm class were positively correlated with soil drainage classes and negatively with leaf area index values. Mortality rates in the dbh ≥ 10 cm class were negatively correlated with initial tree basal areas. Tree recruitment rates were positively correlated with drainage classes and soil pH for trees of the 5 ≤ dbh < 10 cm and dbh ≥ 10 cm classes, respectively. Gain rates of tree basal area were negatively correlated with initial tree basal areas while loss rates of tree basal area were positively correlated with drainage classes.

Significant trends emerged from the analysis of population dynamics of the 12 most abundant tree species (Tab. 5). *Allophylus edulis*, *Mollinedia widgrenii* and *Galipea jasminiflora*, all sub-canopy species were the only to show a significantly higher number of recruited over dead trees and are probably expanding in tree density. The former two also showed a net increase in basal area in the period. The opposite trend, *i.e.* significantly higher number of dead over recruited trees, was registered for five other species: *Piptadenia gonoacantha*, *Sebastiania commersoniana*, *Machaerium stipitatum*, *Dendropanax cuneatum* and *Platycyamus regnellii.* The four remaining species, *Acacia polyphylla*, *Cupania vernalis*, *Eugenia acutata* and *Myrciaria floribunda* showed no significant pattern.

Discussion

Sylvigenesis is the chain of structural changes that a certain forest area undergoes after a disturbance event disrupts tree community biomass and organization (Oldeman 1983; 1989; Nascimento & Viana 1999). This regeneration process may be classified into phases that are recognized by some tree community features, particularly size distribution, species composition and dynamic trends. Changes in tree demography and biomass, traditionally expressed by density and basal area, may stand for key diagnostic features for recognizing regeneration phases. We here propose a hypothetical model of sylvigenesis based on both aspects of tree community dynamics and on the manifold possible paths connecting the regeneration phases (Fig. 4). The *Stability* phase corresponds to the ‘climax’ or ‘mature’ stage of a forest area or eco-unit, where both density and basal area fluctuate moderately under a low impact disturbance regime, *i.e.* without the formation of canopy gaps (*e.g.*, branch-falls and death of sub-canopy trees). This phase may be disrupted by a moderate to severe disturbance event that opens the forest canopy and causes a cutback in both tree density and basal area, characterizing the *Degradation* phase. This phase can be either very brief, as happens after sudden multiple tree-falls caused by wind storms, or last for longer time spans, as when canopy gaps are formed by the gradual crumbling of standing trees and when tree death escalates, because the area is reached by the permeating effects of a nearby disturbance (*e.g.*, edge-effects). Once disturbance effects are ceased,

Table 2. Tree community dynamics per diameter class (dbh) in the Mata da Lagoa, between 2000 e 2005, given for the whole sample and its four soil habitats. Values within parentheses are expected frequencies of trees in 2005 and dead trees based on the frequencies of trees in 2000. Mort. = mortality rates; inter-class migrants: outgr. = outgrowth, recr. = recruits, ingr. = ingrowth.

Diameter	Number of trees					Mort.	Inter-class migrants			Poisson counts	
classes (cm)	2000	2005		dead		(% yr^{-1})	outgr.	recr.	ingr.	*Z*	*p*
Whole sample:											
5≤ dbh <10	641	654	(613.0)	92	(94.7)	3.1	41	136	10	0.778	ns
10≤ dbh <20	405	345	(387.3)	73	(59.8)	3.9	32	0	45	4.899	0.001
20≤ dbh <40	196	188	(187.5)	22	(28.9)	2.4	11	0	25	1.050	ns
40≤ dbh <80	65	63	(62.2)	6	(9.6)	1.9	2	0	6	0.535	ns
Totals	1307	1250		193		3.1	86	136	86		
Upper Argisols:											
5≤ dbh <10	95	100	(88.9)	20	(19.9)	4.6	5	29	1	0.674	ns
10≤ dbh <20	76	57	(71.1)	20	(15.9)	5.9	3	0	4	3.657	0.001
20≤ dbh <40	21	24	(19.6)	1	(4.4)	1.0	0	0	4	1.342	ns
40≤ dbh <80	9	7	(8.4)	1	(1.9)	2.3	1	0	0	1.414	ns
Totals	201	188		42		4.6	9	29	9		
Lower Argisols:											
5≤ dbh <10	199	200	(187.3)	14	(23.0)	1.4	10	25	0	0.143	ns
10≤ dbh <20	138	115	(129.9)	23	(15.9)	3.6	11	0	11	3.429	0.001
20≤ dbh <40	78	73	(73.4)	12	(9.0)	3.3	4	0	11	0.962	ns
40≤ dbh <80	27	28	(25.4)	2	(3.1)	1.5	0	0	3	0.447	ns
Totals	442	416		51		2.4	25	25	25		
Upper Nitosols:											
5–<10	130	126	(124.2)	23	(23.7)	3.8	13	31	1	0.485	ns
10–<20	61	58	(58.3)	11	(11.1)	3.9	6	0	14	0.539	ns
20–<40	30	26	(28.7)	7	(5.5)	5.2	2	0	5	1.069	ns
40–<80	4	5	(3.8)	0	(0.7)	0.0	0	0	1	1.000	ns
Totals	225	215		41		3.9	21	31	21		
Lower Nitosols:											
5≤ dbh <10	217	228	(213.0)	35	(29.2)	3.5	13	51	8	1.063	ns
10≤ dbh <20	130	115	(127.6)	19	(17.5)	3.1	12	0	16	2.188	0.050
20≤ dbh <40	67	65	(65.8)	2	(9.0)	0.6	5	0	5	0.577	ns
40≤ dbh <80	25	23	(24.5)	3	(3.4)	2.5	1	0	2	0.816	ns
Totals	439	431		59		2.8	31	51	31		

ns = non significant

forest building takes place through either of two paths. In the first, an *Early Building* phase, with increasing tree density and basal area, ensues immediately. In the second path, this phase is preceded by an *Early Building with Degradation* phase during which the loss of biomass persists, caused by the death of larger trees, while a new generation of smaller trees is recruited (Oldeman 1983). The declining basal area is therefore accompanied by increasing density. The ensuing *Late Building* phase is characterized by the opposite trend, *i.e.* increasing basal area and decreasing density, the so-called 'self-thinning' process (Oliveira-Filho *et al.* 1997), when a few trees that survive the escalating competition accumulate biomass and grow bigger while many others die, most of which are small. As a result, the forest structure changes from a high density of small trees to a lower tree density with increasing concentration of biomass towards larger trees (the J-reverse distribution). Additional disturbance may intervene during any of the building phases and cause setbacks in the regeneration process and, in strict terms, tree community structure hardly ever attains a long-lasting stability phase (Swaine & Hall 1988).

From the perspective of the above model one can easily infer that small and disturbed man-made forest fragments such as Mata da Lagoa are quite unstable and degradation and building phases probably predominate all-over the area for a period of unforeseen duration. Man-made fragments of tropical forests undergo far-reaching and long-lasting changes in both species composition and physiognomic structure caused by both edge-effects and eco-geographical isolation (Noss & Csuti 1997; Pulliam & Dunning 1997; Laurance 2000; Laurance *et al.* 2002). As usual in other small forest fragments lodged within intensively farmed areas, Mata da Lagoa has been subjected

Table 3. Contingency table with the frequencies of dead trees in each death category and soil habitat of the Mata da Lagoa. Values within parentheses are expected frequencies.

		Death categories				Chi-squared	
Habitats		Felled	Fallen	Standing	Broken	χ^2	*p*
Upper Argisols		0 (2.0)	16 (15.2)	16 (17.3)	5 (2.4)	2.971	0.179
Lower Argisols		2 (6.6)	56 (49.4)	58 (56.1)	4 (7.9)	4.782	0.109
Upper Nitosols		3 (4.0)	33 (29.7)	36 (33.6)	0 (4.7)	4.206	0.139
Lower Nitosols		16 (8.4)	52 (62.6)	68 (71.0)	16 (10)	10.845	0.006
Chi-squared	χ^2	9.831	2.655	0.265	10.054	22.804	0.013
	p	0.006	0.379	0.928	0.005		

Table 4. Coefficients of correlation and their significance ($p < 0.01$) for the relationships between dynamics rates and five environmental variables in $N = 29$ sample plots (20 × 20 m) used to survey the Mata da Lagoa. Coefficients are non-parametric (Spearman's) for correlations with drainage classes and parametric (Pearson's) for the others. Tree mortality and recruitment rates are split into two diameter (dbh) classes.

	Environmental variables				
Dynamics rates	Drainage class	Soil pH	Basal area	Leaf area index	Edge factor
Mortality ($5 \leq$ dbh < 10 cm)	0.55**	0.23^{ns}	-0.25^{ns}	-0.60***	-0.17^{ns}
Recruitment ($5 \leq$ dbh < 10 cm)	0.53**	0.09^{ns}	-0.20^{ns}	-0.28^{ns}	0.07^{ns}
Mortality (dbh ≥ 10 cm)	0.09^{ns}	-0.03^{ns}	-0.53**	-0.03^{ns}	-0.15^{ns}
Recruitment (dbh ≥ 10 cm)	0.25^{ns}	0.55**	-0.27^{ns}	-0.11^{ns}	0.40^{ns}
Loss (basal area)	0.15^{ns}	0.00^{ns}	-0.53**	0.10^{ns}	-0.07^{ns}
Gain (basal area)	0.50**	0.23^{ns}	-0.40^{ns}	-0.27^{ns}	-0.13^{ns}

**, $p = 0.01$; ***, $p = 0.001$; ^{ns}, non significant

Table 5. Population dynamics for 12 tree species surveyed in 2000 and 2005 in the Mata da Lagoa, expressed as number of trees and basal areas. Regeneration (Regen.) guilds: Pion = pioneer, SubCan = sub-canopy, LightCan = light-demander canopy. Number of trees: N1 = initial (2000), N2 = final (2005), D = dead, R = recruits, Z = Poisson parameter, *p* = significance. Basal area: AB1 = initial (2000), AB2 = final (2005).

	Regen.	Number of trees						Basal area (m^2)	
Species	guilds	N1	N2	D	R	Z	*p*	AB1	AB2
Acacia polyphylla	Pion	46	48	8	10	0.47	^{ns}	0.066	0.079
Allophylus edulis	SbCan	20	27	0	7	2.65	**	0.002	0.003
Eugenia acutata	SbCan	31	30	2	1	0.58	^{ns}	0.131	0.148
Cupania vernalis	LgtCan	24	20	5	1	1.63	^{ns}	0.006	0.005
Dendropanax cuneatum	SbCan	28	24	4	0	2.00	*	0.003	0.004
Galipea jasminiflora	SbCan	203	215	15	27	1.85	*	0.273	0.233
Machaerium stipitatum	LgtCan	27	20	7	0	2.65	**	0.017	0.008
Mollinedia widgrenii	SbCan	82	91	5	14	2.06	*	0.206	0.208
Myrciaria floribunda	SbCan	26	27	2	3	0.45	^{ns}	0.004	0.004
Piptadenia gonoacantha	Pion	57	44	16	3	2.98	**	0.109	0.046
Platycyamus regnellii	LgtCan	66	61	5	0	2.24	*	0.786	0.811
Sebastiania commersoniana	SbCan	95	74	26	5	3.77	***	0.111	0.075

*, $p = 0.05$; **, $p = 0.01$; ***, $p = 0.001$; ^{ns}, non significant

to a great number of additional impacts, particularly cattle trampling, selective logging, burning of adjacent pastures, and forest clearing at the edges. Therefore, it is no surprise that *Degradation* phases prevailed all over the area between 2000 and 2005 with a generalized cutback of both tree density and basal area. The prevalence of *Degradation* phases entails that drawbacks promoted by disturbance impacts prevailed over tree regeneration. Nevertheless it is almost impossible to tell apart the effects of either past or current disturbances, *i.e.* occurring prior to or between the two surveys.

The 25% reduction of the fragment area through forest felling performed in 1985, *i.e.* fifteen years before the studied

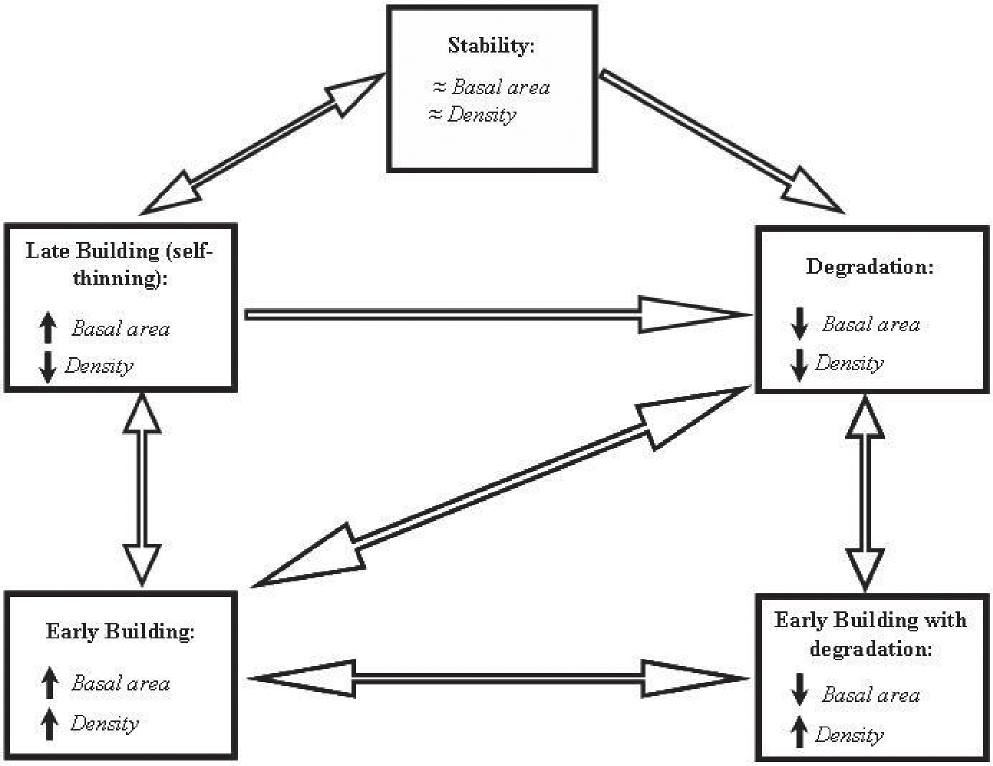

Figure 4. Flow diagram representing the interactions among hypothetical forest regeneration phases and their respective tree community dynamics trends expressed as changing demography (density) and biomass (basal area).

interval, is the strongest candidate among the disturbance forces causing generalized degradation. The impact of this felling probably accentuated edge-effects over the whole fragment, as the area is small enough to be totally made up of forest edges if we take into account that strong edge-effects in tropical forests are detectable at distances of up to 200 m from the edges and two or more decades after edge creation (Laurance & Yensen 1991; Laurance 2000). Another evidence of the greater impact of the fragment reduction was the generalized concentration of decreasing tree density in the second diameter class ($10 \leq$ dbh < 20 cm). This probably reflects a past disturbance event that affected mostly the seedlings and saplings in the understory and created a recruiting gap that smoothes down along time but also appears at increasingly larger size classes. Seedlings, saplings and smaller trees are actually the most affected immediately after edge creation (Viana *et al.* 1997; Laurance *et al.* 1998; 2002).

Other relevant and additional sources of disturbance were cattle trampling and selective logging but their effects were not evenly distributed, as evidenced by the higher density of cattle tracks in the two Upper soil habitats and higher proportion of felled trees in the Lower Nitosols. Nearness was probably the key-reason in both cases, because the Upper habitats are adjacent to the cattle-grazing pastures while the Lower Nitosols are more accessible for collectors of both wood and palm-heart of *Syagrus romanzoffiana*. The higher frequency of broken trees in this site is probably due to the 'domino effect' (Crawford & Yaoung 1998) triggered by fall of large trees; half of tree deaths in the larger diameter class took place in the Lower Nitosols. Additional spatial heterogeneity was registered for other dynamics trends despite the generalized drop of both tree density and basal area in the Mata da Lagoa. Generally speaking, tree community dynamics was more rapid in the Upper habitats than in the Lower ones, though this was clearer for the Argisols. Spatial heterogeneity of disturbance may be once more evoked here because forest edge areas felled in 1985 were much larger near the Upper habitats. In addition, these habitats are more trampled by cattle. Disturbance impacts are therefore more severe in the Upper habitats and this probably gives rise to more unstable and quickly changing community than in the other habitats.

Despite all this, one can not disregard that substrate heterogeneity may also be involved as, for instance, water availability is lower in the Upper habitats and soil drainage classes were significantly correlated with both mortality and recruitment rates of trees in the $5 \leq$ dbh < 10 cm class as were gain rates of tree basal area. Thus, the lower was the water availability the higher were the rates of mortality and recruitment of smaller trees while larger ones (dbh $\geq$ 10 cm) were unaffected. Smaller trees probably have less access to deeper ground water stocks than larger ones, and this is particularly critical in Brazilian seasonal forests that experience a water shortage season (Furtini *et al.* 2003). As a consequence, the higher water shortage of the Upper habitats may have contributed to locally intensify the disturbance effects. In a similar way, the increasing mortality rates of smaller trees with increasing light availability probably reflected the higher canopy openness of more disturbed sites, which may, in turn, have aggravated the water shortage during the dry seasons (Sterck & Bongers 2001). Water- and light-related factors would then be inextricably linked with disturbance at affecting the dynamics of smaller trees. If no correlation was found with the edge factor, this must have to do with the small size of the fragment that assigns the status of forest edge to the whole area.

The only substrate-related variable correlated with tree dynamics apparently with no connection with disturbance was the increasing recruitment rates of larger trees (dbh ≥ 10 cm) with increasing soil pH. The higher nutrient availability of Nitosols is probably contributing to the higher survival and growth rates of trees above a certain size. The dynamics of larger trees was also related to the initial basal area, which represents the standing tree biomass at the beginning of the study period and, putatively, the competition environment. Contrary to what was expected (Machado *et al.* 2008), the higher was the initial basal area of a site the lower were both the mortality rates of larger trees and the loss rates of tree basal area. In fact, as *Degradation* phases prevail all over the fragment, competition was certainly not the main force driving the dynamics of larger trees as expected in *Building* phases. The trend probably reflects, once more, different levels of disturbance and sites with higher initial basal areas and lower loss and mortality rates simply represent the less advanced stages of forest degradation.

Tropical forests normally experience very low rates of change in species composition and five years of observation is a very short time to reveal significant species replacement for long-living organisms such as trees (Swaine & Lieberman 1987; Condit *et al.* 1992). As in the present case, studies of short-term dynamics of tropical forests generally record less than 10% of species disappearing and appearing between surveys and, obviously, among those represented by few individuals (Taylor *et al.* 1996; Kellman *et al.* 1998; Nascimento *et al.* 1999; Werneck *et al.* 2000; Pinto & Hay 2005). Despite all this, a significant decrease in species richness was detected in the Lower Argisols and this was probably related to the lower recruitment rates at this habitat. The relevant fact here is that forest degradation processes caused by severe impacts may result in local species extinction in a very short time span.

Tree population changes of more abundant species are much easier to detect in short-term studies than changes in species richness. Five out of the 12 analyzed populations showed the same degradation trend of the whole community and four populations showed no significant change. Both groups included species of all regeneration guilds. The only noteworthy trend was that the three species expanding in the period, contrasting with the overall degradation trend, were all sub-canopy dwellers. This trend is possibly related to the significant drop in the density of trees of the 10 ≤ dbh < 20 cm class that could have opened spaces for small sub-canopy trees. On the other hand, there is also the possibility that this trend is merely a result of selective logging of trees belonging to this size class because they are preferred for firewood, tool handles, props and poles.

The findings of the present study showed that processes of tree community dynamics can be spatially heterogeneous even in small forest fragments where the same dynamics trend is observed all over the area. This spatial heterogeneity was chiefly determined by the particular disturbance history of each site while environmental heterogeneity may have played a secondary but significant role. Apart from this, as shown in similar studies (Oliveira-Filho *et al.* 2004; Appolinario *et al.* 2005) it was also clear, that the causes of variations in community dynamics in both space and time are often obscure particularly when the interacting factors involve past disturbance events which are difficult to recover with satisfactory precision and detail.

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