Tree community dynamics in a submontane forest in southeastern Brazil: growth, recruitment, mortality and changes in species composition over a seven-year period

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ABSTRACT

In order to assess long-term community dynamics in tree populations, we investigated trees with a diameter at breast height (DBH) ≥ 5 cm in an 11-ha fragment of submontane tropical forest in southeastern Brazil, at the beginning and end of a seven-year period. We observed a general tendency toward decreasing numbers of trees and toward stability in basal area. The stability in basal area was associated with an equilibrium between the loss of trees and the basal area gain from the horizontal growth of surviving trees, as well as from recruits The abundance of dead trees was significantly higher than was that of recruits. Changes in tree abundance occurred mainly in the lower DBH classes, whereas changes in basal area occurred mainly in the intermediate DBH classes. Among trees with a DBH ≥ 10 cm, the observed rates of mortality and recruitment (2.4% yr^{-1} and 1.8% yr^{-1}, respectively) were similar to those reported for other tropical forests. When we examined only trees with a DBH ≥ 10 cm, we found the half-life to be 29.5 years, which places the forest fragment studied among the most dynamic of tropical forests. Over the seven-year period evaluated, the tree community lost ten species, with no new records. The most abundant species showed the highest rates of mortality and recruitment. Climax species, whether shade-tolerant or light-demanding, accounted for more species and individuals than did pioneer species, suggesting that the former group has a greater influence on forest dynamics. The results suggest that the tree community studied is in or is approaching a state of dynamic equilibrium, the changes in community structure and composition being attributed to periodic fluctuations.

Key words: submontane tropical forest, Poço das Antas Biological Reserve, Brazil, Atlantic Forest, community dynamics

Introduction

In forest communities, trees play an important ecological role, determining the architecture and microclimate within the forest (Matlack 1993; Laurance *et al*. 1998), as well as representing the main component of forest diversity (Denslow 1987). Therefore, changes imposed on trees can have a major influence on forest dynamics. Studies in tropical forests have demonstrated variations in spatial dynamics (Lieberman & Lieberman 1987) and temporal dynamics (Manokaran & Kochummen 1987), caused by the influence of environmental variables such as disturbance (Gomes *et al*. 2003; Higuchi *et al*. 2008) and fragmentation (Oliveira-Filho *et al*. 2007).

Within the Atlantic Forest Biome of Brazil, particularly in the central coastal lowlands of the state of Rio de Janeiro, human activity and fragmentation are major sources of disturbance (Siqueira *et al*. 2004; Guedes-Bruni *et al*. 2006; Pessoa & Oliveira 2006; Carvalho *et al*. 2007, 2008). Human activities, mainly timber extraction, burning, cattle grazing, sand mining, artificial drainage and river channelization, have contributed to modifying the vegetation cover. The original forest has been transformed into a mosaic of isolated forest fragments (of various sizes and at different successional stages), surrounded by grassland formations, and most of those fragments have been highly disturbed. This puts many local animal and plant species at risk (Kierulff & Ryland 2003; Figueiredo & Fernandez 2004; Pessoa & Oliveira 2006). There is a lack of studies on the dynamics of these communities. Such studies are essential to understanding the processes and mechanisms by which the communities are maintained.

Here, we analyze the dynamics of a tree community and changes in tree populations in a submontane forest fragment over a period of seven years (1999-2006). We attempted to determine whether the tree community and populations remained stable during the study period, as well as to identify and explain any changes observed. To our knowledge, this is the first study of forest dynamics in a dense, moist, submontane forest in Brazil.

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Material and methods

Study site

The study was carried out in a fragment of tropical dense, moist, submontane forest (Veloso *et al.* 1991) consisting of 11 ha situated in the Poço das Antas Biological Reserve (22°30'-22°35'S; 42°14'-42°19'W), within the municipality of Silva Jardim, in the state of Rio de Janeiro, which is in southeastern Brazil. According to Köppen classification system, the climate is type As - wet tropical with a dry winter, high mean monthly temperatures for most of the year and an averageprecipitation of 1500-2000 mm per year. The soil types are varied: Ultisols and Tropepts at low elevations; and Aquepts, Histosols and Fluvents on floodplains (Lima *et al.* 2006). The fragment studied is circular in shape and is surrounded by grassland, the distance to the nearest neighboring fragment being ca 65 m. The fragment studied belongs to a group of eight forest fragments situated at low elevations. They are located on a vast plain where the water supply was modified by dam construction in 1984, causing a decrease in fragment size. That also changed surrounding vegetation formations, facilitating fires which in turn modified to varying degrees the edge or interior regions of the eight fragments. The first survey was completed in 1999, after which two fires burned much of the matrix between the fragments, and a small portion of the northern edge of the surveyed fragment was slightly affected, with damage to the herb and litter layers. The structure of the fragments is characterized by many species with low densities, trees in the lowest diameter at breast height (DBH) classes showing the highest densities and those in the highest DBH classes showing the lowest densities. These forest fragments are distinguished by high richness and density of species pertaining to the families Myrtaceae, Lauraceae, Fabaceae, Sapotaceae, Euphorbiaceae, Moraceae, Rubiaceae and Annonaceae, the following species being predominant (Pessoa & Oliveira 2006): *Senefeldera verticillata* (Vell.) Croizat, *Actinostemon verticillatus* (Klotzch) Baill., *Mabea piriri* Aubl. (Euphorbiaceae), *Anaxagorea dolichocarpa* Sprague & Sandwith (Annonaceae), *Helicostylis tomentosa* (Poepp. & Endl.) Rusby (Moraceae), *Ecclinusa ramiflora* Mart. (Sapotaceae), *Pterocarpus rohrii* Vahl (Fabaceae), *Guapira opposita* (Vell.) Reitz (Nyctaginaceae) and *Faramea multiflora* A. Rich. ex DC. (Rubiaceae).

Sampling and data analyses

In 1999, Pessoa & Oliveira (2006) established two transects (running north-south and east-west, respectively), arranged in 26 contiguous plots of 10×25 m each (13 plots per transect), totalizing 0.65 ha. All individuals with a diameter at breast height (DBH) $\geq$ 5 cm were tagged; heights and diameters were recorded; and voucher specimens were collected (Pessoa & Oliveira 2006). In 2006, we conducted a second survey in the same plots. We collected survival and mortality data for all of the first-survey trees, as well as recruitment and diameter growth data for all trees with DBH $\geq$ 5 cm in the initial survey.

Tree community dynamics

We calculated parameters of community dynamics, mortality rates and recruitment rates, as well as the rates of gain and loss in basal area. In calculating mortality rates and recruitment rates, we assumed that changes in population size constituted a constant proportion of the initial tree population per time interval (Sheil 1995; Sheil *et al.* 1995, 2000). Mean annual mortality (M), recruitment (R), loss (L) and gain (G) in basal area were calculated using the following expressions (Sheil *et al.* 1995; 2000):

$$M = [1 - (N_s/N_o)^{1/\Delta t}] \times 100$$
$$R = [1 - (1 - r/N_t)^{1/\Delta t}] \times 100$$
$$L = [1 - (BA_s + BA_d/BA_o)^{1/\Delta t}] \times 100$$
$$G = 1 - \{1 - [(BA_r + BA_g)/BA_t]^{1/\Delta t}\} \times 100$$

where M is the mean annual mortality rate, N_s is the size of the surviving population in the second survey, N_o is the size of the population in the initial survey, Δt is the elapsed time in years, R is the mean annual recruitment rate, r is number of individuals recruited between the two time points, N_t is the size of the population in the second survey, L is the mean annual loss in basal area, BA_s is the sum of the basal areas of surviving individuals in the second survey, BA_d is the basal area lost by the surviving individuals (diameter decrease and partial loss of trunk), BA_o is the total basal area in the initial survey, G is the mean annual gain in basal area, BA_r is the sum of the basal areas of recruits, BA_g is the basal area gained by the surviving individuals, and BA_t is the total basal area in the second survey. The rate of gain is calculated on the basis of the estimated number of individuals recruited (Sheil *et al.* 2000).

Half-life and doubling time were used in order to assess changes in the community. Half-life is defined as the time required for the stand to decrease its size by half at the current mortality rate. Doubling time is defined as the time required for the stand to double its size at the current recruitment rate. These indices were calculated using the following expressions (Korning & Balslev 1994):

$$T_H = ln(0.5)/ln(1 + M)$$
$$T_D = ln(2)/ln(1 + R)$$

where T_H is the half-life, ln is the natural log, and T_D is the doubling time. We obtained the turnover rate from the individual count (Phillips & Gentry 1994) and from the basal area (Oliveira-Filho *et al.* 1997; Werneck & Franceschinelli 2004), as calculated by the following expressions:

$$T_N = (M + R)/2$$
$$T_{BA} = (L + G)/2$$

where T_N is the individual turnover rate, and T_{BA} is the basal area turnover rate. The difference between the number of dead trees and the number of recruited trees was determined by comparing Poisson counts (Zar 1996).

We analyzed tree dynamics by diameter class, using the same DBH class intervals adopted in other studies of neotropical forest dynamics (Appolinário *et al.* 2005; Oliveira-Filho *et al.* 2007; Higuchi *et al.* 2008): 5.0-10.0 cm; 10.1-20.0 cm; 20.1-40.0 cm; and > 40.1 cm. Modifications that occurred between the two surveys in each diameter class were determined by recording the number of trees that remained in the class, as well as the numbers of individuals that died, were recruited, immigrated (from another diameter class) and emigrated (to another diameter class), as well as by calculating the losses and gains in basal area. For each diameter class, the difference between the number of trees added (recruits + immigrants) and the number of trees subtracted (dead individuals + emigrants) was determined by comparing Poisson counts (Zar 1996). The chi-square goodness-of-fit test was used in order to determine whether the frequency of live trees and dead trees in 2006 was independent of diameter class, on the basis of the frequencies expected from the diameter distribution reported in the 1999 survey.

Changes in tree populations

To analyze changes in tree populations, we selected 17 species that had been represented by ≥ 10 individuals in the first survey. We calculated the following parameters of forest dynamics: mortality; recruitment; and basal area (gains and losses). Differences in frequency between the number of recruits and the number of dead trees in each of the 17 populations were examined by comparing Poisson counts. In order to determine the influence of species groups on the dynamics in the fragment studied, we classified the 17 species by ecological group, using the classification system proposed by Swaine & Whitmore (1988) for trees in tropical rain forests, as follows: pioneer species; light-demanding climax species; and shade-tolerant climax species. The species are distinguished by their light requirements for germination and establishment. Seeds of pioneer species require solar radiation to germinate, their seedlings and saplings being found in open areas of the forest. Light-demanding climax species need solar radiation for seedling growth and typically grow rapidly under such conditions. Shade-tolerant climax species require little or no solar radiation for seedling growth. The classification of the species by ecological group was based on the literature and on ten years of experience in the forest formation under study.

Results

Tree community dynamics

From 1999 to 2006, there was a general tendency toward a decrease in the numbers of trees, as well as toward stability in basal area (Tab. 1). The number of dead trees surpassed the number of recruits in 21 of the 26 sample plots. The abundance of dead trees was significantly higher than that of recruits (Z=6.72, p=0.00). The observed stability in basal area was associated with the fact that losses in basal area were offset by gains related to the growth of the surviving trees (Tab. 1). In the analysis of changes in tree abundance by diameter class, we observed differences between the two time points in distribution by diameter, the difference being greatest for the 5.0-10.0 cm diameter class (Fig. 1). Between 1999 and 2006, there was a reduction in tree abundance in the 5.0-10.0 cm, 10.1-20.0 cm and > 20-40 cm diameter classes, as well as an increase in the number of dead trees in all classes. Tree numbers increased only in the > 40.1 cm diameter class. However, the diameter distribution for the sample did not differ significantly between 1999 and 2006 (χ^2=2.38, p=0.5). As can be seen in Tab. 2, abundance values were higher than expected only in the > 40.1 cm diameter class. The highest dead tree counts were recorded for the two smallest diameter classes, and there were no significant differences among the diameter classes in terms of mortality (χ^2=2.65, p=0.45). Mortality was higher than expected in the intermediate (10.1-20.0 cm and 20.1-40.0 cm) diameter classes. In the two smallest diameter classes, the number of trees subtracted (dead individuals + emigrants) was significantly higher than the number of trees added (recruits + immigrants). Differences were not significant for the other diameter classes. These results show that the smaller diameter classes are primarily responsible for changes in tree abundance, whereas an imbalance in basal area is due to a loss in basal area among trees in the intermediate diameter classes.
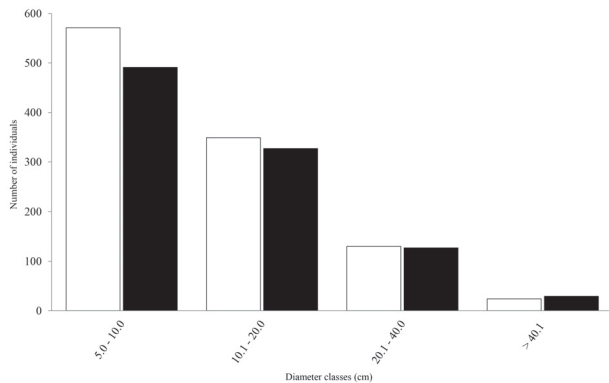
The mortality rate of 2.2% yr⁻¹ resulted in a half-life of 31.2 years. Recruitment was 0.9% yr⁻¹, resulting in a doubling time of 77.2 years, with an individual turnover rate of 1.57% yr⁻¹ and a basal area turnover rate of 2.1% yr⁻¹. However, if the minimum DBH is raised to ≥ 10 cm, the values differ considerably, with mortality at 2.4% yr⁻¹ and recruitment at 1.8% yr⁻¹, translating to a half-life of 29.5 years and a doubling time of 37.9 years.

Changes in tree populations

In 1999, there were 150 tree species, compared with only 140 in 2006, and there were no new additions between the two time points. Population abundance changed very little during the period. Forty-two species (28%) suffered losses or gains of at least one tree. Sixteen species lost or gained two to five trees, and only five species lost more than five trees.

Table 1. Dynamics of the tree community in an area of tropical submontane forest over a seven year period (1999-2006) in the Poço das Antas Biological Reserve, Brazil.

Characteristcs	Total sample
Number of trees	
1999	1074
2006	974
Surviving	913
Dead	161
Recruits	61
Mortality rate (% yr^{-1})	2.25
Recruitment rate (% yr^{-1})	0.9
Turnover rate (% yr^{-1})	1.57
Basal area	
1999 (m^2)	20.26
2006 (m^2)	20.24
Dead (m^2)	2.86
Recruits (m^2)	0.14
Growth of surviving trees (m^2)	2.7
Loss rate (% yr^{-1})	2.11
Gain rate (% yr^{-1})	2.14
Turnover rate (% yr^{-1})	2.1

Figure 1. Distribution of trees, by diameter at breast height, in a fragment of submontane tropical forest within the Poço das Antas Biological Reserve, in the state of Rio de Janeiro, Brazil, in 1999 (□) and 2006 (■).

Population abundance decreased in 41 species and increased in three, remaining unchanged in the remaining species. Between the two time points, there were individual deaths in 60 species, whereas there was recruitment of individuals in 25. All ten of the species that were lost from the community were comprised of only one or two individuals and were therefore considered rare species. Among the surviving species, losses (in terms of the number of dead trees) were greatest from *Senefeldera verticillata* (n = 34), *Anaxagorea dolichocarpa* (n = 16), *Mabea piriri* (n = 12), *Astrocaryum aculeatissimum* (n = 10) and *Faramea truncata* (n = 8), which collectively accounted for 49.7% of the total mortality. Recruitment (in terms of the number of trees added) was greatest among *S. verticillata* (n = 15), *A. dolichocarpa* (n = 9), *F. truncata* (n = 6) *Actinostemon verticillatus* (n = 4) and *M. piriri* (n = 3), which collectively accounted for 60.6% of the total recruitment. Among the 17 species that had been represented by ≥ 10 trees in 1999, we observed significant differences between recruitment and mortality in three species, mortality rates being higher than recruitment rates in all three of those species: *S. verticillata* (Z=2.71, p=0.005); *A. aculeatissimum* (Z=2.71, p=0.01); and *M. piriri* (Z=2.32, p=0.02). Seven species decreased in abundance and lost basal area, *A. aculeatissimum* (45%), *M. piriri* (25%) and *Virola gardneri* (A.DC.) Warb. (25%) showing the greatest reduction in number of trees. There was only one species (*Ecclinusa ramiflora* Mart.) in which abundance remained unchanged and there was a gain in basal area. Seven species showed reduced abundance and yet made gains in basal area. In one species (*Bathysa mendoncaei* K. Schum.), abundance and basal area both increased, whereas in another (*Rinorea guianensis* Aubl.) there was a decrease in abundance and no change in basal area. The species *A. aculeatissimum*, *Faramea multiflora*, *Tetraplandra leandrii* Baill. and *Guapira opposita* showed the greatest losses in basal area (Tab. 3). Therefore, among the species that were the most abundant in the two surveys, eight had populations with dynamics similar to those presented by the entire community. We observed a tendency toward a decline in the number of trees and toward stabilization of the basal area.

Among the species whose populations declined in abundance and in basal area, two were pioneer species, three were shade-tolerant climax species, and two were

Table 2. Dynamics of the tree community per diameter class for a tropical submontane forest over a seven year period (1999-2006) in the Poço das Antas biological Reserve, Brazil. Expected values (exp.), Emigrant (emgr.), Imigrant (imgr.), Recruits (recr.). Poisson count: values of Z and P.

Diameter class (cm)	Number of trees				Dead			Loss % yr^{-1}	Gain % yr^{-1}	Emgr. N°	Imgr. N°	Recr. N°	Poisson Z	Count P
	1999	2006	exp.	N°	exp.	%yr^{-1}								
5-10	571	491	(556.9)	81	(85)	2.1	2.1	2.99	61	1	61	5.60	0
› 10-20	349	327	(354.5)	58	(53)	2.6	2.2	0.9	26	62	-	2.56	0.01
› 20-40	130	127	(134.8)	21	(19.7)	2.4	2.6	1.33	7	25	-	0.41	ns
› 40-80	24	29	(27.8)	1	(3.3)	0.6	1.3	2.79	-	6	-	1.89	ns
Total	1074	974		161					94	94	61		

light-demanding climax species. Of the seven species that declined in abundance and increased in basal area, one was a pioneer species, two were light-demanding climax species, and four were shade-tolerant climax species. A simultaneous increase in abundance and basal area was seen in only one species, a light-demanding climax species. Ecological species group distribution indicates eight light-demanding climax species, six shade-tolerant climax species and three pioneer species. The rates of individual turnover and basal area turnover were highest for *Astrocaryum aculeatissimum*. Only the species *Faramea multiflora* presented a similarly high basal area turnover rate (Tab. 3).

Discussion

The results of this study indicate that, for the period evaluated, the community dynamics of the forest fragment under study were characterized by an imbalance between mortality and recruitment rates, the rates of the former being higher than those of the latter. However, there was a tendency toward an equilibrium between losses and gains in basal area. An analysis of tree distribution by diameter class suggested that tree size does not influence mortality. In tropical rain forests, mortality has been found to be independent of tree size for trees with a DBH ≥ 5 cm or ≥ 10 cm, meaning that the risk of death is the same for small trees as it is for large trees (Lieberman *et al*. 1985; Gentry & Terborgh 1990; Swaine 1990). The logarithmic decline in tree numbers in parallel with an increase in individual tree size is a consequence of forest dynamics, allowing the coexistence of trees of different sizes and the recruitment of new trees (Rankin-de-Merona *et al*. 1990; Swaine 1990). The results are consistent with the picture presented above and a general feature of steady-state tropical forests (Swaine *et al*. 1987; Whitmore 1998). The variance here observed in tree mortality and recruitment might reflect periodic fluctuations (Manokaran & Kochumnen 1987) more than a response to post-disturbance recovery (Oliveira-Filho *et al*. 1997; Appolinário *et al*. 2005) or long-term successional changes (Foster 1990; Gentry & Terborgh 1990). Underscoring this idea is the maintenance of a great proportion of species in the later successional stages. The great proportion of species of later ecological status might have resulted in the lower recruitment rate found. Because such species show slow growth, the length of census interval might not have allowed new trees to reach the 5 cm minimum DBH cut-off used in this study. Fragment size is another point that cannot be neglected. The small size of the fragment (11 ha) could have a direct influence on the persistence of species, mainly those present at low density. Populations with low density can be affected by processes at the population level, through genetic or demographic events (Gilpin & Soulé 1986), and processes at the community level, such as loss of pollinators or seed dispersers, can compromise reproductive success and establishment (Aizen & Feinsinger 1994). Species lon-

Table 3. Tree population dynamics for the 17 most abundant species in a submontane forest over seven years time (1999-2006) in the Poço das Antas Biological Reserve, Brazil. Ecological group: CST= climax shade-tolerant, CLD = climax light-demanding, PI = pioneer. Number of trees: N_o = initial (1999), N_f= final (2006), D= dead, R= recruit. Basal areal: BA_0 = initial (1999), BA_f = final (2006). T_N = turnover rate in tree numbers. T_{BA} = turnover rate in basal area.

| Species | GE | Number of trees | | | | Basal area (m²) | | T_N | T_{BA} |
		N_0	D	R	N_f	BA_0	BA_f		
Senefeldera verticillata (Vell.) Croizat	CST	243	34	15	223	3.456	3.476	1.47	2.32
Anaxagorea dolichocarpa Sprague & Sandwicth	CST	97	16	9	90	0.612	0.591	1.89	1.80
Actinostemon verticillatus (Klotzch) Baill.	CST	78	5	4	77	0.586	0.622	0.83	0.78
Faramea truncata DC.	CST	52	8	6	50	0.360	0.387	2.04	1.58
Mabea piriri Aubl.	PI	48	12	3	39	1.002	0.849	2.33	2.32
Helicostylis tomentosa (Poepp. & Endl.) Rusby	CST	33	3	2	31	0.570	0.642	1.36	1.28
Ecclinusa ramiflora Mart.	CLD	26	1	1	26	0.386	0.401	0.55	0.85
Astrocaryum aculeatissimum (Schott) Burret	PI	22	10	1	13	0.156	0.085	4.63	5.12
Aparisthmium cordatum (A. Juss.) Baill.	PI	21	5	2	18	0.103	0.116	2.69	1.91
Guapira opposita (Vell.) Reitz	CLD	17	2	1	16	0.324	0.251	1.79	2.69
Bathysa mendoncaei K. Schum.	CLD	18	-	2	20	0.118	0.133	0.73	1.12
Faramea multiflora A.Rich. ex DC	CLD	14	2	1	12	0.051	0.041	2.27	3.47
Virola gardneri (A.DC.) Warb.	CST	12	3	1	10	0.303	0.292	2.71	1.76
Rinorea guianensis Aubl.	CLD	12	1	-	11	0.150	0.150	0.61	1.05
Pseudolmedia laevigata Trécul.	CLD	12	1	-	11	0.065	0.066	0.61	1.89
Tetraplandra leandri Baill.	CLD	11	2	1	10	0.158	0.127	2.12	2.95
Swartzia apetala var. *glabra* (Vogel) R.S. Cowan	CLD	10	1	-	9	0.054	0.055	0.73	0.73

gevity and relative abundance are among the main features linked to patterns of tree mortality (Swaine *et al.* 1987).

Compared with the mean mortality rates reported for trees with a DBH ≥ 10 cm in other neotropical rain forests by Korning & Balslev (1994) and Phillips *et al.* (1994)—0.70% yr^{-1} and 3.01% yr^{-1}, respectively—the 2.38% yr^{-1} obtained in the present study is relatively high. For trees with a DBH ≥ 5 cm and ≥ 10 cm, we recorded mean half-life values of 31.7 years and 29.5 years, respectively, which are also comparable to the mean of 46.5 years (range, 22.5-139.3 years) previously recorded for tropical forests (Phillips & Gentry 1994). Therefore, the forest studied here is among the most dynamic forests in the world. The half-life of 29.5 years found for trees with a DBH ≥ 10 cm is even more similar to the 28 years previously obtained for a 10-ha fragment in Central Amazonia (Laurance *et al.* 1998). Unfortunately, the dynamic parameters indicated do not allow other comparisons between the two studies, which could be very interesting considering the similarity of the two study areas in terms of size and isolation. In the present study, when trees ≥ 5 cm DBH were considered, the doubling time was more than twice the half-life, indicating a rapid decrease in density in the study area. This shows the influence that the DBH cut-off point had on the results, which is probably linked to the fact that, although small trees are numerous in tropical forests, their mortality rates are typically much higher than are those of larger trees (Swaine 1990). It should be borne in mind that the growth and survival of small trees can be negatively affected by the proximity of co-specific adults, as well as that, within the population, mortality rates can vary by size class (Hubbell & Foster 1990a; 1990b).

Over the seven-year period evaluated, the community under study showed a decrease in species richness, the losses being concentrated in those species with low abundances. This suggests demographic problems in some species populations, which, due to low numbers of recruits, have trouble surviving in the community (Pessoa & Oliveira 2006). In forest fragments, the space and conditions that support and increase the chances of germination and establishment are, in general, reduced (Benitéz-Malvido 1998; Scariot 2000; Laurance *et al.* 2001), which has implications for the maintenance of populations occurring at low density. Although the presence of species at low density is said to be a feature of tropical forests (Hubbell & Foster 1986), such species are more predisposed to local extinction, due to environmental and demographic variations, genetic problems and natural events (Gilpin & Soulé 1986; Nason *et al.* 1997). Therefore, it is possible that the species at low density are not self-maintaining and that their populations have been sustained by the importation of propagules from neighboring fragments (Pessoa & Oliveira 2006). Because trees typically live for decades, many species may be responding slowly, persisting locally only as adults trees (Foster 1990; Gentry & Terborgh 1990; Williams-Linera *et al.* 1998; Laurance *et al.* 2006), full populations being impracticable (Kageyama

et al. 1998). Consequently, species recorded in the second survey might not be present in a few years or constitute witnesses of the past. The changes in demographics and growth patterns observed in the present study might also be linked to species-specific needs. Because species differ in their needs for germination, growth and reproduction, community dynamics parameters can be influenced by local species composition; persistence of the species can also be imposed by local environmental conditions (Hubbell & Foster 1990a). In the present study, only three species showed considerable reductions in density; that is, the mortality rate had a direct influence on those species. The preponderant pattern among the most abundant species was that of a reduction in abundance and in basal area. Among such species, mortality was proportionally higher among the individuals of greater diameter, resulting in losses in basal area that surpassed the gains from growth. In various studies of tropical forests, the relationship between size and mortality has not been examined (Lieberman & Lieberman 1987; Gentry & Terborgh 1990). In studies evaluating that relationship, the mortality of large trees has been associated with the dry season (Hubbell & Foster 1990b), although drought events have also been associated with mortality in small trees (Hartshorn 1990). This relationship and its importance in maintaining the tree species composition in the forest fragment studied here remains unclear. The predominance of species in the later successional stages might be a factor, because such species typically exhibit slow growth. Therefore, the annual gain in basal area derived from diameter growth of individuals is low.

The analogy between ecological group and demographic changes in these same species showed few pioneer species. In tropical forests, the low abundance of pioneer species has been associated with conditions of little disturbance (Hartshorn 1980), although it has also been associated with post-disturbance recovery (Oliveira-Filho *et al.* 1997; Sheil *et al.* 2000; Werneck *et al.* 2000; Gomes *et al.* 2003; Werneck & Franceschinelli 2004; Oliveira-Filho *et al.* 2007). The history of our study area does not indicate drastic events in the community, great transformations being limited to the matrix and to the border region between the forest and matrix. In fact, the loss of forest coverage that previously occupied the matrix resulted in oscillations in temperature and air humidity, as well as in wind speed, mainly in regions near the fragment edge (Siqueira *et al.* 2004). In addition, due to interruptions in the vegetation continuum, some interactions can be lost or seriously altered. However, it is plausible that the low abundance of pioneer species is related to moderate disturbance conditions in the fragment, where the forest structure provides an environment less suitable for their germination and growth. The fact that climax species are more numerous and abundant than are pioneer species suggests that the former, whether shade-tolerant or light-demanding, have a greater influence on forest dynamics. Some studies in tropical forests have found the risk of death

to be higher among slow-growing trees than among fast-growing trees (Swaine *et al*. 1987). It is therefore also possible that climax species influence the mortality rate of the community and, consequently, the community dynamics.

Our results suggest that the tree community studied is in, or is approaching, a state of dynamic equilibrium and call attention to the possibility that the resilience of the community is low. The demographic changes observed tended to favor mortality, and the individual distribution by diameter class suggests that modifications in mortality and recruitment were associated with periodic fluctuations rather than being a result of post-disturbance recovery processes. The changes in community structure were reflected in the tree species composition, which featured a reduction in diversity. Ten low-density species disappeared, presaging a similar future for those that are currently at low density. Those species are not self-maintaining in the forest, and their populations might be sustained at their current levels by the continual arrival of immigrants from neighboring fragments. The small size of the fragment studied and the conditions in the surrounding matrix can make this system more vulnerable to fires and storms; that is, less resistant to stochastic events and human activities.

Acknowledgments

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