Community structure of vascular plants in treefall gaps and fire-disturbed habitats in the Atlantic rainforest, southern Bahia, Brazil

ADRIANA MARIA ZANFORLIN MARTINI[1,5], FLAVIO ANTONIO MAËS DOS SANTOS[2], PAULO INÁCIO PRADO[3] and JOMAR GOMES JARDIM[4]

ABSTRACT – (Community structure of vascular plants in treefall gaps and fire-disturbed habitats in the Atlantic rainforest, southern Bahia, Brazil). The effects of disturbances on plant community structure in tropical forests have been widely investigated. However, a majority of these studies examined only woody species, principally trees, whereas the effects of disturbances on the whole assemblage of vascular plants remain largely unexplored. At the present study, all vascular plants < 5m tall were surveyed in four habitats: natural treefall gaps, burned forest, and their adjacent understorey. The burned area differed from the other habitats in terms of species composition. However, species richness and plant density did not differ between burned area and the adjacent understorey, which is in accordance to the succession model that predict a rapid recovery of species richness, but with a different species composition in areas under moderate disturbance. The treefall gaps and the two areas of understorey did not differ among themselves in terms of the number of individuals, number of species, nor in species composition. The absence of differences between the vegetation in treefall gaps and in understorey areas seems to be in agreement with the current idea that the species present in treefall gaps are directly related to the vegetation composition before gap formation. Only minimal differences were observed between the analyses that considered only tree species and those that considered all growth habits. This suggests that the same processes acting on tree species (the best studied group of plants in tropical forests) are also acting on the whole assemblage of vascular plants in these communities.

Key words - atlantic forest, fire, growth habits, natural treefall gaps, species richness

RESUMO – (Estrutura da comunidade de plantas vasculares em clareiras naturais e em área perturbada por fogo em uma floresta pluvial tropical Atlântica no Sul da Bahia, Brasil). Os efeitos das perturbações sobre parâmetros da estrutura de comunidade de plantas em florestas tropicais têm sido freqüentemente analisados. Porém, a maioria dos estudos realizados até o momento tem considerado somente plantas lenhosas, principalmente árvores, e o efeito de perturbações sobre toda a comunidade de plantas vasculares ainda não havia sido avaliado. No presente estudo, todas as plantas vasculares menores que 5 metros de altura foram amostradas em clareiras naturais, em uma área de floresta queimada em um incêndio acidental e em áreas de sub-bosque adjacentes. A área queimada diferiu das outras áreas em relação à composição de espécies, porém a riqueza de espécies e a densidade de indivíduos não foi diferente entre a área queimada e as áreas de sub-bosque. Estes resultados estão de acordo com os modelos sucessionais que prevêem que em locais sujeitos a perturbações de intensidade moderada ocorre uma rápida recuperação da riqueza de espécies, porém com uma composição de espécies diferenciada. As clareiras naturais e as áreas de sub-bosque não diferiram quanto ao número de indivíduos e de espécies, nem em relação à composição de espécies. A ausência de diferenças entre a vegetação em clareiras e no sub-bosque sugere que as espécies encontradas em clareiras estão diretamente relacionadas às espécies presentes antes da formação das clareiras. Foram observadas apenas pequenas diferenças entre os resultados das análises que consideraram somente as espécies arbóreas e as análises considerando todos os hábitos de crescimento, sugerindo que os mesmos processos que atuam sobre as espécies arbóreas estão também atuando sobre toda a comunidade de plantas vasculares nestas florestas.

Palavras-chave - clareiras naturais, Floresta Atlântica, fogo, hábitos de crescimento, riqueza de espécies

1. Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Rodovia Ilhéus - Itabuna km 16, 45650-000 Ilhéus, BA, Brazil.
2. Universidade Estadual de Campinas, Departamento de Botânica, Caixa postal 6109, 13083-970 Campinas, SP, Brazil.
3. Universidade de São Paulo, Departamento de Ecologia Geral, Rua do Matão, Travessa 14, 321, 05508-900 São Paulo, SP, Brazil.
4. Universidade Estadual de Feira de Santana, Departamento de Ciências Biológicas, Programa de Pós-Graduação em Botânica, Avenida Universitária, s/n, 44031-460 Feira de Santana, BA, Brazil.
5. Corresponding author: amartini@uesc.br

Introduction

One of the central topics of tropical forest ecology during the last three decades has been the relationship between the astonishing plant diversity and natural disturbances, especially treefall gaps. Some hypotheses have been put forward to explain this relationship. According to the intermediate disturbance hypothesis (Connell 1978), natural treefall gaps impose a medium-level disturbance regime in these ecosystems in terms of extension, frequency, and intensity, that allows the

coexistence of pioneer as well as late-secondary sucessional species.

The gap partitioning hypothesis (Denslow 1980) proposes that determined groups of plants retain characteristics that allow them to efficiently colonize gaps of a certain size (or specific micro-habitats within those gaps). According to this hypothesis, tropical forest plant species have narrow regeneration niches (*sensu* Grubb 1977) that permit the co-existence of a large number of species. The principal evidence supporting the niche-based hypothesis is the existence of pioneer tree species that are rare in the forest understorey but abundant in large gaps (Brokaw & Busing 2000). These species would thus appear to have a narrower regeneration niche than most tropical tree species.

If natural treefall gaps had an important role in the maintenance of species diversity in tropical forest through niche differentiation, it would be expected that they would show a species composition different from the adjacent understorey, and/or a higher number of species. Treefall gaps could have a higher species richness as a function of an increased density of individuals (the density effect of Denslow 1995).

Contrary to the hypothesis put forward by Denslow (1980), Hubbell & Foster (1986) have suggested that the majority of tropical forest species have broad regeneration niches, and are able to become established under a variety of light environments. The regeneration success of a given species would therefore seem to be a result of chance, or of local historical factors.

A thirteen-year study of gaps in a 50 ha permanent plot at Barro Colorado, Panama, demonstrated no differences between the estimated species richness in treefall gaps and understorey forest areas, and revealed that the species composition of gaps is not predictable (Hubbell *et al*. 1999). Even pioneer species do not occur in predictable patterns in gaps of any given size or age, and they demonstrate low levels of establishment in gaps. These results suggest that the niche-based hypotheses cannot explain the species diversity observed in those gaps.

Recent reviews have pointed out the weak evidence supporting the niche-based hypotheses for tropical tree species in gaps, and stress the apparent importance of random events in determining species diversity (Brokaw & Busing 2000, Busing & Brokaw 2002). Nonetheless, according to Schnitzer & Carson (2000) there is a strong evidence that niche-based hypotheses do not apply to shade-tolerant tree species – the most studied group in tropical forest systems – but it may still be too early to discard them, as there have been very few studies

undertaken of the herbaceous-shrub vegetation or other growth habits. Most of these studies focused on a specific growth habit, such as lianas (Putz 1984, Schnitzer *et al.* 2000), shrubs (Denslow *et al.* 1990), or herbs (Goldblum 1997), but the effects of disturbances on the whole assemblage of vascular plants remain largely unexplored.

In general, the hypotheses cited above seek to understand the relationship between species diversity and disturbances under natural conditions. However, a comparison of the vegetation in habitats affected by both natural and anthropogenic disturbances may help to elucidate the processes that underlie the establishment of species, and the ways in which human actions can influence diversity and community structure. Few studies have directly compared forest recovery following anthropogenic and natural disturbances (Chazdon 2003).

Fires are normally exogenous and infrequent in tropical forest areas, so that the organisms there are presumably less resistant to their effects (Connell 1978, Kauffman 1991). Fire can completely alter the floristic composition and community structure of a tropical forest area through: i) initial elimination of the herbaceous-shrub layer and the advanced regeneration plants (Uhl *et al*. 1989); ii) the sudden flush of nutrients derived from burning of large quantities of organic material (Vinha *et al*. 1983, Uhl & Jordan 1984); and iii) the survival or re-sprouting of more resistant species (Uhl & Jordan 1984, Kauffman 1991).

The alterations in the plant community seem to be strongly related to burn intensity and land-use history (Uhl *et al.* 1988a, Cochrane & Schulze 1999). Several studies have examined the responses of the plant community to slash-and-burn, but only a few studies have been conducted in tropical forests burned by accidental fires, without previous vegetation cut (Woods 1989, Nykvist 1996, Ivanauskas *et al.* 2003). More information about changes in vegetation structure and species composition after this type of disturbance are greatly needed to understand this pathway of succession. The increasing fire susceptibility of tropical forests due climatic changes (Woods 1989, Cochrane & Schulze 1999, Nepstad *et al*. 2004) call the attention to these issues.

The present study investigated the influence of a natural disturbance (treefall gaps) and an anthropogenic disturbance (an accidental fire) on the community structure of small and medium-sized vascular plants of all growth habits in a tropical forest ecosystem. These disturbed habitats were compared with adjacent areas of intact understorey.

Revista Brasil. Bot., V.30, n.2, p.303-313, abr.-jun. 2007

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Specifically, the following questions were addressed: i) do disturbed habitats (treefall gaps and burned areas) differ in number of individuals and species composition from their adjacent understorey? ii) Is the species richness higher in treefall gaps than the adjacent understorey? iii) Is the opposite trend observed in the anthropogenically disturbed habitat?

Since most similar studies have focused only on tree species, the analyses of plant community structure were done for both the total set of vascular plants (including all growth habits) and only for tree species, in order to allow comparisons.

Material and methods

Study area – This study was undertaken in the Una Biological Reserve, located in the municipality of Una, Bahia, Brazil (15º10' S and 39º03' W) and situated within the "Mata Atlântica" (Atlantic Forest) domain, one of the ten most endangered biomes of the world (Mittermeier *et al.* 1999, Myers *et al*. 2000). Southern Bahia is among the regions of Atlantic Forest that have the highest levels of plant diversity and endemism (Thomas *et al.* 1998).

The Una Biological Reserve occupies approximately 7,022 ha, and 78% of its area is considered well conserved forest (Marques *et al.* 2002). The remaining areas were recently disturbed or are undergoing regeneration. The Reserve is composed predominately of lowland dense rain forest (floresta ombrófila densa de terras baixas - IBGE 1992).

The soils in the study area are predominately red-yellow latosols, variation Colônia (typic haplortox). They are nutrient poor, although exhibiting a good physical structure (Ibama/ MMA 1998).

The climate is characterized by the absence of a definite dry period and a total rainfall greater than 1,300 mm year^{-1} (type Af in the system of Köppen, Mori *et al.* 1983). Vegetation sampling – All natural gaps within an area of 3.5 hectares (Area 1) of an old-growth forest within the Una Biological Reserve were mapped. Gaps were defined as open areas in the canopy, representing a discontinuity in the vertical gradient of the forest. They are generally associated with fallen trees. Only gaps where the vegetation was up to 5 meters tall and/or where the trees had a maximum diameter of 8 cm at ground level were considered. In order to calculate the area of the gaps, their centre was determined visually and the distance between the two trees (diameter at ground level greater than 8 cm) at the furthest opposite edges were measured. The distance between the two trees in a perpendicular axis to the first one was then measured. The area was estimated using the formula for an ellipse as proposed by Runkle (1982). Within the 3.5 hectares sampled, 43 treefall gaps were found, ranging from 30.6 m^2 to 260.9 m^2. The mean gap size was 87.4 (± 54.7) and the median was

65 m^2. Eighty six percent of treefall gaps were smaller than 150 m^2.

Among the 43 gaps measured, six of the largest and up to 4 years old (determined by the presence of well-preserved bark and thin twigs on the terminal branches of the principal fallen tree) were chosen for this study. These six selected treefall gaps had areas between 65.4 to 260.9 m^2, and the linear distances among them varied from 25 to 300 m.

Adjacent to each gap and at a minimum distance from it equivalent to the maximum diameter of the gap, a sample plot of equal shape and size was established in the forest understorey. The minimum distance between understorey and gap plots edges was ca. 25 m, and the maximum was 50 m.

Six sample plots were established within an area of forest burned during an accidental fire occurred in February, 1995, *i.e.* 5 years before the study. The fire was of medium intensity, which allowed some canopy trees to survive, although the understorey vegetation was completely eliminated. This burned area was located approximately 1 km from Area 1 described above,

Additionally, six other sample plots were established in the understorey of an old-growth forest area approximately 200 m from the burned area.

In order to minimize the influence of plot size and the spatial configuration of the samples, the plots in the burned area and in the forest understorey near the burned area were laid out with the same spatial pattern and the same shape and size as the 6 gaps of Area 1.

The sampling habitats thus defined will be referred to as follows: Treefall Gaps (G), Understorey near Gaps (UG), Burned area (B), Understorey near Burned area (UB).

The sample plot was lozenge-shaped and defined by the two axes of the treefall gaps described above. Within each sample plot, six 1-m^2 sub-plots were randomly located (total of 36 in each habitat), and all vascular plants between 0.2 and 5 m tall were surveyed. Taxonomic knowledge of local flora by JGJ and the comprehensive plant collection at Herbarium CEPEC allowed to a nearly full-resolved separation of specimens in morphs, and the identification of most of them. These plants were classified in ten growth habits according to the definitions adopted by Amorim *et al.* (unpublished data), based on field observations in the region: trees, treelets, shrubs, sub-shrubs, herbaceous, woody vines, vines, hemi-epiphytes, scandent and epiphytes. The plants up to 0.2 m tall were only counted. Detailed descriptions of taxonomic identification, a complete checklist and the proportion of species and individuals in each growth habit are presented in Martini (2002).
Data analysis – The few plants > 0.2 m that could not be identified, nor even separated into morphospecies (*n* = 27), were excluded from analyses of species richness and composition. Hence, the number of individuals in species richness and vegetation composition analyses does not correspond exactly to the total number of individuals used in the density analysis computations.

A single-factor analysis of variance was used to test differences in the number of individuals among habitats. Residuals of this analysis were checked for the assumptions of normality and equality of variances .

For each habitat, mean species accumulation curves were calculated (Gotelli & Colwell 2001) employing the Independent Sampling algorithm in the EcoSim 6.0 program (Gotelli & Entsminger 2001). The mean richness estimated for an equal number of individuals was compared using their 95% confidence intervals.

A Detrended Correspondence Analysis (DCA) of species abundance was performed for each plot in order to analyse the similarity of species composition among plots in similar habitats. The abundances of species rarer than Fmax/5 (where Fmax is the frequency of the commonest species) were downweighted in proportion to their frequency. Species commoner than Fmax/5 were not downweighted (McCune & Mefford 1999).

A Multiple Response Permutation Procedure (MRPP) analysis was performed, using the Sørensen distance between plots, in order to determine if species composition differed among the habitats examined (McCune & Mefford 1999). This analysis examines if the similarity in species composition among plots within the same habitat is greater than would be expected if the plots were randomly assigned to one of the habitats. The degree of similarity is expressed by the chance-corrected within-group agreement. This index (called "A") varies from zero to one, and would have a maximum value (of 1) if all plots within an habitat had exactly the same species composition.

The Indicator Species Analysis (ISA) was used to verify if there were species that served as indicators for each of the habitats examined. This statistical method employs a combination of the Relative Frequency and the Relative Abundance of species in the plots in each habitat in order to calculate an Indicator Value. The Monte Carlo randomization estimates the probability that the Indicator Value of a given species would differ from the expected value if plots were randomly distributed among habitats.

All analyses (DCA, MRPP, and ISA) were performed using the software program PC-ORD - version 4.1 (McCune & Mefford 1999).

As the majority of studies on vegetation in treefall gaps considers only young individuals of tree species (Schnitzer & Carson 2000), statistical analyses were also performed considering only trees and treelets (*sensu* Amorim *et al.*, unpublished data), thus allowing for better comparisons with previously published literature.

Results

All growth habits – A total of 3,001 individuals were surveyed, of which 55.7% belonged to the smallest height class (< 0.2 m; table 1). No significant differences in mean number of individuals per plot of any height class were observed among the four different habitats (table 1). The largest variation among plots was seen in the understorey near the burned area (UB), principally among the smallest height classes. This variation was associated with the large number of individuals (213) found in one of the plots (UB5), a value significantly above the mean of 125 individuals plot^{-1} for all habitats combined (table 1).

The estimated number of species (S_{est}) for a sample size of 200 individuals was significantly lower in the burned area (B) when compared to gaps (figure 1). Understorey plots (UG and UB) did not differ among themselves, nor in relation to the other habitats (table 2).

The first axis of the DCA showed a clear separation between habitats. Burned plots (B) and a group formed by plots at the treefall gaps (G) and the understorey (UG) were ordered at opposite ends of the 1st axis, while the understorey plots near the burned area (UB) were at intermediate position (figure 2). Second axis expressed idiosyncrasies of some plots. At this axis, one plot of the understorey near the burned area (UB4), and the gap plot G1 were separated from the other plots of the same habitat. This separation was due in large part to the absence of *Merostachys* sp. (Poaceae) and *Psychotria purpurascens* Müll. Arg. (Rubiaceae), and

Table 1. Mean number of individuals (SD in parentheses) of all vascular plants within different height classes of the four habitats analysed (G = Treefall gaps; UG = Understorey near treefall gaps; B = Burned area; UB = Understorey near burned area).

Height (m)	G (n = 6)	UG (n = 6)	B (n = 6)	UB (n = 6)	TOTAL (n = 24)	P* (ANOVA)
< 0.20	77.5 (16.6)	76.7 (12.6)	54.2 (22.9)	70.2 (24.1)	69.7 (20.6)	0.175
0.2 to 1	47.0 (15.6)	41.0 (15.6)	29.7 (9.4)	36.2 (25.5)	38.5 (17.6)	0.393
1 to 5	13.5 (4.3)	16.8 (6.1)	19.7 (4.1)	17.8 (5.2)	17.0 (5.2)	0.218
0.2 to 5	60.5 (13.4)	57.8 (21.4)	49.3 (12.1)	54.0 (27.1)	55.4 (18.7)	0.774
All	138.0 (25.0)	134.5 (22.6)	103.5 (24.4)	124.2 (45.3)	125.0 (31.8)	0.238

* Probability values for the analysis of variance of the mean number of individuals among the four habitats, for each height class.

to the presence of a larger number of individuals of *Philodendron surinamense* (Miq.) Engl. (Araceae). These two axes accounted for 59.6% of the total variance observed.

The comparison of the species composition among the four habitats using the MRPP demonstrated significant differences when all individuals > 0.2 m were considered (A = 0.084; *P* < 0.0001). This analysis mode can be recalculated while excluding any of the habitats, and thus allows one to determine which habitat(s) is(are) in fact different from others (McCune & Mefford 1999). In paired comparisons, burned area differed significantly from all other habitats (G: A = 0.1044; *P* < 0.001, UG: A = 0.1089; *P* < 0.001, UB: A = 0.0893; *P* < 0.001). When the other habitats (G, UG, and UB) were compared as pairs, no significant differences were observed in their species composition.

The burned area contained the highest number of indicator species (10) according to the Indicator Species Analysis (ISA). The principal indicator species were *Pteridium aquilinum* (L.) Kuhn, a sub-shrub fern, *Scleria secans* (L.) Urban, a scandent Cyperaceae, and *Miconia mirabilis* (Aubl.) L.O. Williams, an arboreal Melastomataceae frequently associated with human-disturbed environments (table 3). Treefall gaps showed three indicator species: two arboreal (*Pouroma mollis* Trécul and *Protium heptaphyllum* (Aubl.) Marchand), and one hemi-epiphyte Cyclanthaceae (*Evodianthus funifer* (Poit.) Lindm). In the understorey adjacent to the treefall gaps, two hemi-epiphyte species of Araceae (*Philodendron surinamense* and *Rhodospatha latifolia* Poepp. & Endl.) had high values as indicator species. In the understorey near the burned area, only the sub-shrub palm *Geonoma pauciflora* Mart. was considered an indicator species.

A total of 409 individuals of tree species (including treelets) between 0.2 and 5 meters tall were sampled. These represented approximately one third of all plants sampled in this study within this height class.

The burned area had a significantly lower mean number of trees than treefall gaps (*F* = 3.489; *d.f.* = 3, 20; *P* = 0.0035). However, the other habitats (UG and UB) did not differ from either the burned area or treefall gaps (table 4).

The estimated species richness for samples of 60 individuals was smaller in the burned area in relation to treefall gaps and to the understorey near the gaps, but did not differ from the understorey near the burned area (table 4). The estimated tree species richness did not differ among treefall gaps and the two understorey areas.

Tree species composition differed among the four habitats (MRPP; A = 0.0712; *P* < 0.0001). However, when the burned area was excluded, no significant differences were noted (A = 0.0079; *P* = 0.2275) among the three remaining habitats (G, UG e UB).

The tree species *Miconia mirabilis* (*P* = 0.001), *Cecropia pachystachya* Trécul (*P* = 0.0035), and *Henriettea succosa* (Aubl.) DC. (*P* = 0.0365) were the best indicators for the burned area, while *Pouroma mollis* and *Protium heptaphyllum* were indicators for treefall gaps. The understorey areas had no tree species with significant indicator species indices.
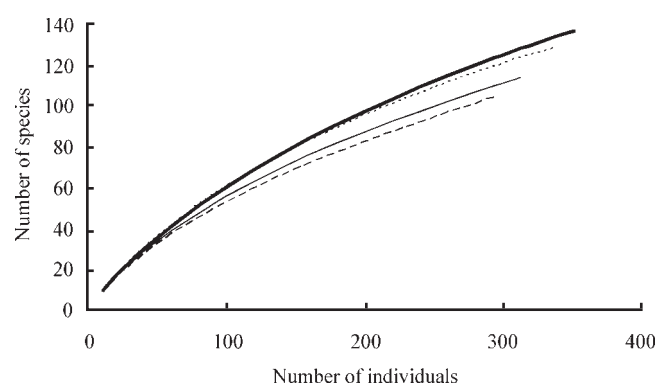

Figure 1. Mean species accumulation curve (2.000 randomisations) for each habitat analysed. Legend: Solid thick line = Treefall gaps (G); Dotted line = Understorey near treefall gaps (UG); Dashed line = Burned area (B); Solid fine line = Understorey near burned area (UB).

Table 2. Observed and estimated species richness of all vascular plants in the four habitats analysed (N = total number of individuals in each habitat (identification confirmed); S_{OBS} = Observed species richness; S_{EST} = estimated species richness; LOWCI/UPPCI = Lower and upper confidence intervals for estimated species richness. G = Treefall gaps; UG = Understorey near treefall gaps; B = Burned area; UB = Understorey near burned area).

HABITAT	N	S_{OBS}	S_{EST}*	LOWCI	UPPCI
G	354	137	96.9	89.29	104.59
UG	340	129	95.2	87.74	102.75
B	294	104	82.3	75.57	88.98
UB	314	114	87.0	80.17	93.81

* Mean estimated species richness for 200 individuals.

Discussion

This is the first study that sampled small and medium-sized plants of all growth habits in tropical forest environments subjected to different degrees of disturbance. Most previous studies have focused on specific growth habits in disturbed areas, usually tree
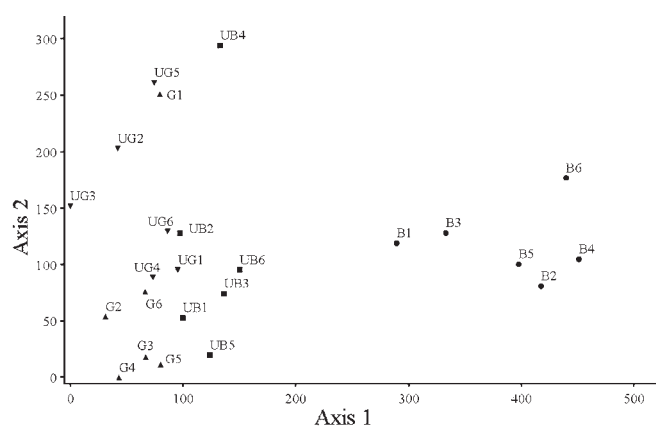

Figure 2. Detrended correspondence analysis (DCA) ordination of plots, based on species abundance. (G = Treefall gaps; UG = Understorey near gaps; B = Burned area; UB = Understorey near burned area).

Table 3. Indicator species of the four habitats, according to the Indicator Species Analysis (ISA). Values in parentheses indicate the probability (*P*), which represents the proportion of randomisations (Monte Carlo) that had the Indication Index greater than or equal to the observed value (refer to the Methods section). Species are ordered according to their "*P*" values (G = Treefall gaps; UG = Understorey near treefall gaps; B = Burned area; UB = Understorey near burned area).

HABITAT	INDICATOR SPECIES
G	*Pourouma mollis* (0.008)
	Protium heptaphyllum (0.028)
	Evodianthus funifer (0.038)
UG	*Philodendron surinamense* (0.009)
	Rhodospatha latifolia (0.031)
B	*Pteridium aquilinum* (0.001)
	Scleria secans (0.001)
	Miconia mirabilis (0.002)
	Passiflora haematostigma (0.002)
	Becquerelia clarkei (0.003)
	Cecropia pachystachya (0.005)
	Cyrtocimura scorpioides (0.037)
	Miconia sp2 (0.037)
	Henriettea succosa (0.038)
	Vismia guianensis (0.043)
UB	*Geonoma pauciflora* (0.037)

or shrub species (Brokaw 1985, Uhl *et al.* 1988b, Tabarelli & Mantovani 1998, Nicotra *et al.* 1999, Carvalho *et al.* 2000, Denslow & Guzman 2000, Dickinson *et al.* 2000). Other studies have examined all growth habits, but only in non-disturbed environments (Gentry & Dodson 1987, Galeano *et al.* 1998). A great effort was done to have the plant *taxa* as fully-resolved as possible. Only 2% of the plant specimens (> 0.2 m tall) could not be attributed to a morph, and 64% of the morphs were identified to species level. These values indicate a high level of identification for tropical plant communities, especially when including all growth habits.

For the sake of comparison of all vascular plants among the four habitats we were not able to have a large number of plots in each habitat, and this should be considered in the following discussion. Large differences among habitats could be properly detected with this sampling effort, but if small differences eventually do exist, they would require a larger sample size to become apparent.

Among the habitats analysed here, the burned area had the clearest differentiation from the others in terms of species composition. Somewhat surprisingly however, it did not demonstrate further differences in other aspects of community structure.

There was no difference in the mean number of individuals observed in the burned area and the other environments, which goes against the idea that a larger number of individuals could establish after fire disturbance due to the greater availability of nutrients and the liberation from above- and below soil level competition (Uhl & Jordan 1984, Sundarapandian & Swamy 1996). A majority of the studies on post-fire regeneration have evaluated areas that had previously been cut (slash and burn agriculture), a situation that produces a cleaner post-burning environment. The present study, however, evaluated an area in which numerous trees had survived fire disturbance and had re-sprouted (thus continuing to utilize soil nutrients). Shading by these trees may have inhibited to some extent plants that require high light levels for optimal growth.

Additionally, the community in the present study was analysed 5 years after the fire event, time enough for plants capable of rapid growth to have grown significantly and to asymmetrically (Freckleton & Watkinson 2001) utilize the mineral resources liberated by the fire, to shade the smaller plants and restrict the establishment of smaller class sizes. This seems to be the case for *Scleria secans* (Cyperaceae), *Miconia mirabilis* (Melastomataceae), and *Pteridium aquilinum*

Table 4. Density of individuals, mean number of individuals per plot (SD in parentheses), observed species richness (S_{OBS}), and estimated species richness (S_{EST}) for tree species. Lower (LOWCI) and upper (UPPCI) confidence intervals are indicated (G = Treefall gaps; UG = Understorey near treefall gaps; B = Burned area; UB = Understorey near burned area). Note: different superscript letters represent significant differences ($P < 0.05$) within the same column.

Habitat	Total number of individuals	Mean number of individuals[#]	S_{OBS}	S_{EST}*	LOWCI	UPPCI
G	130	21.7[a] (± 5.68)	59	36.3	31.54	41.13
UG	123	20.5[ab] (± 10.62)	57	36.2	31.39	41.06
B	72	12.0[b] (± 3.69)	32	28.5	25.74	31.23
UB	84	14.0[ab] (± 4.69)	41	33.6	29.97	37.22

[#] ANOVA ($P < 0.05$).
* Mean estimated species richness for 60 individuals.

(Dennstaeditiaceae), which dominated the taller height classes in the burned area.

In the burned area, the sample-corrected mean number of species of all growth habits was equivalent to that encountered in the two understorey areas. Some sucessional models attempt to explain this lack of significant differences (Connell 1978, Roberts & Gilliam 1995, Guariguata & Ostertag 2001). These models predict a rapid recovery of species richness in areas that have suffered only moderate disturbance, although with a different species composition, dominated at first by fast-growing, short-lifespan species. Also, the lower number of species in the burned area compared to the treefall gaps could be related to the strong dominance of these species in the burned area. The situation observed in the burned area is quite similar to that prediction, principally in light of the sharp separation of the burned area plots in both the DCA and the MRPP analyses.

Considering only tree species, there was no difference in the estimated number of species richness between the burned area and the adjacent understorey. Hence, species richness of trees have been re-established very early during succession. The rapid recovery in richness and some other community parameters were also observed in slash-and-burned plots in tropical forests, where a rapid stocking of pioneer and primary forest trees follows a short phase of dominant grasses and forbs (Uhl & Jordan 1984, Castellani & Stubblebine 1993).

Although the number of species did not differ, the tree species composition differed significantly between the burned area and the adjacent understorey, mainly because pioneer tree species such as *Miconia mirabilis* (Melastomataceae), *Cecropia pachystachya* (Cecropiaceae) and *Henriettea succosa*

(Melastomataceae), have occurred exclusively in the burned area. Otherwise, some species common in the forest understorey, such as *Euterpe edulis* Mart. (Arecaceae), *Licania hoehnei* Pilg. (Chrysobalanaceae) and *Ecclinusa ramiflora* Mart. (Sapotaceae), were recorded in the burned area, showing that species that built up the mature forest were established near the beginning of the succession (Uhl & Jordan 1984). In fact, the species composition in the burned area was different from the other three habitats, while the treefall gaps did not differ from the understorey areas. These results suggest that the fire is a factor of higher importance than light in determining changes in species composition after disturbances. Additionally, the community that has been established in the burned area will determine the composition and abundance of seeds in the seed rain and thus will affect the assemblage of the plant community and of the seed bank in the future (Young *et al*. 1987, Walker & Neris 1993).

The natural treefall gaps and the two areas of understorey were consistently similar in regards to their species composition, species richness, and density of individuals in the different size classes. The remarkable similarity observed between the two understorey areas (adjacent to the gaps or adjacent to the burned area) in all variables analysed in the present study suggests that the forest structure and composition was the same before the disturbances in the whole studied area.

The absence of differences in plant density among the treefall gaps and the two understorey areas goes against the idea that natural disturbances (such as those formed by treefalls) provides a local increase in plant density that is stimulated by the liberation of resources such as light and by diminished competition from the fallen tree itself (Brokaw 1985, Denslow 1995). An initial increase in the number of individuals that become

established in treefall gaps (Brokaw 1985, Hubbell *et al*. 1999, Goldblum 1997) would cause an increase in species richness, and this "density effect" would help maintain species diversity (Denslow 1995, Brokaw & Busing 2000). However, a number of surveys that sampled woody plants or trees did not record different densities of individuals in treefall gaps and control understorey plots (Arévalo & Fernández-Palácio 1998, Tabarelli & Mantovani 1998, Carvalho *et al*. 2000, Dickinson *et al*. 2000). The present study generated similar results, in terms of both the whole plant community, including all growth habits and tree species alone.

The lack of any difference in species richness between treefall gaps and the understorey was associated with a similar lack of difference in species composition. There was no large number of species occurring specifically in treefall gaps, as might have been expected from the hypothesis that treefall gaps play an essential role in promoting and maintaining species diversity (Denslow 1980, 1986, 1987). Only three species occurred preferentially in treefall gaps in this survey (*Evodianthus funifer*, *Pouroma mollis*, and *Protium heptaphyllum*). Numerous studies have demonstrated the lack of significant differences between plant communities in treefall gaps and in the nearby understorey vegetation (Barton 1984, Brokaw & Scheiner 1989, Arévalo & Fernández-Palácio 1998, Tabarelli & Mantovani 1998, Carvalho *et al*. 2000, Dickinson *et al*. 2000).

In general, the treefall gaps in the present study did not show larger numbers of individuals or species than the adjacent understorey, nor a distinct plant community, as would be expected by the niche-based hypotheses. These results seems to be in agreement with the current hypotheses that species composition in treefall gaps is strongly determined by the composition of the understorey before gap formation (Uhl *et al*. 1988b) and not by niche differences (Hubbell *et al*. 1999, Brokaw & Busing 2000).

Additionally, the absence of differences in species composition between treefall gaps and the understorey could be attributed to the relatively small size of the gaps sampled in this study. Some authors had suggested that large gaps - greater than 400 m^2 (Denslow 1987) or 1.000 m^2 (Hartshorn, 1978) - are required to the establishment of pioneer species or large gap specialists (Denslow 1980). However, in previous studies carried on sites that are not usually exposed to large disturbances such as hurricanes or cyclones, the largest gaps sampled were less than 400 m^2 (Abe *et al*. 1995, Midgley *et al*.

1995, Arévalo & Fernandez-Palácio 1998, Carvalho *et al*. 2000) and gaps with more than 120 or 150 m^2 were considered large (Yavitt *et al*. 1995, Dickinson *et al*. 2000, Tabarelli & Mantovani 2000). In the present study, all gaps were less than 400 m^2, but they represent the largest gaps in this forest and all but one were greater than 120 m^2. In summary, the very high richness of tree species observed in the studied forest (Thomas *et al*. unpublished data, Mori *et al*. 1983) could not be attributed to niche partitioning among gap specialists and shade-tolerant species.

Under such disturbance regime dominated by small gaps, it could be expected an increase in the growth rate of the plants established in the area before the gap formation, instead of changes in the species composition (Putz *et al*. 1983). The analysis of growth and survival rates of the established plants in treefall gaps and understorey areas might help to elucidate the role of this mode of disturbance in the forest dynamics.

Schnitzer & Carson (2000) have called attention to the fact that the ideas of Brokaw & Busing (2000) were essentially based on analyses of tree species, and that it would be necessary to undertake studies on plants with other growth habits. In the lower stratum analysed, for each arboreal individual surveyed, 2.7 individuals of other growth habits were also present. Likewise, for every tree species, 2 non-tree species were observed (Martini 2002). These values highlight the importance of sampling non-tree individuals because they could be potential competitors of the arboreal individuals in the lower stratum. In the present study, the same pattern was observed when all growth habits were considered together, and with tree species alone. Hence, the observed patterns of species richness for either tree species or all vascular plants in this forest could not be attributed to gap-niche partitioning.

Even though the niche-based hypotheses did not seem to be supported by our results, natural disturbances such as those seen in treefall gaps may still be important in maintaining species diversity by benefiting rare and/or competitively inferior species, as suggested by the hypotheses of compensatory mortality (Connell *et al*. 1984, Wright 2002) and recruitment limitation (Tilman & Pacala 1993).

The relations described here were observed in a forest formation located in an area with poor soils, high rainfall, and no marked dry period. Coomes & Grubb (2000) have suggested that the dominant species in this type of environment may not depend on natural treefall gaps in order to become established. As such, it would

be interesting to conduct similar studies (including species of all growth habits) in areas with a strong seasonal component, in order to verify if the same processes are involved.

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