

## Relief influence on tree species richness in secondary forest fragments of Atlantic Forest, SE, Brazil

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**RESUMO** – (Influência do relevo na riqueza de espécies arbóreas em fragmentos de floresta secundária de Mata Atlântica, SE, Brasil). O objetivo deste trabalho foi explorar a relação entre a riqueza de espécies arbóreas com as características morfológicas do relevo no Planalto de Ibiúna (SE, Brasil). Foram amostrados 61 blocos de 0,30 ha, sistematicamente estabelecidos em 20 fragmentos de floresta secundária (2-274 ha) e em três áreas de uma floresta secundária contínua, a Reserva do Morro Grande (9.400 ha). Em cada bloco, 100 árvores com diâmetro à altura do peito > 5 cm foram amostradas pelo método do quadrante centrado, e as riquezas total e por grupo de dispersão e sucessão foram obtidas. O relevo foi caracterizado pela média e variância da declividade, altitude, orientação e posição na vertente. Não houve relação significativa entre a heterogeneidade do relevo e a riqueza de espécies arbóreas. Os parâmetros do relevo afetaram pouco a riqueza da vegetação, mas a altitude foi particularmente importante, especialmente na floresta contínua. Apesar da pouca extensão na variação de altitude (150 m), a riqueza aumentou com este fator. As áreas mais altas também foram aquelas com as maiores coberturas florestais e os mais baixos graus de perturbação, o que deve contribuir para a maior riqueza dessas áreas. Nossos resultados indicam uma influência indireta do relevo, pelo fato das áreas mais altas serem também as menos desmatadas, e não uma influência direta de fatores abióticos relacionados ao gradiente de altitude.

**Palavras-chave:** relevo, riqueza e composição de espécies arbóreas, Mata Atlântica, uso da terra

**ABSTRACT** – (Relief influence on tree species richness in secondary forest fragments of Atlantic Forest, SE, Brazil). The aim of this work was to explore the relationship between tree species richness and morphological characteristics of relief at the Ibiúna Plateau (SE Brazil). We sampled 61 plots of 0.30 ha, systematically established in 20 fragments of secondary forest (2-274 ha) and in three areas within a continuous secondary forest site, Morro Grande Reserve (9,400 ha). At each plot, 100 trees with diameter at breast height > 5 cm were sampled by the point centered quarter method, and total richness and richness per dispersal and succession class were obtained. The relief was characterized by the mean and variance of slope, elevation, aspect and slope location. There was no significant relationship between relief heterogeneity and tree species richness. Relief parameters generally did not affect tree richness, but elevation was particularly important especially in the continuous forest. Despite the limited range of altitudinal variation (150 m), species richness increases with elevation. The highest areas were also those with the largest forest cover and the lowest disturbance degree, which should contribute to the greater richness of those sites. Our results suggest an indirect influence of relief, due to the fact that deforestation is less intense in higher regions, rather than a direct influence of abiotic factors related to the altitudinal gradient.

**Key words:** relief, tree species richness and composition, Atlantic Forest, land use

### Introduction

Among the factors that potentially influence tree species richness, parameters related to relief and its heterogeneity are often important. Aspect controls the exposure to sunlight and the moisture intercepted by the vegetation. Slopes with higher irradiation, i.e. north and west in the Southern Hemisphere, have elevated

temperatures and rates of evapotranspiration with a consequent reduction in soil moisture content and in humidity (Spurr & Barnes 1973), besides changes in chemical characteristics of the soil and in vegetation composition (Simonetti personal communication). Slope may also accelerate or attenuate irradiation effects on the vegetation, by influencing the loss of soil nutrients by erosion (Furley 1976). Some studies have indicated

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that the physical and chemical characteristics of the soil, which vary as a function of the relief, showed a direct relationship with the vegetation (Oliveira Filho *et al.* 1994, 1998; Chen *et al.* 1997; Carvalho *et al.* 2000; Bertani *et al.* 2001; Lyon & Sagers 2003). Resende *et al.* (1988) described the relief and soil texture as important factors controlling drainage, water availability, moisture retention, permeability and amount of nutrients absorbed by the plants or lost through leaching. In altitudinal gradients, climatic factors are important, mainly due to temperature variations (Kapelle *et al.* 1995; Pendry & Proctor 1996). In tropical regions there is strong evidence of relationships between relief features and tree species richness (Ashton 1964; Austin *et al.* 1973; Riezebos *et al.* 1982; Riezebos 1983; Lieberman *et al.* 1985; Basnet 1992; Clark *et al.* 1995; Newbery *et al.* 1996; Clark *et al.* 1998).

Besides morphological characteristics, relief heterogeneity may influence vegetation diversity, richness and composition (Ayyad & Dix 1964; Killingbeck & Wali 1978; Swanson 1988; Nichols *et al.* 1998; Stephenson & Mills 1999) in continuous (Rosenzweig 1995), as well as in fragmented habitats (Kohn & Walsh 1994). For example, along the Potomac River (USA), relatively homogeneous banks have fewer niches in comparison with heterogeneous ones, consequently having low species richness (Everson & Boucher 1998). In Rhode Island, also in USA, areas that present diverse geomorphological characteristics support richer and more varied plant communities than areas with limited geomorphological variation (Burnett *et al.* 1998).

In the Atlantic forest region, previous studies have shown that the high tree richness observed in semideciduous montane forests can be partially related to environmental heterogeneity, particularly to the heterogeneity of soils and topography (Espírito-Santo *et al.* 2002; Souza *et al.* 2003; Machado *et al.* 2004). Similar results were also observed in altitudinal forest in SE Brazil (Dalanesi *et al.* 2004). According Budke *et al.* (2007) and Oliveira Filho *et al.* (2001), the local influence of soils on the vegetation is related to relief and hydrological dynamics, since soil properties are a direct consequence of these factors.

In order to better understand the relationship between the relief features and richness of Atlantic Montane Rainforest tree communities, we sampled fragments of secondary forests and continuous forest sites at Ibiúna Plateau (SE, Brazil) to test two null hypotheses: i) tree species richness does not depend

on morphological characteristics of relief; ii) there is no relationship between relief heterogeneity and tree species richness.

Hasui (1975) considers as the most important tectonic element in the region the group of subvertical faults (60 to 90°), the most significant being those at Taxaquara, Jundiuvira and Caucaia. In the light of current theoretical knowledge, these faults are actually ductile shear zones (Ramsay & Huber 1983) which are common in southeastern Brazil. These huge structures are hundreds of kilometers long and their width can reach hundreds of meters.

The predominant crystalline basement in the Ibiúna Plateau is composed of rocks of a high metamorphic grade, as the migmatites, and magmatic rocks, as granite. According to the American Soil Taxonomy, the main soils in the region are: Alfisols, Ultisols, Oxisols and Inceptisols (Ross & Moroz 1977). The occurrence of sesquioxide iron in the study region gives the soil a reddish coloration characteristic of highly drained subtropical soils.

The climate of Ibiúna was characterized as mild hot and humid, *Cfa* type (Köppen, 1948; CIIAGRO/IAC 2003). Maximum and minimum average monthly temperatures are 27 °C and 11 °C, respectively. Average temperature in the hottest month is above 22 °C and average precipitation in the driest month varies from 30 to 60 mm. Annual precipitation is about 1,300-1,400 mm, with seasonal variations, April-August being the driest months with the lowest average temperatures. The frequent occurrence of winds and mist make the climate relatively cold.

The original forest in the region has been classified as a Lower Montane Rainforest (Oliveira Filho & Fontes 2000) and can be considered a transition between coastal rain forest and mesophyllous semi-deciduous forest of inland São Paulo state (Catharino *et al.* 2006). About 32% of the investigated fragmented landscape is covered by natural forests of different successional stages (early-, mid- and old-growth forests, *ca.* 2,795 ha). There is a predominance of the intermediate stage, with 60-80 year-old forests, which encompass 18% of the landscape. Canopy height is usually > 10 m, with emergent trees up to 25-30 m, and the most abundant tree species are *Guapira opposita*, *Clethra scabra*, *Casearia sylvestris*, *Myrcia multiflora*, *Matayba elaeagnoides*, *Rudgea jasminoides*, *Rapanea umbellata* and *Croton floribundus* (Catharino *et al.* 2006; Bernacci *et al.* 2006).

Historical deforestation within the studied region was strongly linked to urban development in São Paulo,

which included forest cutting for charcoal and power production, especially during World War II, and conversion of forests for agricultural production. The Ibiúna Plateau is part of the green belt of the city of São Paulo, and the main agricultural activities in the region are potato and tomato crops, fowl breeding and several other crops (fruits and vegetables). With the reduction in coal supply after World War II, an intense process of forest regeneration started, resulting in many of the actual fragments of the study region (Teixeira personal communication). Adjacent to the fragmented landscape is the Morro Grande Forest Reserve, with about 9,400 ha of forest at different successional stages. This forest was partly clear-cut in the past and has regenerated since the early 1920s, when two dams were built. As this forest is part of a Reserve, human disturbances are more homogeneous and controlled than those of the forest fragments.

## Material and methods

**Study site** – The study site is located at the Ibiúna Plateau (Ponçano *et al.* 1981), in the municipalities of Cotia and Ibiúna, state of São Paulo, SE Brazil (23°35'S, 23°50'S and 46°45'W, 47°15'W). A map of the study area is presented in Durigan *et al.* (2008). The Ibiúna Plateau is part of the Atlantic Plateau, a highland region mainly composed of Pre-Cambrian crystalline rocks cut by Tertiary-Mesozoic basic intrusive rocks, and by the covers of the sedimentary basins of São Paulo and Taubaté (Almeida 1964). In the same region, Ponçano *et al.* (1981) identified the following relief types: mountain plateau with steep hillslopes, mountain with moderate to gentle hillslopes, and alluvial plains.

**Sample sites** – The morphological data on relief and tree species richness were collected in 61 150×20 m plots (*i.e.* 0.30 ha) established in 20 forest fragments varying in size from 2 to 175 ha, as well as in three sites within the Morro Grande Forest Reserve, with a predominant intermediate stage of succession, at least 2 km apart from each other (Tab. 1). These plots were systematically distributed in each studied site, independently of the relief, 200 m apart from each other (Fig. 1). The number of plots per site was proportional to patch size (Tab. 1). Distances between sampled fragments range between 491-3217 m (mean: 1398 m), and were similar to the ones observed at Morro Grande (Durigan *et al.* 2008).

**Tree richness** – In each plot, 100 trees with diameter

at breast height > 5 cm were sampled by the point centered quarter method (Cottam e Curtis 1956). The 25 vegetation sampling points were arranged at 10-meter intervals in two parallel rows of 13 and 12 points, distant 10 meters from each other (Fig. 1).

The observed richness per plot was then considered as dependent variables. Besides the overall richness, we considered also the richness per dispersal category (anemochorous, barochorous and zoochorous) and succession class (pioneer, early secondary and late secondary trees, and typical understory species labeled “ombrophilous”). This classification was based on literature information (Lorenzi 1998 and volumes of Flora Ilustrada Catarinensis, published by P.R. Reitz), as presented in Catharino *et al.* (2006) and Bernacci *et al.* (2006).

**Relief morphological data** – In order to test the first hypothesis, we measured the following morphological parameters of relief in each plot: i) Average aspect in

Table 1. Main characteristics of the sites studied and sampling effort (number of plots) used for vegetation and relief analyses (Ibiúna Plateau, SE, Brazil).

Sites	Area (ha)	Number of sampling plots	Number of plots at an intermediate successional stage
Morro Grande A	9400.61 *	4	0
Morro Grande B	9400.61 *	4	0
Morro Grande C	9400.61 *	4	0
Zezinho	274.33	4	4
Pedroso	175.1	4	3
Takimoto	99.39	4	4
Mioko	52.17	4	4
Pedro	53.07	4	4
Reizinho	18.33	3	0
Beto	14.08	3	2
Godoy	12.92	2	2
Dito André	18.78	3	3
Nelson	31.22	3	1
Lila	28.88	3	2
Agostinho	47.87	3	2
Lacerda	14	2	2
Carmo Messias	5.48	1	1
Luiza	3.63	1	0
Dito	4.98	1	0
Maria	3.81	1	1
Manoel	4.56	1	1
Japonês	4.57	1	0
Tereza	1.96	1	0
Total		61	36

\* Connected with a large forest area (> 700.000 ha) situated in the Paranapiacaba Mountain Range.

relation to geographic north, obtained for each vegetation point with a geological compass (Brunton). The mean value was obtained using circular statistics (Batschelet 1981; Zar 1996); ii) Average slope (in degrees) obtained from 100 measures utilizing a Brunton compass; iii) Average elevation (meters in relation to sea level), obtained by positioning the sample plots on the topographical map (scale 1:10,000) produced by the São Paulo state government (1979). Elevation values were defined by the average of three measures along each plot; iv) Slope location, classified as lowland, slope or top, or as a combination of these positions.

To the test the second hypothesis, the following parameters were considered: i) Variance in aspect, obtained by circular statistics from the 25 measures of aspect in each plot; ii) Variance in slope, obtained from the 100 slope measures in each plot; iii) Amplitude of elevation, consisting of the difference between the higher and the lower points of the sample plots; iv) Heterogeneity of positions in the slope, measured by the frequency of positions on the slope, ranging from one (plots having only top, slope or lowland) to three (plots including top, lowland and slope areas).

This experimental design was not planned to control possible effects of soil characteristics. At the detailed scale considered here (0.30 ha), there is a

strong correlation between soils and relief as the result of the physical and chemical interactions between morphogenesis (relief formation and evolution) and pedogenesis (soil formation and evolution). Considering the concept of toposequence (or catena) defined by Milne (1935, in Jenny 1980), soil properties vary continuously as the average gradient of the hill slope increases or decreases though the soil properties remain unaltered along the same contour line. According to Duchaufour (1991), pedogenesis on the hill top influences the other parts of the hill. Therefore, there is a strong genetic relationship among the different types of soil, which occur on a steep hill. We can then consider that the effects of relief and soils cannot be distinguished in the present study.

Data Analysis – The relationship between number of species and relief was always tested per plot, *i.e.* considering 100 individuals in a constant area of 0.30 ha, irrespective of the total area of the fragments. In the case of the first null hypothesis, tests were conducted to explore the relationship between tree richness and the average values of the four morphological parameters (aspect, slope, elevation and location). As the same hypothesis was tested with four variables, we opted to utilize a significance level of  $p < 0.0125$  (Bonferroni's adjustment). We did not use a unique multiple regression due to the impossibility of

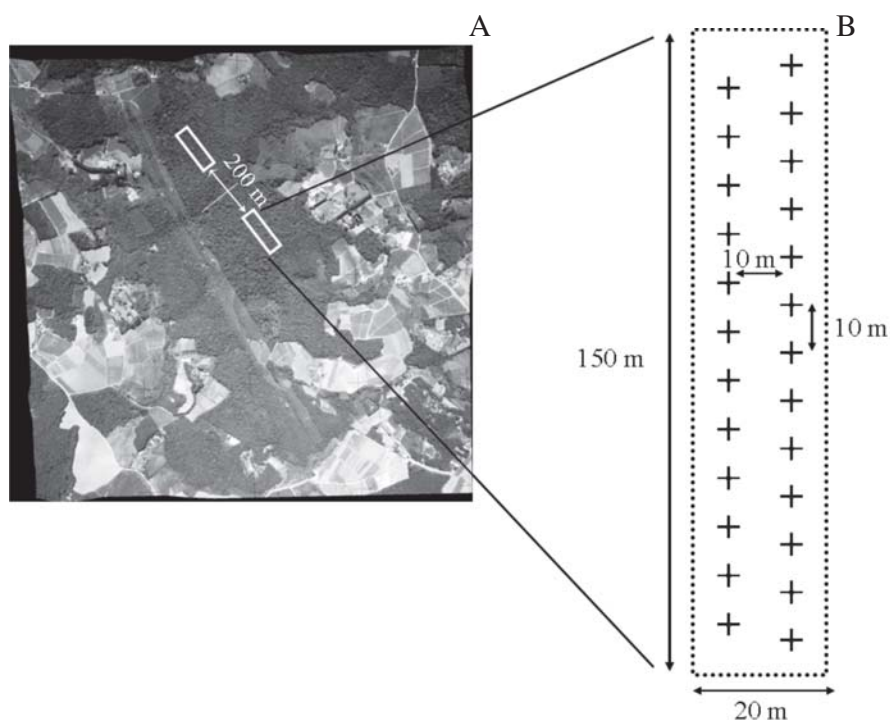


Figure 1. Spatial arrangement of (A) two sampling plots within one studied fragment and (B) 25 sampling points within a plot.

including circular variables (aspect) and categorical variables (slope location) in a linear regression. The relationship between richness and slope as well as with elevation were tested with simple linear regressions ( $n = 61$ ). The significance of the relationship between aspect and tree species richness was obtained using the Test of Rayleigh (Batschelet 1981; Zar 1999), generated by the Circular<sup>TM</sup> Statistics software. In this case, due to software limitations, it was not possible to use Bonferroni's adjustment. The relationship with slope location was obtained by analysis of variance, considering only categories with more than eight plots (slope, slope and lowland, slope and top,  $n = 59$ ). All tests presented homogeneity of variances (Levene's test). The Statistica<sup>TM</sup> software was used for regression and variance analyses.

For the second null hypothesis, data on tree richness were related to the variances of the relief parameters by means of linear regressions. Once more, Bonferroni's adjustment was employed, considering a significance level  $< 0.0125$ .

In order to attenuate possible effects of forest succession and human disturbances on the observed relationships between tree richness and relief, all tests for hypotheses 1 and 2 were repeated for two situations: considering only the plots at an intermediate successional stage ( $N = 36$ , Tab. 1), and considering only the plots inside the Morro Grande Reserve ( $N = 12$ ), where human disturbance is lower. The successional stages were defined taking into account criteria related to forest height, density, and tree diameter.

## Results

**Tree richness** – From the 6,100 individuals sampled, 311 species were surveyed, 296 being classified to the species level. The tree community was essentially composed of early- (133 species, 42%) and late- (97.31%) secondary species. Pioneer (25) and ombrophilous (40) species were uncommon. We observed a predominance of zoochorous species (234, *i.e.* 75%) in relation to anemochorous (62) and barochorous (15) species. Overall richness was strongly connected to richness of zoochorous (Pearson,  $r = 0.904$ ,  $n = 61$ ,  $P < 0.001$ ) and late secondary ( $r = 0.702$ ,  $n = 61$ ,  $P < 0.001$ ) species. The number of species per sample plot (100 individuals) ranged from 26 to 61 species (Tab. 2). Richness per dispersal category and succession class also varied greatly among sampled plots (Tab. 2).

Table 2. Basic descriptive statistics of the tree species richness in the 61 studied plots (Ibiúna Plateau, SE, Brazil).

Richness	Mean	Minimum	Maximum	Standard deviation
Total	41.0	26.0	61.0	7.2
Anemochorous	6.9	1.0	12.0	2.6
Barochorous	1.8	0.0	6.0	1.2
Zoochorous	32.3	19.0	51.0	7.7
Pioneer	3.1	0.0	12.0	2.3
Initial secondary	14.3	7.0	20.0	3.5
Late secondary	19.5	6.0	34.0	6.0
Umbrophilous	3.5	0.0	9.0	2.2

**Relief parameters** – Average slope varied from 6.5 to 27.8 degrees, staying between 5.1 and 20 degrees in 90% of the plots. The aspect averages were well distributed: 30.6% faced East, 30.6% faced North, 21% faced West and 17.7% faced South. The elevations found for the sample plots were between 876.3 and 1025.4 m, and plot location on the slopes basically included three classes: only on the slopes ( $n = 39$ ), on the slopes and lowlands ( $n = 11$ ) and on the slopes and tops ( $n = 8$ ). Slope and elevation were positively correlated in 61 plots (Pearson,  $r = 0.376$ ,  $P = 0.003$ ), and negatively related inside the Morro Grande Reserve ( $r = -0.686$ ,  $N = 12$ ,  $P = 0.014$ ).

**Relationship between richness and morphological characteristics of the relief** – There was no significant variation in overall tree species richness as a function of slope location, average aspect or slope. On the other hand, tree species richness appears to be related to elevation: richer communities were observed in higher regions (Tab. 3). This relationship was marginally significant when considering all plots sampled ( $p = 0.024$ ) and highly significant when only the plots at Morro Grande Forest Reserve were considered ( $p = 0.006$ ).

The richness of species per group of dispersal and succession showed little significant relationship as a function of the relief characteristics (Tab. 3). The most significant relationships were those observed for the two groups with less species: barochorous (15 species) and pioneers (25 species). These groups showed greater richness in areas of higher slope and elevation when all plots were considered, and also when only plots at intermediate successional stage were taken into account. There was a significant increase in the number of zoochorous species and a tendency for the late secondary species to increase with elevation at Morro Grande Reserve (Tab. 3), which is expected

Table 3. Linear regressions between tree species richness and average elevation per plot. adj R<sup>2</sup>: adjusted coefficient of determination; P: significance level; (-): negative relationship. Significant results are in bold.

	All plots (N = 61)		Intermediate regeneration plots (N = 36)		Morro Grande Reserve plots (N = 12)	
	adj R <sup>2</sup>	P	adj R <sup>2</sup>	P	adj R <sup>2</sup>	P
Total	0.07	0.024	0.02	0.577	<b>0.50</b>	<b>0.006</b>
Anemochorous	0.01	0.621	0.03	0.806	0.10	0.982
Barochorous	<b>0.11</b>	<b>0.009</b>	0.07	0.061	0.04	0.464
Zoochorous	0.02	0.127	0.03	0.787	<b>0.63</b>	<b>0.001</b>
Pioneer	<b>0.11</b>	<b>0.004</b>	0.11	0.028	0.10	0.915
Initial secondary	(-) 0.01	0.753	(-) 0.04	0.127	0.10	0.994
Late secondary	<0.01	0.494	0.02	0.648	0.41	0.014
Umbrophilous	<b>0.14</b>	<b>0.001</b>	0.11	0.026	0.10	0.169

because of the high correlation of the richness of these groups with the overall species richness.

**Relationship between richness and relief heterogeneity** – There was no significant relationship between overall richness or richness per functional group of tree species and variability of morphological parameters of the relief in any of the conditions examined. There was only a tendency, with the increase in relief heterogeneity, for the richness of a large part of the functional groups to increase: anemochorous species in relation to slope, aspect and slope location (the last two relationships at Morro Grande); barochorous species and slope (Morro Grande); pioneers and slope (plots at intermediate successional stage); early-secondary species and aspect in the plots at intermediate successional stage. However, in all these cases, the variance explained by relief heterogeneity was always low (< 8% for all plots, < 10% for the plots at intermediate successional stage and < 38% at Morro Grande). In some cases, the tendencies were contrary to expectation, such as reduction in the number of zoochorous species with the increase in variance of slope at Morro Grande and in relief heterogeneity in all plots and at the Morro Grande Reserve, or the reduction in late secondary species with the heterogeneity of relief locations. Finally, the number of marginally significant relationships for the 61 plots (four relationships) did not tend to increase when we considered only the plots at similar (intermediate) successional stages (three marginally significant relationships) or less subject to recent disturbances (Morro Grande; five relationships).

## Discussion

Unlike the findings of other authors, there were few significant relationships between the morphological

parameters of relief and tree species richness. Results with the same data set showed that species composition is also weakly related to relief (W. G. Silva, unpublished data). Many factors may have contributed to this apparent absence of relationships. First, the relationships may have been masked by human disturbance. In general, significant correlations between parameters of tree community structure and relief were obtained in studies carried out in old-growth, less disturbed forests (Killingbeck & Wali 1978; Lieberman *et al.* 1985; Kapelle *et al.* 1995; Chen *et al.* 1997; Botrel *et al.* 2002). At the Ibiúna Plateau, the situation is completely different. As all the studied fragments were, at least in part, deforested in the past, the forests investigated are not remaining fragments essentially composed of mature forests, but predominantly secondary fragments resulting from forest regeneration (Teixeira, personal communication), being that more preserved sites at Morro Grande have greater diversity (Bernacci *et al.* 2006; Catharino *et al.* 2006). The results partly demonstrate that the different successional stages and degrees of disturbance might have influenced the results. The main relationships were found when the whole community was observed inside the Morro Grande, where disturbances are less intense and the forest has a longer history of protection. On the other hand, some relationships between relief and tree richness were only observed when all plots were considered, as is the case of richness of anemochorous species and variance of slope. Therefore, there was a change in the pattern of relationship between tree richness and relief parameters as a function of the group of plots considered in the analyses. However, the number of significant relationships did not increase as the successional stage or the degree of disturbance were

controlled. These changes suggest that, in each of the three studied situations, the relief might influence different ecological or human processes, such as the choice of areas for agriculture settlement, or processes related to seedling and sapling survival, soil formation or characteristics. Therefore, it does not appear that there is a simple masking effect of relief related to human disturbance or successional stages, but distinct processes occurring in each situation.

Secondly, much of the evidence of relief influence on vegetation was observed in areas subject to periodic disturbance and, in some cases, intense, like those observed on river banks (Everson & Boucher 1998; Bertani *et al.* 2001) or on steep slopes subject to landslides (Simonetti personal communication). The sites studied in the Ibiúna Plateau were not subject to frequent flooding or landslides. Under these conditions, relief location and slope probably have lower effects on the loss of soil nutrients by erosion (Furley 1976) and on the physical-chemical characteristics of the soil, which could influence the vegetation (Oliveira-Filho *et al.* 1994; 1998; Carvalho *et al.* 2000; Bertani *et al.* 2001; Lyon & Sagers 2003). Thirdly, despite having considered the concept of toposequence (Jenny 1980), there is huge complexity in the relationships between relief and vegetation, partially related to superficial hydrological dynamics and soil characteristics (Austin *et al.* 1973; Lieberman *et al.* 1985; Kapelle *et al.* 1995; Newbery *et al.* 1996; Pendry & Proctor 1996; Chen *et al.* 1997; Tanner *et al.* 1998), which may hide the identification of the individual effects of relief parameters on the vegetation (Takyu *et al.* 2002). In this way, the weak relationship between tree richness and relief characteristics seems to reflect a real situation, not being masked by anthropogenic disturbances or by the fact that there were forests sampled at different successional stages. Apparently, this relationship can be weak when there are no strong natural stressing factors (*e.g.* inundations, landslides), as is the case of the present study.

The most significant results refer to an increase in the total number of species with elevation at Morro Grande, and an increase in the richness of barochorous and pioneer species with elevation and slope. As elevation and slope were significantly related, it was not possible to distinguish the individual effects of these parameters. Theoretically, areas with steeper slopes would allow more light penetration and would be more subject to landslides (C. Simonetti, personal communication), which could reflect on the greater richness of pioneer species. As the majority of pioneer

species are barochorous, this relationship would also be reflected on this group. Moreover, as in greater elevations there are steeper declivities, pioneer and barochorous species would also be favored by regions having greater elevations. However, these expected relationships should be weak in the study region, since the observed declivities were relatively low (*e.g.* 10-15 degrees, with a maximum average of 28 degrees), which would not favor the occurrence of landslides in forested regions.

The positive relationship between elevation and tree species richness was opposite to the expected, where a reduction in richness with an increase in elevation is the common result (Gentry 1988; Lieberman *et al.* 1996; Vasquez & Givnish 1998; Wang *et al.* 2003). According to Kent & Coker (1995), elevation is not really an environmental variable that influences the vegetation directly, but a complex gradient, inside of which many environmental factors vary and act together on the structure and composition of the vegetation. Among those factors are temperature, precipitation, humidity, wind speed, luminosity, chemical and physical characteristics of the soil, topography and drainage (Proctor *et al.* 1983; Harrison *et al.* 1989; Huggett 1995). A reduction in the number of species occurs with an increase in elevation due to the decrease in temperature. This happens both in temperate areas (Harrison *et al.* 1989) and in tropical mountains (Grubb & Whitmore 1963; Proctor *et al.* 1983; Huggett 1995). A possible explanation for this would be a decrease in decomposition rates proportionally to a decrease in temperature. Wang *et al.* (2003) pointed out that richness and diversity of types of forests and pastures reach a peak at intermediate portions of the altitudinal gradient. Sanchez (personal communication), in regions within the Atlantic Forest, and Lieberman *et al.* (1996), in Costa Rica, found the highest tree richness at elevations of 300 meters, decreasing above and below this altitude. However, in Southwest Asia, Proctor *et al.* (1988) and Pendry & Proctor (1997) found a tendency towards an increase in abundance and tree species richness with elevation, without the occurrence of a threshold.

At the studied sites, there was a small altitudinal variation between the sample vegetation plots (about 150 m), which must represent a difference of less than 1 °C between the extreme points of the altitudinal gradient, considering an average reduction of about 0.6 °C for each increase of 100 m in elevation in humid climates (Begon *et al.* 1996). At the Morro Grande Reserve, where the relationships with elevation were

more evident, the amplitude is even smaller (61 m). In these conditions, climatic changes occurring with elevation should not interfere with the vegetation drastically.

Other environmental gradients, which vary with elevation, might explain the greater richness in higher areas. Considering regional mapping scales (1/50,000 to 1/500,000), there are no significant differences in the type of geological or soil formation with elevation (Mello 2003). There is only a tendency towards the occurrence of a more rugged relief in the higher areas, which was already reflected on the significant relation between elevation and slope in the sample plots. On the other hand, the highest areas at the fragmented landscape and the Morro Grande Reserve are closer to an extensive continuous forest (Paranapiacaba Mountain range). As a consequence, these areas could be favored by a higher regional availability of species and by their proximity to seed sources for regeneration (Silva *et al.* 2007). Possibly, in these larger forest areas there was also less human disturbance in the past, as well as conversion of land into farmland and, therefore, the soils should be less impoverished. Our data suggested that the richer communities in higher and steep regions would not be determined by a direct influence of environmental parameters, such as temperature, type of soil or superficial hydrological dynamics, but would be more likely related to landscape structure (higher continuity and proximity among forest patches) or to a record of less intense soil conversion and agricultural use.

Few studies have previously related relief heterogeneity directly to species richness and diversity (but see Burnett *et al.* 1998; Nichols *et al.* 1998). The weak relationships observed in the present study indicate that species richness variations in the studied fragmented landscape (Bernacci *et al.* 2006, Durigan *et al.* 2008) are not related to relief heterogeneity. The Morro Grande Reserve, which contains a lower number of tree species, is also the place with the lowest elevation, slope and variations in these two parameters. This topographic situation and higher homogeneity in terms of relief could be contributing to lower tree species richness. However, if higher values and variances in elevations and declivities favor richness, then the largest fragments should be the richest fragments. Nevertheless, they only have intermediate richness, much below of that observed for fragments with intermediate size. In this way, it was not possible to find any clear influence of relief heterogeneity on the significant richness variations observed as a

function of fragment size. However, it is not possible to discard environmental heterogeneity as potential factor acting on species richness. Environmental heterogeneity is composed of a series of other parameters, besides those investigated here, such as physical and chemical characteristics, soil moisture, temperature, seasonality, frequency and duration of inundations, variations in the litter, light conditions, winds, etc., which could potentially act on species richness (Bertani *et al.* 2001; Takyu *et al.* 2002).

In summary, there was no direct relationship between relief heterogeneity or location and tree richness under the study site conditions. There were only few significant relationships between relief characteristics and tree community richness, and successional stage or degree of disturbance of the forests does not appear to influence this pattern. The most significant relationship (richness increase with elevation and slope) seems to reflect an indirect influence of the relief, due to the fact that deforestation is less intense in higher regions, rather than a direct influence of abiotic factors related to the altitudinal gradient.

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