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ORGANIZAÇÃO, ESTRUTURA E AMOSTRAGEM EM UMA FLORESTA ESTACIONAL SEMIDECÍDUA

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RESUMO

Neste estudo foram investigados aspectos teóricos relacionados à organização comunitária em uma floresta Estacional Semidecídua no sudeste do Brasil (Mata Ribeirão Cachoeira, Campinas, São Paulo). A área amostral com 6,5 ha, situa-se em uma vertente com declividade média de 15% e é delimitada em sua porção mais baixa pelo ribeirão Cachoeira, porém, sem sofrer inundações. Trata-se, portanto, de um gradiente ambiental sutil representado pela variável elevação do terreno. Outro gradiente ambiental é condicionado pelo regime natural de perturbação da floresta, através da contínua abertura e reconstituição arquitetural de clareiras. Este gradiente foi representado pela variável altura da vegetação. As duas variáveis foram correlacionadas com a variação estrutural da floresta após a exclusão do efeito da proximidade espacial entre parcelas. A correlação foi significativa mostrando que a topografia e o regime de perturbação exercem algum controle sobre a estrutura florestal em escala local. A diversidade variou ao longo da encosta mostrando desvio de dominância ecológica, ou seja, um aumento em dominância acima do que poderia ser esperado pela simples redução do número de espécies. Esses resultados sugerem ausência de equivalência ecológica entre as espécies e dão suporte ao modelo de montagem de comunidades por diferenciação de nicho. Foi possível identificar manchas de floresta com diferentes estruturas e a disposição espacial das manchas também apresentou correlação com a elevação do terreno. Contudo, a variação estrutural foi gradual e, em boa parte, não pôde ser explicada pelas variáveis ambientais, sugerindo a influência de eventos históricos e estocásticos. As implicações para a recuperação de áreas degradadas incluem a necessidade de escolha apropriada de espécies de acordo com as variações ambientais locais, ainda que sutis e graduais. O contexto teórico de organização comunitária delineado motivou a abordagem de questões metodológicas relativas à investigação de padrões comunitários em meso escala (1-100 km^2). Assim, a heterogeneidade do universo amostral representado pela floresta estudada foi avaliada relativamente às suas implicações para a estimativa de abundância das espécies e para a estabilidade do rank de abundância. Métodos de reamostragem e inferência estatística revelaram baixa precisão e estabilidade, portanto, comparações entre florestas baseadas na inspeção visual do rank de abundância devem ser evitadas. A existência de um gradiente vegetacional determinístico foi usada como justificativa para um refinamento dos métodos utilizados na tomada de amostras de composição de espécies voltadas à investigação de padrões comunitários em meso escala. Este refinamento consiste na estratificação do universo amostral e na descrição dos diferentes estandes de vegetação separadamente. A análise de suficiência amostral revelou que o reconhecimento de estandes na área de estudo requer um tamanho de amostra de oitenta parcelas de 10 x 10 m. Por outro lado, estimativas de atributos indicadores do status de conservação como diversidade, dominância, área basal e densidade total podem atingir boa precisão e acurácia com cinqüenta parcelas. As estruturas de abundância dos dois estandes identificados apresentaram diferenças conspícuas reforçando a importância da estratificação. A comparação de atributos indicadores de status de classificação e conservação com valores referência mostrou que a vegetação estudada pode ser considerada uma típica e bem conservada floresta Estacional Semidecídua.

Palavras-chave: Biodiversidade, Coexistência, Florestas tropicais, Reamostragem, Suficiência amostral, Técnicas de amostragem, Teoria Neutra

ABSTRACT

In this study, we investigated theoretical aspects related to community organization in a Semideciduous Atlantic forest in SE Brazil (Ribeirão Cachoeira forest, Campinas municipality, São Paulo state). The 6.5 ha sampling area is located on a slope with an average steepness of 15% and is delimited in its lowest portion by Cachoeira stream, which, however, is not subject to flooding. We dealt, therefore, with a subtle environmental gradient represented by the variable "terrain elevation". Another environmental gradient was conditioned by the forest natural disturbance regime through continuous gap opening and architectural reconstruction. This gradient was represented by the variable "vegetation height". Both variables were correlated with the forest structural variation after the exclusion of the effects of spatial autocorrelation. The correlation was significant, showing that topography and disturbance regime exert some control on the forest structure at local scale. Diversity varied along the slope showing a deviation in ecological dominance, that is, a dominance increase above what could be expected from the reduction of species number alone. These findings suggest the absence of ecological equivalence among species and give support to the model of community assembly by niche differentiation. It was possible to identify forest patches with different structures and the spatial disposition of patches also presented a correlation with terrain elevation. However, transition between patches was gradual and, to a great extent, could not be explained by environmental variables, suggesting the influence of historical and stochastic events. The practical implications of these results in the restoration efforts of degraded forest areas include the necessity of an appropriate species choice, according to local environmental variation, no matter how subtle or gradual it might be. The theoretical context that was delineated for community organization motivated us to address methodological questions related to community patterns investigation at meso-scale (1-100 km^2). Thus, the heterogeneity of the whole sampling universe represented by the studied forest was evaluated in relation to the implications for species abundance estimation and stability of the abundance rank. Resampling methods and statistical inference revealed low precision and stability, hence comparisons among forests based on visual inspection of the abundance rank should be avoided. The existence of a deterministic vegetation gradient was used as justification for a refinement of the methods used in the collection of species-composition samples aimed at investigation of community patterns at meso-scale. This refinement consists of stratification of the sampling universe and of the description of different vegetation stands separately. The sampling sufficiency analysis showed that the stand recognition in the studied area demands a sampling size of eighty 10 x 10 m plots. On the other hand, estimation of conservation status indicator attributes such as diversity, dominance, total basal area and density may reach satisfactory precision and accuracy with a sampling effort of fifty plots. The abundance structure of both identified stands revealed conspicuous differences, reinforcing the importance of stratification. Comparison of conservation and classification status indicator attributes with reference values evidenced that the studied vegetation can be considered a typical well-conserved Semideciduous Atlantic forest.

Palavras-chave: Biodiversity, Coexistence, Neutral theory, Resampling, Sampling sufficiency, Sampling techniques, Tropical forests

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INTRODUÇÃO GERAL

A variação espacial e temporal da estrutura de comunidades vegetais tem recebido diferentes tratamentos teóricos na tentativa de se compreender como as comunidades são organizadas ou montadas. De acordo com a Teoria Neutra, essa variação pode ser prevista por uma dinâmica em que eventos demográficos como nascimento e morte sejam inteiramente atribuídos ao acaso (Hubbell & Foster 1986, Hubbell 1997, Hubbell 2001). Em outros termos, a probabilidade de um indivíduo na comunidade morrer ou se reproduzir não depende da espécie a que este indivíduo pertence. De acordo com esse modelo, a distribuição de abundância entre as espécies de uma comunidade poderia ser descrita por um modelo matemático multinomial (Hubbell 1997, Hubbell 2001, Chave 2004). A dinâmica neutra estabilizaria as relações de abundância entre espécies, contudo, devido a estocasticidade demográfica, as espécies poderiam mudar de posição no rol de abundância no tempo e no espaço, fenômeno conhecido como de deriva comunitária (Hubbell & Foster 1986) ou ecológica (Hubbell 2001).

A dinâmica neutra pressupõe que todas as espécies da comunidade sejam ecologicamente equivalentes, tanto em termos de ajuste às condições abióticas quanto em habilidade competitiva (Hubbell 1997, Hubbell 2001, Chave 2004). Relaxar essa premissa do modelo significa atribuir probabilidades de morte ou reprodução espécie-específicas aos indivíduos da comunidade, situação em que as equações do modelo neutro prevêem uma drástica redução do tempo de persistência das espécies na comunidade (Zang & Lin 1997, Yu et al. 1998). Por outro lado, é notória a existência de diferenças interespecíficas, em termos de tolerância e requerimentos ambientais e habilidade competitiva em comunidades vegetais (Leigh 1999, Wright 2002, Leigh et al. 2004, Turnbull et al. 2004). Portanto, a teoria neutra não poderia explicar a elevada diversidade alfa observada em florestas tropicais. O modelo alternativo de organização comunitária, que considera as diferenças ecológicas entre as espécies, é o modelo de montagem por diferenciação de nicho (Hubbell 1997), que tem recebido considerável suporte empírico (Poorter & Arets 2003, Tuomisto et al. 2003a, Tuomisto et al. 2003b, Aiba et al. 2004, Enoki & Abe 2004, Obiri & Lawes 2004, Cannon & Leighton 2004, veja revisões em Wright 2002 e Leigh et al. 2004). De acordo com o modelo, espécies com requerimentos ecológicos diferentes ocupariam ou dominariam porções da comunidade com características abióticas distintas, sendo, portanto, a coexistência facultada pela heterogeneidade ambiental (Leigh 1999, Wright 2002). Neste caso, a variação estrutural da comunidade seria conseqüência de respostas ecofisiológicas dos indivíduos a diferentes condições ambientais expressas na taxa de crescimento líquido populacional e, portanto, na abundância específica. Dessa forma, seria possível correlacionar inequivocamente a variação espacial da estrutura comunitária com a variação de fatores ambientais. Dentre os fatores mais comumente relacionados à variação estrutural em florestas tropicais, a disponibilidade hídrica no solo tem papel de destaque (Rodrigues et al. 1989, Oliveira-Filho 1994, Oliveira-Filho et al. 1997, Sabatier et al. 1997, Cardoso & Schiavini 2002, Martins et al. 2003). A disponibilidade hídrica no solo varia consideravelmente com a posição ao longo de uma vertente (Furley 1976, Oliveira-Filho 1994, Oliveira-Filho et al. 1997, Sollins 1998, van der Berg & Oliveira-Filho 1999). Por outro lado, a estrutura florestal também varia no espaço em resposta a mudanças nas condições ambientais impostas pelo regime natural de perturbação da floresta, caracterizado pela contínua abertura e reconstituição arquitetural de clareiras (Oliveira-

Filho et al. 1997, Oliveira-Filho et al. 1998, Poorter & Arets 2003, Aiba et al. 2004, Enoki & Abe 2004).

Apesar da importância atribuída a mecanismos determinísticos, como a diferenciação de nicho, para a manutenção da diversidade alfa em florestas tropicais (Leigh et al. 2004), o modelo neutro também tem recebido suporte empírico (Condit et al. 2002, Tuomisto et al. 2003a, Tuomisto et al. 2003b). É possível que mecanismos determinísticos e eventos estocásticos interajam na montagem de comunidades vegetais e, neste caso, a importância relativa de ambos os tipos de processos pode variar entre comunidades (Hubbell 2001). Portanto, a investigação da diferenciação de nicho em florestas tropicais, em diferentes contextos ecológicos, constitui um esforço relevante para o desenvolvimento da teoria ecológica. Contudo, identificar relações ecológicas entre a comunidade e fatores abióticos não é uma tarefa fácil. Processos espacialmente estruturados tais como a reprodução das espécies e a dinâmica da água no solo podem ocasionar autocorrelação espacial positiva em variáveis como número de indivíduos e umidade. Dessa forma, correlações espúrias entre variáveis bióticas e abióticas podem surgir a partir de estruturas espaciais coincidentes, mesmo sob uma dinâmica comunitária neutra (Legendre & Legendre 1998). Portanto, relações causais só podem ser efetivamente comprovadas após o controle da estrutura espacial das variáveis através de modelagem causal (Legendre & Legendre 1998).

Este trabalho teve como objetivos gerais a) o estudo da organização de uma floresta Estacional Semidecídua, considerando os diferentes modelos de montagem de comunidades; e b) correlacionar aspectos teóricos e metodológicos da Ecologia de Comunidades enfatizando as possíveis aplicações práticas das informações obtidas.

No capítulo 1 (Position on slope, disturbance, and tree species coexistence in a Seasonal Semideciduous forest in SE Brazil), a variação da estrutura comunitária em uma floresta de 6,5 ha (parte da Mata Ribeirão Cachoeira, Campinas, São Paulo) foi correlacionada, através de modelagem causal, com a elevação do terreno e com a altura da vegetação, considerada uma medida simples de perturbação. No capítulo 2 (Deterministic local-scale community spatial structure in Semideciduous Atlantic forest), o foco foi a relação entre variação estrutural e elevação do terreno, buscando explorar o viés aplicado da organização comunitária no contexto de fragmentação da floresta Estacional Semidecídua.

Os resultados obtidos nos dois primeiros capítulos definiram um embasamento teórico que direcionou a investigação de aspectos metodológicos nos três capítulos seguintes. A relação entre teoria e método é bastante discutida na literatura ecológica (e.g. Cain & Castro 1971, Mueller-Dombois & Ellengerg 1974). A base teórica mencionada inclui modelos determinísticos que consideram o ambiente abiótico e as interações interespecíficas como importantes fatores determinando a estrutura de comunidades vegetais, respectivamente, modelos de diferenciação de nicho (Leigh 1999, Wright 2002) e de regras de montagem (Silvertown & Wilson 1994, Wilson et al. 2000). Tais modelos são coerentes com a noção de comunidade ecológica, que se estabeleceu a partir do debate iniciado com as opiniões divergentes de Clements (1916) e Gleason (1926), ou seja, a de um conjunto de populações que apresentam similaridades em seus requerimentos e tolerâncias ecológicas, porém, com propriedades emergentes resultantes da interação entre indivíduos (Anderson & Kikkawa 1986, Moravec 1989). Dessa forma, os três últimos capítulos enfocaram aspectos metodológicos distintos relativos à investigação de padrões comunitários em pequena escala espacial (meso escala).

No capítulo 3 (Precision and stability of the tree species abundance rank in Semideciduous Atlantic forest), a precisão das estimativas de abundância das espécies e a estabilidade do rank de abundância foram avaliadas e as implicações dessas variáveis para a investigação de padrões estruturais foram discutidas. No capítulo 4 (Sampling sufficiency analysis for stand recognition and estimation of conservation status indicator attributes in the Semideciduous Atlantic forest), a variação estrutural da floresta, associada à elevação do terreno, foi tomada como justificativa para o refinamento dos métodos de tomada de amostras de composição de espécies visando à investigação de padrões estruturais em meso escala. Inicialmente, a suficiência amostral para o reconhecimento de diferentes estandes na floresta foi avaliada. Também se avaliou a suficiência amostral para a estimativa de descritores de atributos que podem ser considerados indicadores de status de conservação da floresta, como diversidade, área basal e densidade total.

O refinamento metodológico mencionado foi aplicado no capítulo 5 (Describing forest stands outlined through objective entitation and assessing classification and conservation status in the Semideciduous Atlantic forest), na descrição da estrutura de abundância da floresta que foi alvo deste estudo. Dessa forma, a floresta foi descrita como um todo e também foram apresentadas descrições separadas para cada um dos dois estandes de vegetação identificados. A vegetação dos estandes foi comparada para evidenciar a importância da estratificação. No mesmo capítulo, o status de classificação e conservação da floresta foi avaliado através da descrição de atributos indicadores e comparação com valores de referência disponíveis na literatura.

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CAPÍTULO 1

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Position on slope, disturbance, and tree species coexistence in a Seasonal Semideciduous forest in SE Brazil

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Abstract

We investigated the influence of position on a slope (plot relative elevation) and vegetation disturbance (the tallest tree height per plot) on community composition and diversity in a SE Brazilian Seasonal Semideciduous forest (46º55' W, 22º50' S). Trees with dbh ≥ 5 cm were sampled in one hundred 10 x 10 m plots randomly placed in a 6.5-ha forest area. Through partial Mantel test, floristic dissimilarities among plots (Jaccard index computed with species abundance in each plot) were correlated with environmental distances among plots (Euclidian distance index computed with relative elevation and the tallest tree height values in each plot). Relative elevation and the tallest tree per plot height were individually correlated with floristic gradients expressed by PCA axes scores using Pearson's correlation coefficient. Through resampling, we compared diversity (richness, Berger-Parker *D* and Shannon *H'*) among plots in the drier (up) and moister (low) ends of the slope. Floristic dissimilarities were significantly correlated with environmental distances even after geographic distances among plots have been partialled out ($r_m = 0.1274$, $p < 0.001$). The first two PCA axes accounted for 22% of the total variance. After Bonferroni and Dutilleul's corrections, axis 1 showed a marginally significant correlation with plot relative elevation ($r = -0.4097$, $p = 0.0309$), and axis 2 was significantly correlated with the tallest tree height per plot ($r = 0.2953$, $p = 0.0106$). Position on the slope and vegetation disturbance were reliable predictors of community composition, thus suggesting the operation of niche assembly organizing processes. Richness and diversity (*H'*) decreased

and dominance (D) increased with elevation on the slope. Dominance increase from $D_{(300)}$ = 0.11 (confidence interval = 0.091 – 0.131) to $D_{(300)}$ = 0.19 (CI = 0.165 – 0.210) surpassed the expected dominance increase based on the reduction of richness alone: $D_{(300)}$ = 0.13 (CI = 0.110 – 0.140), thus highlighting the niche partitioning assembly of the community, especially among abundant species. Given the great amount of floristic variability remaining unexplained, stochastic processes, such as those related to dispersal limitation, may also have influence on the community composition. Therefore, both niche assembly and chance events can operate even on a fine local scale.

Introduction

The processes determining the composition of plant communities have received considerable attention in tropical regions, where, due to the high diversity, the researchers have sought to answer the following question: How can so many species coexist on fine local scales? A variety of explanations have been considered (Hubbell and Foster 1986; Hubbell 1997; Leigh 1999; Hubbell 2001; Wright 2002; Leigh et al. 2004). According to the niche assembly model, different species would exhibit different habitat preferences, so that the coexistence of species would be favored by environmental heterogeneity (Leigh 1999; Wright 2002). On the other hand, the lack of conspicuous patterns found in some tropical communities has given rise to explanations without any niche assembly appeal, in which the composition of communities would be the result of fortuitous combinations of ecologically equivalent species competing strongly, but in a diffuse way (Hubbell and Foster 1986; Hubbell 1997; Hubbell 2001; Chave 2004). These two conceptual frameworks were called respectively the niche assembly and the dispersal assembly perspectives of community organization (Hubbell 1997). Leigh (1999) revised the arguments of these two approaches, and concluded that tropical plant communities do have several gradients of arboreal diversity, which are consistently related to environmental variables. Therefore, the coexistence of species could not be attributed purely to chance, but to a set of factors that would play a role in the community organization, among them environmental heterogeneity and associated trade-offs (Leigh 1999; Wright 2002; Leigh et al. 2004).

Studies performed in tropical forests have demonstrated that, even on a fine scale (some hectares or less), environmental variables can influence the composition of the community (Lescure and Boulet 1985; Rodrigues et al. 1989; Oliveira-Filho 1994; Oliveira-Filho et al. 1997; Sabatier et al. 1997; van den Berg and Oliveira-Filho 1999; Cardoso and Schiavini 2002; Aiba et al. 2004; Koponen et al. 2004). The role of environmental heterogeneity can be assessed by investigating species distribution patterns in the space, that is, by highlighting regularities in the occurrence or abundance of species in relation to a gradient of an environmental variable. On fine scales, floristic patterns have mainly been associated to chemical and physical soil properties (Lescure and Boulet 1985; Rodrigues et al. 1989; Oliveira-Filho 1994; Oliveira-Filho et al. 1997; Sabatier et al. 1997; Cardoso and Schiavini 2002; Martins et al. 2003; Valencia et al. 2004). Physical and chemical soil properties, including soil water regime, covary on fine scales with topographic position (Sollins 1998; van den Berg and Oliveira-Filho 1999). On the other hand, variables influenced by gap opening, such as light, soil and air temperature, soil nutrient availability, and relative air humidity (Bazzaz and Pickett 1980), also have an important role in the determination of fine-scale floristic patterns (Oliveira-Filho et al. 1997; Oliveira-Filho et al. 1998; Poorter and Arets 2003; Aiba et al. 2004; Enoki and Abe 2004).

Therefore, the variables related to fine-scale floristic patterns may be divided in two sets: 1) variables not related to the forest natural disturbance history; and 2) variables related to the forest natural disturbance history. Though artificial, this division may help to investigate community organizing processes. Both sets of variables can interact or overlap in the determination of forest composition, but it is possible to detect the patterns related to each set of variables individually. Type-1 variables are mainly edaphic, such as soil fertility, pH, P and Al content, texture and water availability, and they do not rely on disturbances to vary. As they can vary along a slope, these variables are influenced by the position on the relief or horizontal space (Furley 1976; Rodrigues et al. 1989; Oliveira-Filho 1994; Oliveira-Filho et al. 1997; Sollins 1998; van den Berg and Oliveira-Filho 1999; Martins et al. 2003). Type-2 variables comprise soil and atmosphere properties that vary along time, following gap regeneration after a disturbance event. The theory of gap dynamics (Whitmore 1982; Oldeman 1983) considers the forest as a mosaic of patches at different successional stages, each patch occupied by species with different environmental demands (Budowski 1965; Swaine and Whitmore 1988; Whitmore 1989). Thus, the variation of type-2 variables along time may be expressed by the variation of the regeneration phases or disturbance status of several patches in the space.

Type-1 and 2 variables are descriptors of species' ecology and can be represented by niche axes against which species performance can be plotted (Hutchinson 1957). In this model, species coexistence relies on the number and length of niche axes, the degree of specialization of the species, and degree of tolerable overlap between adjacent species' niches. This model, however, has limited application in plant community ecology when dealing with resources (Crawley 1997). In this case, an alternative model will plot competitive trade-off solutions instead of species' performance on niche axes (Tilman 1982; Tilman and Pacala 1993). In this model, species coexistence will rely on the species capability to acquire complementary trade-off solutions to exploit the resources and on the spatial heterogeneity of resource supply levels (Tilman 1982; Tilman and Pacala 1993). Both models assume spatial heterogeneity and some degree of habitat partitioning among species, which are the base of the niche assembly perspective of community organization. They also allow the interpretation of floristic and diversity spatial patterns.

Floristic and diversity spatial patterns can be viewed as evidence of niche assembly organizing processes. In tropical tree communities, decrease of diversity is associated with stress-related factors, such as intensity and duration of the dry season, incidence of frosts, soil impoverishment, and water saturation (Leigh 1999; Boubli 2002; Cielo-Filho et al. 2002; Konopen et al. 2004). Hence, floristic patterns are expected to be accompanied by diversity patterns if an underlying environmental gradient represents a stress gradient, as is the case, for example, of an environmental gradient associated with a slope. For instance, soil water availability varies considerably with position on a slope (Furley 1976; Oliveira-Filho 1994; Oliveira-Filho et al. 1997; Sollins 1998; van den Berg and Oliveira-Filho 1999). Thus, a slope may also correspond to a water availability gradient, mainly in seasonal tropical climates, in which there is a rainy and a dry season.

However, detecting floristic and diversity patterns does not constitute an exact proof in favor of the niche assembly perspective. Dispersal assembly model (neutral theory) can also predict floristic gradients (Condit et al. 2002; Chave 2004) and, since vegetation and environmental variables can be spatially autocorrelated, spurious correlations between vegetation and environmental variables can arise by chance (Legendre and Legendre 1998; Aiba et al. 2004). Furthermore, neutral theory can also predict reduction in richness and, as a consequence, increase in dominance (Hubbell 2001). Thus, it is not easy to infer the relative importance of dispersal *versus* niche assembly perspectives from floristic and diversity spatial patterns. One possible way to address this question is by examining whether the increase of dominance along an environmental gradient is larger than the expected increase of dominance generated by reduction of richness alone. This situation was taken here as indicating ecological dominance deviation, evidence of niche assembly of the community (Hubbell 2001).

The objective of this paper was to answer the following questions: Can floristic and diversity variation in a Seasonal Semideciduous forest area be related to position on a slope and disturbance, as would be expected if type-1 and 2 variables were playing a role in the community organization? Is increase of dominance along an elevation gradient larger than the expected increase generated by reduction of richness alone, that is, is there evidence of ecological dominance deviation?

Methods

Study site

This work was carried out in the Ribeirão Cachoeira forest, the second largest forest fragment (245 ha) in a region where forest cover was highly fragmented (Santin 1999). It is located in the Environmental Protection Area of the municipality of Campinas, São Paulo state, with the coordinates 46º55' W and 22º50' S (Fig 1a). The fragment is crossed in the east-west direction by the Cachoeira stream, a tributary of Atibaia River (Fig. 1b). The vegetation may be classified as Seasonal Semideciduous forest due to the climatic seasonality and deciduousness observed in about 30% of the highest trees during the dry season (IBGE 1992). The climate is Koeppen's Cwa, with a hot rainy season from October to March, with monthly average temperatures between 22 ºC and 24 ºC and average total precipitation of 1057 mm; and a dry season from April to September, with monthly average temperatures between 18 ºC and 22 ºC and average total precipitation of 325 mm (1961-1990 observation period, Ortolani et al. 1995). Altitude varies from 630 to 760 m a. s. l., the relief is hilly with steepness varying from 12% to more than 45% (Instituto Geológico 1993). Soil is Chromic Luvisol, with sandy texture and many rock fragments (Embrapa 1999).

The sampling area is 6.5 ha, located in the south portion of the forest fragment, on the left of the Cachoeira stream (Fig. 1b). It was selected with the aid of a 1:25,000 aerial photograph and examination in the field. To choose this area, we avoided great declivity variations and the presence of too large gaps. As one physiognomical extreme, the vegetation has a few small gaps; as the other, it has a continuous canopy with 15 to 18 m in height and emergent trees of up to 30 m. There are no signs of recent anthropogenic disturbances in the area, such as charcoal on the ground surface, soot on trunks, and presence of stumps or coppiced trees. The sampling area is located on a slope, approximately 270 m in length, with average steepness of 15%, and 40 m of difference between the up and low ends. The boundary of the sampling area in its lower portion corresponds to a trail alongside the Cachoeira stream, and does not undergo periodic flooding (Fig. 1c).

Sampling

The sampling was made in plots arranged in accordance with the unrestricted randomization procedure proposed by Greig-Smith (1983). A system of coordinated axes was used, one with 400 m in length (the X axis, following the trail along Cachoeira stream, approximately in the E-W direction) and the others with 200 m in length (the Y axes, imaginary straight lines originating orthogonally from the principal axis, all directed approximately to the South). The coordinates of each plot northeastern vertex were obtained by drawing random number pairs, one number corresponding to the position on the X axis, the other corresponding to the position on one of the Y axes (Fig. 1c). A hundred 10 x 10-m plots were installed, with vertices demarcated by permanent PVC pipe stakes. The position on the slope was represented by the relative elevation of each plot, which was obtained with the aid of a transparent hose almost completely filled with water. We started from the lowest plot on the slope and measured the differences of the water column height in each end of the hose, which was positioned in the centre of two nearest plots.

We sampled all living trees ≥ 5 cm dbh from July to December 1999. We tagged each tree with a numbered aluminum label, and recorded its height and dbh. We established *a priori* two inclusion and two exclusion sides for each plot: all individuals that touched the plot limit line at the inclusion sides were included in the sample, and the ones that touched the exclusion sides were excluded. Provisional tree identification to species was made in the field, based on vegetative and reproductive characters. Nomenclature of plant species followed Santos and Kinoshita (2003). Definitive identification was made by means of published identification keys and comparison with material lodged in the Campinas State University Herbarium (UEC). Taxon specialists confirmed definitive identifications. The vouchers were lodged in UEC collection.

Data analysis

To evaluate whether floristic variation in the forest is related to the position on the slope and disturbance, we used simple and partial Mantel tests based on Pearson correlation coefficient (Legendre and Legendre 1998). We started from three primary matrices from which three secondary matrices were computed:

1. A primary matrix of 81 species and 100 plots, composed of the number of individuals of each species per plot. The species sampled with only one individual were not included in the species *versus* plot matrix. *Almeidea lilacina* St.-Hil., an understory Rutaceae tree densely clumped in a few plots, was also excluded. This matrix was used to compute the floristic dissimilarity matrix among plots, namely the secondary floristic matrix. To do so, we used Jaccard dissimilarity index (2B/(1+B), where B is the Bray-Curtis dissimilarity (Faith et al. 1987).
2. A primary matrix of two environmental variables and 100 plots. Environmental variables were the position on the slope, represented by the relative elevation of each plot, and disturbance, represented by the tallest tree height in each plot (a simple, efficient disturbance descriptor, since disturbed plots have lower trees). This matrix was used to compute an environmental distance matrix among plots, namely the secondary environmental matrix. To do so, the Euclidian index was used after standardization ($\bar{x} = 0$, $s^2 = 1$) of environmental variables.
3. A primary matrix of two geographic variables and 100 plots. Geographic variables were the coordinates of plots in two orthogonal straight axes plotted on figure 1c. This matrix

was used to compute a geographic distance matrix among plots, namely secondary geographic matrix. To do so, the Euclidian index was used.

The Mantel tests were performed on the secondary matrices. First, we correlated biological and environmental matrices through a simple Mantel test. As the analyses dealt with spatial structures, it was necessary to eliminate the influence of autocorrelation in space, which could generate spurious correlations between the variables analyzed. To do so, we used the secondary geographic matrix to partial out the effect of inter-plot geographic distance on the correlation between biological and environmental matrices, through a partial Mantel test. Monte Carlo permutation (1000 permutations) was used to evaluate the statistical significance of the correlations. R-package software (package vegan) was used to compute dissimilarity and distance matrices and to run Mantel tests.

Furthermore, we used an unconstrained ordination method to extract the principal floristic gradients in our data. We hypothesized that the environmental variables position on the slope and disturbance could have some degree of correlation with these floristic gradients if type-1 and 2 variables were playing a role in the community organization. The investigation of floristic gradients was made through Principal Component Analysis – PCA (Legendre and Legendre 1998) performed with the software Fitopac (Shepherd 1996). The PCA was applied to a matrix of covariances, obtained from the data matrix of 81 species and 100 plots, composed of the number x of individuals of each species per plot after a logarithmic transformation ($\log x + 1$). The stability of the PCA axes was evaluated through comparison of the eigenvalues obtained in the analysis with the ones expected according to the broken stick model (Frontier 1976; Jackson 1993). The relationships between floristic gradients, represented by the plot scores on the PCA axes, and the relative elevation and the tallest tree height per plot were analyzed through Pearson's correlation coefficient (Zar 1999). We correlated plot scores on axis 1 against both plot relative elevation and the tallest tree height per plot separately, and did the same for plot scores on axis 2. In order to control for type-I error we used the sequential Bonferroni correction (Rice 1989) for $\alpha = 5\%$. To test the significance of correlations we used the CRH procedure (Clifford et al. 1989) modified by Dutilleul (1993). This procedure considers the amount of autocorrelation in the data in order to calculate an effective sample size. This effective sample size is then used to calculate degrees of freedom, based on which the significance of the correlation can be properly assessed. This procedure is required because, in the presence of spatial autocorrelation, an individual plot will not correspond to a full degree of freedom due to the lack of independence among plots, leading to inflated Type I error probability (Legendre and Legendre 1998). Correlations were performed using PASSAGE software (Rosenberg 2001).

The relationships between species and PCA axes were investigated through analysis of eigenvector diagram. To construct the diagram, we normalized the eigenvectors by the square root of the respective eigenvalues (λ), and plotted them in the reduced space formed by the PCA first two principal axes. Each eigenvector represents a species in the matrix, and in the eigenvector diagram, the cosine of the angle formed between an eigenvector and a PCA axis is proportional to the covariance between the respective species and the axis (Legendre and Legendre 1998). In the eigenvector diagram, we inputted just the species eigenvectors that, when normalized by 1, had a length longer than the equilibrium contribution ($\sqrt{(2/n)}$, being n the number of species in the data matrix). A species with eigenvector shorter than the equilibrium contribution does not contribute to the reduced space defined by two principal axes more than it would by assuming an equal association of this species with all other axes (Legendre and Legendre 1998).

The variation of diversity with relative elevation was evaluated by mean of three diversity measures: richness, Berger-Parker (*D*) dominance index (Berger-Parker 1970) and Shannon (*H'*) diversity index (Shannon 1948). The plots were divided in two groups (subcommunities), one above and the other below the median elevation of the plots. Average values and confidence intervals (95%) of these diversity measures were estimated separately for each group of plots by means of resampling techniques (1000 iterations) using EcoSim software (Gotelli and Entsminger 2000). To test whether the increase of dominance along the elevation gradient was larger than the expected increase generated by reduction in richness alone (e.g. whether there was ecological dominance deviation), we compared the dominance observed in the poor subcommunity with that of a simulated community. We constructed this simulated community by applying neutral theory assumptions to the rich subcommunity data. To construct the simulated community, we standardized the number of individuals to 300 in both poor and rich subcommunities by calculating a mean vector of species abundance for each of them through resampling techniques. Then, we eliminated the species of the standardized rich subcommunity that were lacking in the standardized poor subcommunity until richness in the two subcommunities was equaled (species exclusive of the poor subcommunity were substituted by species with the same abundance in the rich subcommunity). We added the abundance of the species eliminated to the remaining species in the proportion of their abundance in the subcommunity, as could be expected under a zero sum dynamics with ecological equivalence (Hubbell 1997; 2001). EcoSim software (Gotelli and Entsminger 2000) was used to compute dominance indices and respective 95% confidence intervals in order to compare dominance (D_{300}) between the poor subcommunity and the simulated community.

Results

Floristic patterns

In the 100 plots we found 1080 living trees of 119 species, of which 37 were represented by only one individual and so not included in the analyses. A simple Mantel test showed a significant correlation between biological and environmental matrices ($r_m = 0.1636$, $p < 0.001$). This correlation remained significant even after geographic distances among plots have been partialled out by holding the geographic matrix constant ($r_m = 0.1274$, $p < 0.001$).

The first two axes of PCA explained 22% of the total data variance. These axes represented floristic gradients in which abundance of species varied among plots. Therefore, a plot score on an axis summarizes the relative contribution to this plot composition of the species whose abundance varies along the floristic gradient represented by that axis. Since we hypothesized that plot relative elevation and the tallest tree height could be related to the major floristic gradients in the forest, only the first two principal axes were analyzed. These axes seem to represent a stable solution, since the variance associated with them was, on average, twice as large as the expected variance according to the broken stick model (Table 1).

The scattering of points (plots) in the reduced space formed by the first two principal axes showed two floristic gradients (Fig. 2a). Equilibrium contribution was $\sqrt{(2/81)} \approx 0.157$, and ten species had normalized eigenvectors longer than this value (Table 2, Fig. 2b). Joint analysis of figures 2a and 2b revealed that the floristic gradient expressed by axis 1 was primarily defined by differences in the relative contribution to plot composition of *Esenbeckia leiocarpa* and *Savia dictyocarpa*. This interpretation arises from the relatively high length of *E. leiocarpa* and *S. dictyocarpa* eigenvectors and the relatively small covariance angles these eigenvectors formed with axis 1, that is, these species had high covariances with this axis (Legendre and Legendre 1998). These were also the species with greatest abundance in the whole community. The relative contribution of *E. leiocarpa* and *S. dictyocarpa* to plot composition was higher, respectively, on the negative and positive sides of axis 1 (Fig. 2b). The other species with high covariance with axis 1 were *Metrodorea nigra* and *Ocotea beulahiae,* both with a relatively high contribution to plot composition on the positive side of axis 1.

The floristic gradient expressed by axis 2 was defined primarily by abundance differences of *E. leiocarpa* and *S. dictyocarpa* on the positive side, and *Aegiphila sellowiana* and *Urera baccifera* on the negative side. Other species with high covariance with axis 2 were *Actinostemon communis* on the positive side, and *Croton floribundus*, *Aspidosperma polyneuron* and *Astronium graveolens* on the negative side. Although the eigenvectors of the remaining 71 species did not surpass the equilibrium contribution for the first two axes, and so were not included in the above analysis, several of them also contributed to the floristic gradients outlined by these axes. For instance, 32 species differed more than 2-fold in density between negative and positive sides of axis 1, and 39 species on axis 2. The relations observed between floristic gradients expressed by these axes and the explanatory variables position on the slope and disturbance were as follows.

Floristic gradient versus position on slope

The correlation between the floristic gradient represented by axis 1 scores and plot relative elevation was only marginally significant at the table-wide α level of 5% (Table 3). Since axis 1 scores and relative elevation were negatively correlated, *Esenbeckia leiocarpa* showed a tendency to increase abundance towards the higher portion of the slope, whereas *Savia dictyocarpa*, *Metrodorea nigra* and *Ocotea beulahiae* showed the opposite trend (Fig. 2b). This floristic gradient is probably derived from community organizing processes involving type-1 variables. Species with abundance covarying in opposite directions with elevation could have found different solutions for the trade-off between the ability to survive in drier habitats and the ability to grow fast in wetter ones (Leigh 1999).

Floristic gradient versus disturbance

The scores of the axis 2 were significantly correlated with the tallest tree height in the plot (Table 3). Since axis 2 scores and the tallest tree height per plot showed positive correlation, *Esenbeckia leiocarpa*, *Savia dictyocarpa* and *Actinostemon communis* tended to increase abundance in plots with larger tallest tree height, whereas the pioneers *Croton floribundus*, *Aegiphila sellowiana* and *Urera baccifera* had the opposite tendency (Fig. 2b). This floristic gradient is probably derived from community organizing processes involving type-2 variables, promoted by disturbance events that knock down canopy specimens and favor the pioneers that can colonize such gaps. Those two species groups could have developed different regeneration strategies in relation to the trade-off between the ability to survive in shade and the ability to grow fast in gaps (Leigh 1999; Leigh et al. 2004). *Aspidosperma polyneuron* and *Astronium graveolens* are quite abundant in the whole area, and individuals up to 10 m high can be easily found in gaps. The greater wood density of these species (Lorenzi 1992) indicates that they should grow more slowly and that their co-occurrence with the more opportunistic soft-woody species in gaps could be due to their survival, as small-sized individuals, in gap openings.

Floristic patterns associated with plot position on the slope and disturbance were confirmed through Mantel tests and PCA axes correlations with these environmental variables. These patterns probably arise from the responses of several species to the variation of type-1 and 2 variables, although only the most abundant species (which most contributed to the PCA axes) were considered above.

Diversity patterns

We hypothesized a diversity gradient associated with elevation, since elevation could represent a water stress gradient. The results agreed with this hypothesis: richness and H'

were consistently larger in the subcommunity of the less elevated plots than in the one of the more elevated plots, and the contrary happened with dominance (Fig. 3). The rich subcommunity close to the watercourse had 615 individuals and 104 species, whereas the poor subcommunity had 465 individuals and 70 species. In spite of its smaller number of species, the poor subcommunity shelters 15 exclusive species. The dominance in the poor subcommunity ($D_{(300)}$ = 0.19, *CI* = 0.165 – 0.210) was larger than the dominance in the simulated community ($D_{(300)}$ = 0.13, *CI* = 0.110-0.140). This indicates that the increase of dominance in the poor subcommunity is not a simple consequence of a decrease in species richness.

Discussion

Floristic patterns

A partial Mantel test showed a significant correlation between biological and environmental matrices that cannot be entirely attributed to similar spatial structures of the variables considered. This indicates a causal relation between community composition and the environmental type-1 and 2 variables. When variables present positive spatial autocorrelation they can exhibit similar spatial structures and strong correlation, which may be causal or non-causal (Legendre and Legendre 1998). Non-causal correlation may be the result of contagious processes involving the variables analyzed, such as soil water dynamics and plant reproduction; whereas causal correlation may arise when the spatial structure is an intrinsic property of the causal variable. It is possible that the latter case may be applied to the correlation between floristic gradient and position on slope.

Floristic gradient versus position on slope

Considering a single slope, the elevation is by definition a spatially structured variable. So, when taking into account the amount of autocorrelation in the data, the lack of significant correlation between the plot scores on PCA axis 1 and the position on the slope was not a surprise. However, when the autocorrelation is not controlled for, the highly significance of this correlation suggests the existence of an organizing force probably related to type-1 variables. Similar qualitative results were also found by van den Berg and Oliveira-Filho (1999) in a gallery forest in southeastern Brazil. The major floristic pattern in that forest, expressed by the first CCA axis, was significantly correlated with elevation and covaried with type-1 variables. In the present study, 17% of the score variation on the first axis could be explained by relative elevation. Several factors may have contributed to the relatively low explanatory power of position on the slope: 1) soil chemistry, texture and water regime can show complex relations with position on the slope, and the gradients of soil properties may not follow a simple catena (Oliveira-Filho et al. 1997; Sabatier et al. 1997); 2) fertility gradients and pH can themselves be independent of position on the slope (Oliveira-Filho 1994); 3) limitations in the species dispersal capacity can generate aggregated distribution patterns beyond what could be explained by environmental species preferences (Svenning and Skov 2002), making it difficult to detect distribution patterns along shallow gradients (Cannon and Leighton 2004); and 4) dispersal limitation can allow species to win sites by default since competitive superior species may fail to reach all sites favorable to their growth and survival (Hubbell et al. 1999; Condit et al. 2002; Dalling et al. 2002; Obiri and Lawes 2004, Aiba et al. 2004). All these factors may have lessened the power of plot relative elevation to predict variation in the first PCA axis scores (factors 2 to 4 may also have lowered the amount of variance explained by this axis). Factor two may have created floristic gradients expressed in other PCA axis whereas factor four may have introduced stochasticity in the floristic variation.

Floristic gradient versus disturbance

The significant relationship between plot scores on axis 2 and vegetation disturbance, even after taking into account spatial autocorrelation, revealed the existence of an additional organizing force in the community, probably related to type-2 variables. Oliveira-Filho et al. (1998) also reported significant correlation between floristic gradient, expressed by the first axis of a CCA, and a disturbance gradient represented by gap openings in a tropical deciduous forest. In our study, relatively low explanatory power was observed, and only 9% of the score variation in the second axis could be explained by the tallest tree height variation. Several factors may influence the vegetation succession in a site, such as: the surrounding vegetation by means of interspecific interactions, propagule supply, and environmental modification; the seed and seedling bank; the availability of resources; and disturbance levels (Connell 1989; van Hulst 1992). Pioneer species can also partition gaps of different sizes due to seasonal climate-promoted trade-offs (Pearson et al. 2003). These deterministic factors, together with stochastic factors, such as random climatic variability and fluctuations of resources and propagules, and the winning by default chance-factor mediated by dispersal limitation (Connell 1989; van Hulst 1992; Hubbell 1999; Dalling et al. 2002), could have contributed to the low amount of variance explained by PCA axis 2 and the relatively low explanatory power of the tallest tree height per plot on axis 2. According to Obiri and Lawes (2004), except for a few pioneer species, composition of gaps may be largely a chance effect of dispersal and recruitment limitation of the surrounding species pool, so that gap composition can exhibit a great amount of unpredictability.

The results of the Mantel tests and the plot arrangement in the ordination space were expected according to literature on niche assembly community organizing processes. Nevertheless, the great amount of variance that remained unexplained and the low explanatory power of both position on slope and disturbance on floristic gradients could indicate that environmental heterogeneity would contribute little to the observed diversity, in accordance with conclusions of other authors (Leigh 1999; Wright 2002; Leigh et al. 2004; Valencia et al. 2004). The small explanatory power of plot relative elevation and the tallest tree height per plot on the community composition might suggest the necessity of more detailed studies involving a larger number of explanatory variables. However, such studies have already been conducted by other authors and have also left great amounts of variance unexplained (Oliveira-Filho et al. 1997; Oliveira-Filho et al. 1998; van den Berg and Oliveira-Filho 1999). The pervasive noise observed in tropical arboreal vegetation data points out to the importance of stochastic processes, although historical events can also play a role. This importance increases with the reduction of the population size (Shaffer 1981; Hubbell 2001), and most of the tree populations in the Seasonal Semideciduous forests are represented by few individuals (Martins 1993). Stochastic processes related to dispersal limitation seem quite plausible in Ribeirão Cachoeira forest. For instance, 16 out of the 25 most abundant species in the sampling area showed significantly clumped spatial pattern (Cielo-Filho 2001), indicating that seeds produced by these species cannot reach all available sites on the area, since seed rain tends to concentrate around parent trees (Levin et al. 2003). Indeed, in the study area, seedlings of two abundant species, *A. polyneuron* and *E. leiocarpa* (and probably also their seeds), had significantly clumped spatial patterns (Fonseca et al. 2004; A.G. Furtado and F.R. Martins unpubl.).

Diversity patterns and possible related mechanisms of species coexistence

Which processes would contribute to the coexistence of the relatively high number of species observed in the Ribeirão Cachoeira forest? The observed correlation of floristic and diversity gradients with position on the slope does not allow us to immediately discard neutral models of community dynamics (Hubbell 1997; Hubbell 2001; Chave 2004). Species abundance can vary from one point to another in a community under neutral dynamics, so that techniques such as PCA and CCA can extract structure from such community data. It could also be expected that variance distribution among ordination axes deviates from the broken stick model. For instance, dispersal limitation can increase the floristic variation predicted by neutral models (Chave 2004). Condit et al. (2002) showed that a spatially structured neutral model can explain observed decay of similarity in species composition at distances as short as 200 m.

Hubbell’s neutral theory could even predict differences in richness and dominance between the two subcommunities we studied. Since the poor subcommunity is less dense ($t = 3.313$, $Df = 98$, $p = 0.0013$), it could have a smaller fundamental biodiversity number θ (Hubbell 1997; 2001). Considering similar migration rates, the smaller θ would lead to a lower richness and a consequent increase in dominance in the less dense subcommunity (Hubbell 1997; 2001). However, other predictions of Hubbell’s neutral model concerning diversity can qualify the patterns we found as evidence of niche partitioning assembly. For instance, the increase in dominance we observed was above the level expected from the simple decrease in richness. Excess of dominance was called ecological dominance deviation by Hubbell (2001), who argued that it reinforces the importance of niche assembly.

Therefore, diversity and dominance varied along the water stress gradient, represented by the elevation variation, in accordance with the expectancy from the niche assembly perspective. In communities under stress, one or a few ecological resources can have disproportional importance in the determination of species abundance, and species with different competitive abilities in relation to these resources/factors can divide the niche space in a quite hierarchical manner (May 1975). In this case, a decrease in the community niche space would happen, with a consequent reduction in the number of species able to survive in such conditions due to ecophysiological constraints (Grime 1983). Additional reductions in species number would result from competitive exclusion among the remaining species, due to the more hierarchical competitive relationships that would occur among them. On the other hand, in communities of mesic environments, where resources play a similar role in the determination of species abundance, differences in the competitive ability of the species in relation to different resources would allow each species to consume more of the resource that most limits it, and this would result in the co-occurrence of more species and in smaller dominance (Tilman 1982). Given sufficient time, however, such a model would predict monodominance in the subcommunity under water stress, whereas the more humid subcommunity would shelter only as many species as the number of limiting resources it possesses (Tilman 1982; Tilman and Pacala 1993). On the other hand, if species are selected to have different solutions for a competitive trade-off between the ability to exploit water and other limiting resources covarying along the slope, such as light (Leigh et al. 2004), then the resource-ratio hypothesis predicts the co-existence of as many species as the number of complementary competitive trade-off solutions, and change of dominance may occur according to the ratio of resource supply rates (Tilman 1982; Tilman and Pacala 1993).

However, we do not know whether it is possible for as many complementary competitive trade-off solutions as there are species to exist in the Ribeirão Cachoeira forest. Furthermore, the small amount of variance explained by axis 1 and the low explanatory power of relative elevation on axis 1 scores variation indicated that species are not tightly packed along the elevation dimension of the community niche space, as could be expected from the resource-ratio hypothesis. It might not be strictly necessary that all species in Ribeirão Cachoeira forest have found a complementary trade-off solution, that is, a range of ratios of resource supply rates in which each species competitively overcomes all the others, in order to persist in the community (Hurtt and Pacala 1995). For instance, we found evidence that dominant species could respond to habitat heterogeneity and interact under some deterministic model, whereas dispersal limitation could preclude competitively superior species to eliminate other species from their preferential habitats since they would fail to reach all sites favorable to their growth and survival (Hurtt and Pacala 1995; Hubbell et al. 1999). In this case, competitively inferior species could manage to persist in the community by opportunistically winning sites by default.

Practical implications

Ecological restoration constitutes an important action to soften biodiversity loss. Since both deterministic and stochastic processes can play a role in the development of a community, it is necessary to know at which point of the equilibrium–nonequilibrium continuum the focal system is situated (Palmer et al. 1997). Hence, according to Palmer et al. (1997), it is possible to determine the best combination of efforts towards restoration of forest composition (equilibrium communities) *versus* function (nonequilibrium communities). Our study reveals that deterministic processes related to disturbance and position on slope can influence tree species distribution. Therefore, our results point out to the importance of considering deterministic mechanisms of community organization, especially for pioneer and abundant canopy and understory species, in restoration projects. Knowing the demands and ecological tolerances to abiotic factors of these species constitutes the first step in developing models of ecological restoration and the appropriate choice of species to each site. The second step should be to identify the community assembly rules concerning such species (Weiher and Keddy 1995; Wilson 1999), in such a way as to guarantee the choice of appropriated species combinations. The number of abiotic variables to be evaluated constitutes an important aspect in view of the high cost involved in collecting and analyzing these data. Our results showed that position on the slope constitutes an alternative that can reveal useful patterns for the delineation of ecological restoration models.

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Figure legends

Figure 1. (a) location of the Ribeirão Cachoeira forest (RCF) and other remaining forest fragments in Campinas (CA) municipality, São Paulo state, Brazil, adapted from Santin (1999). (b) Ribeirão Cachoeira forest and the location of the 6.5-ha sampling area. (c) sketch showing the hundred 10 x 10-m plots in the Ribeirão Cachoeira forest.

Figure 2. (a) PCA covariance ordination of the 100 plots in the Ribeirão Cachoeira forest. (b) PCA covariance eigenvector diagram showing Elei = *Esenbeckia leiocarpa*, Asel = *Aegiphila sellowiana*, Cflo = *Croton floribundus*, Apol = *Aspidosperma polyneuron*, Agra = *Astronium graveolens*, Mnig = *Metrodorea nigra*, Acom = *Actinostemon communis*, Sdic = *Savia dictyocarpa*, Obeu = *Ocotea beulahiae* and Ubac = *Urera baccifera*.

Figure 3. Average diversity curves and confidence intervals at 95% probability level for different numbers of individuals obtained by resampling two plot sets divided according to their relative elevation on the slope: ♦ = lower plot set; • = upper plot set.

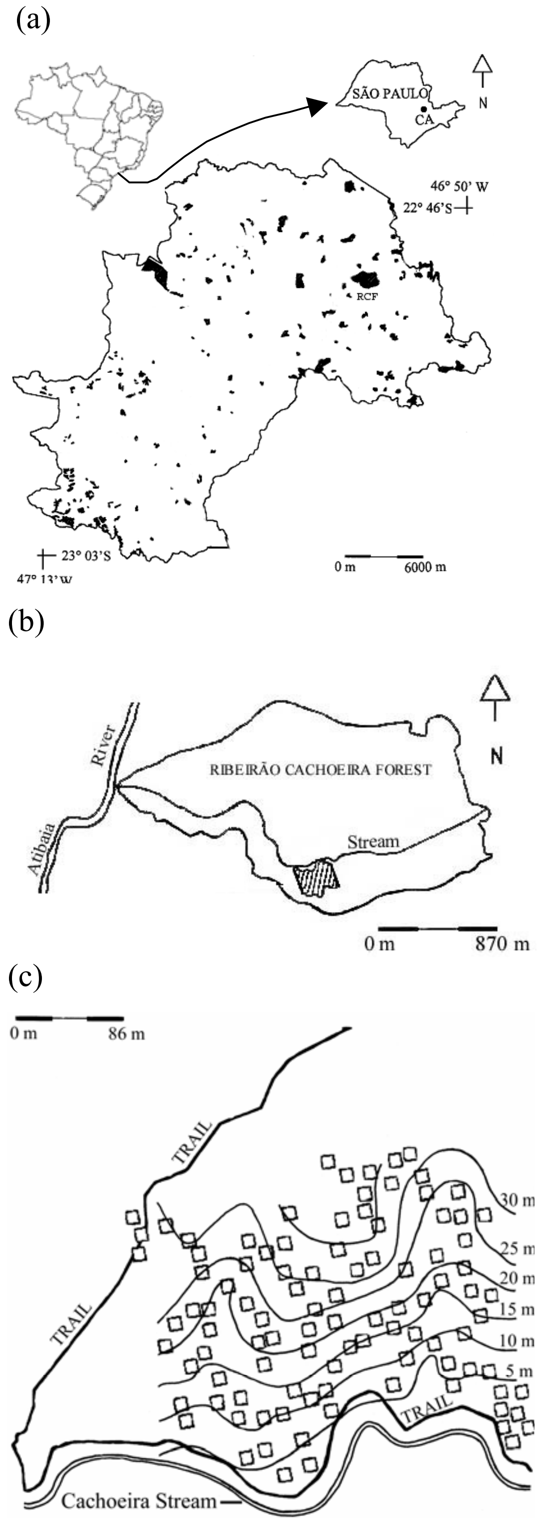
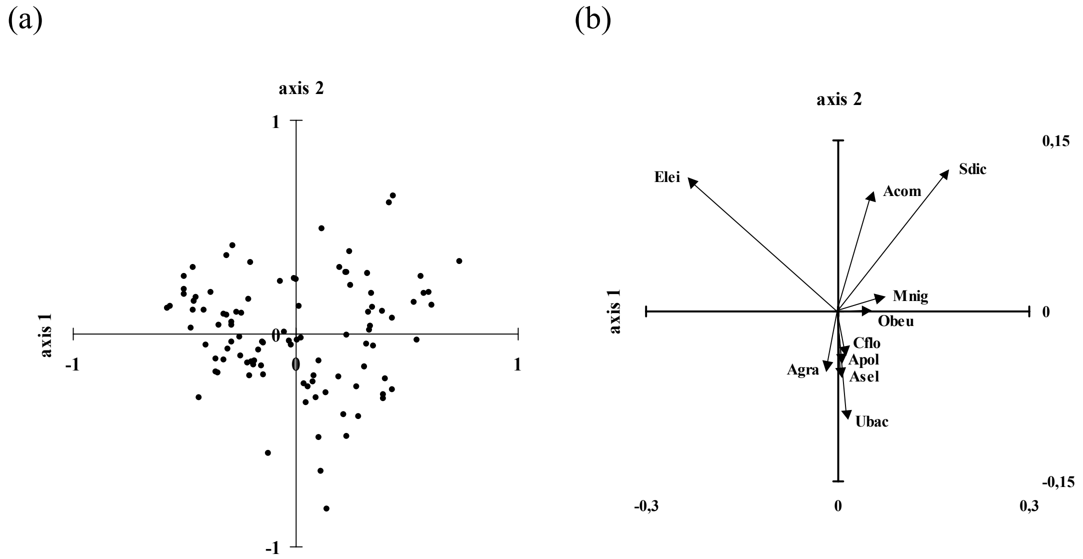

(a)
SÃO PAULO
CA
N
46° 50' W
22° 46'S
RCF
23° 03'S
47° 13' W
0 m
6000 m
(b)
River
Atibaia
RIBEIRÃO CACHOEIRA FOREST
N
Stream
0 m
870 m
(c)
0 m
86 m
TRAIL
TRAIL
TRAIL
TRAIL
30 m
25 m
20 m
15 m
10 m
5 m
Cachoeira Stream

Figure 1.


(a)
axis 2
1
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1
-1
(b)
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0,15
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Ubac
-0,15
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0
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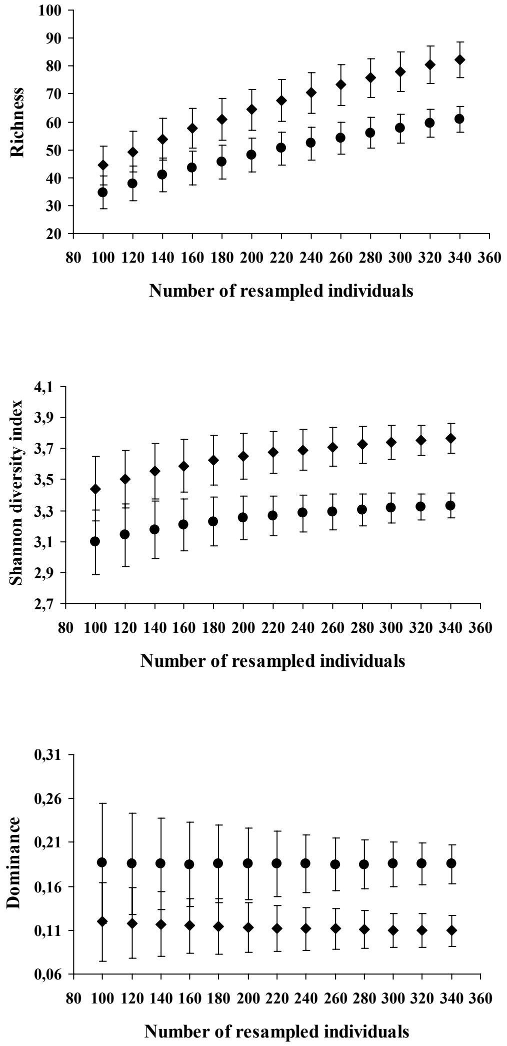
Figure 2.



Richness
100
90
80
70
60
50
40
30
20
80 100 120 140 160 180 200 220 240 260 280 300 320 340 360
Number of resampled individuals
Shannon diversity index
4,1
3,9
3,7
3,5
3,3
3,1
2,9
2,7
80 100 120 140 160 180 200 220 240 260 280 300 320 340 360
Number of resampled individuals
Dominance
0,31
0,26
0,21
0,16
0,11
0,06
80 100 120 140 160 180 200 220 240 260 280 300 320 340 360
Number of resampled individuals

Figure 3.

Table 1. Eigenvalues (λ) of the first two axes of the ordination (PCA-covariance) of 100 sampling units in a Seasonal Semideciduous forest. Var. = variance

Axis	λ	Var. (%)	Accumulated Var. (%)	Broken stick
1	0.10815	13.68	13.68	6.15
2	0.06581	8.33	22.01	4.91

Table 2. Abundant species in Ribeirão Cachoeira forest with eigenvectors greater than the equilibrium contribution and respective abundance.

Family	Species	Number of stems
Rutaceae	*Esenbeckia leiocarpa* Engl.	147
Phyllanthaceae	*Savia dictyocarpa* Müll. Arg.	88
Anacardiaceae	*Astronium graveolens* Jacq.	59
Apocynaceae	*Aspidosperma polyneuron* Müll. Arg.	49
Euphobiaceae	*Actinostemon communis* (Müll. Arg.) Pax	47
Rutaceae	*Metrodorea nigra* A. St.-Hil.	42
Urticaceae	*Urera baccifera* L.	29
Euphorbiaceae	*Croton floribundus* Spreng.	25
Lauraceae	*Ocotea beulahiae* Baitello	22
Lamiaceae	*Aegiphila sellowiana* Cham.	17

Table 3. Correlation between PCA axes 1 and 2 and the two environmental variables relative elevation and the tallest tree height per plot. r = Pearson correlation coefficient, en = effective sample size after Dutilleul's correction, p_1 = probability, p_2 = probability after Dutilleul's correction.

	Relative elevation				Tallest tree height			
PCA axis	r	p_1	en	p_2	r	p_1	en	p_2
1	-0.4097	0.0000	27.85	0.0309	-0.0258	0.7990	82.94	0.8171
2	-0.2380	0.0171	35.17	0.1675	0.2953	0.0029	74.15	0.0106

CAPÍTULO 2

Deterministic local-scale community spatial structure in Semideciduous Atlantic forest

Manuscrito formatado de acordo com as normas da revista *Applied Vegetation Science*.

Tabelas e figuras no final do capítulo.

Deterministic local-scale community spatial structure in Semideciduous Atlantic forest

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Abstract

Question: Can position on slope control species composition in tropical forests at local scales?

Location: São Paulo state, Southeastern Brazil (22º50' S and 46º55' W, 630-760 m a.s.l.).

Methods: In a 6.5-ha sampling area of a Semideciduous Atlantic forest fragment, one hundred 10 x 10 m quadrats were randomly placed on a slope and trees ≥ 5 cm DBH were sampled. PCA axis-1 scores summarized the main gradient of species composition. We used semivariograms and kriging to model spatial dependence of species composition and to investigate the relation between spatial variation of community structure and quadrat position on the slope (elevation). Partial Mantel test was used to evaluate causality of this relationship.

Results: One thousand and eighty trees, belonging to 119 species, were counted. We found close agreement between axis-1 scores and elevation spatial structures. Causal modeling confirmed the causality nature of this relationship through a significant partial Mantel statistic, after common spatial structures have been controlled for.

Conclusions: Our results show that position on slope can control species composition in a Semideciduous Atlantic forest. This suggests that local-scale species composition patterns should be taken into account in tropical forest restoration models.

Keywords: Community organization; Kriging; Niche assembly; Spatial autocorrelation.

Introduction

Vegetation patterns including fine-scale patterns, such as the variation of species composition with altitude, can occur over some kilometers or less (Salis et al. 1995; Torres et al. 1997; van den Berg & Oliveira-Filho 2000). On the other hand, some studies done in Semideciduous Atlantic forests have noticed that even at local scales vegetation can show patterns related to position on slope (Oliveira-Filho 1994; Oliveira-Filho et al. 1997; Cardoso & Schiavini 2002; Martins et al. 2003). If local-scale species abundances are correlated with position along slopes, this relation may be causal or non-causal (Legendre & Legendre 1998) in accordance, respectively, with the niche assembly and dispersal assembly models of community organization (Hubbell 1997, 2001). Spatially structured processes such as, for example, species reproduction and the water dynamics in the soil, can cause positive spatial autocorrelation in variables such as number of individuals and humidity. In this way, spurious correlations between community composition and position on slope can arise from coincidental spatial structures of those variables, and causality can only be attested if some significant relationship between the variables remains after similar spatial structure has been controlled for (Legendre & Legendre 1998). In this case, there is evidence of niche assembly dynamics, that is, species present differences in ecological requirements concerning environmental variables, and local-scale patterns of species composition should also be considered together with landscape and regional patterns in environmental planning and ecological restoration (Palmer et al 1997).

The objectives of this work are: a) to model local-scale spatial structures and to search for similar spatial structures of variables representing species composition and position on slope on a Semideciduous Atlantic forest; and b) to test whether relationship between spatial structures may be considered causal or non-causal.

Methods

Study site and data collection

This work was carried out in the Ribeirão Cachoeira forest, the second largest forest fragment in the municipality of Campinas, Southeast Brazil, with 245 ha (Santin 1999). It is located in the Campinas Environmental Protection Area at the coordinates 22º50' S and 46º55' W (Fig. 1). The fragment is crossed east-west by the Ribeirão Cachoeira stream, a tributary of Atibaia River (Fig. 1). The vegetation may be classified as Seasonal Semideciduous forest due to the prevalence of phanerophytes, climatic seasonality and deciduousness of about 30% of the highest trees during the dry season (IBGE 1992). The climate is Koeppen's Cwa, with a warm, rainy season from October to March, average temperatures between 22 and 24 ºC, and precipitation of 1057 mm; and a dry season from April to September, with average temperatures between 18 and 22 ºC, and precipitation of 325 mm (1961-1990 period, Ortolani et al. 1995). Altitude varies from 630 to 760 m a.s.l.; relief is marked by hills with steepness varying from 12% to more than 45% (Instituto Geológico 1993). Soil is Haplic Lixisol (Prado 2003), with sandy texture and many rock fragments.

The sampling area has 6.5 ha, located in the south portion of the forest fragment, at the left margin of Cachoeira stream (Fig. 1). This area was chosen by examination of an aerial photograph in 1:25 000 scale and visual inspection by walking in the forest. The choice criterion was the range of topography and vegetation physiognomy in order to avoid great declivity variations and the presence of too large gaps. The physiognomic extremes are a few, small gaps and continuous canopy to a height of 15-18 m with emergent trees of up to 30 m. There are no signs of recent anthropogenic disturbances in the area, such as charcoal on the ground surface, soot on trunks, and presence of stumps or coppiced trees. The sampling area is located on a slope of approximately 270 m length with 40 m of difference in the altitudes of the lowest and highest points, and an average steepness of 15% (Fig. 2).

One hundred 10 x 10 m permanent quadrats were allocated in the 6.5-ha sampling area in accordance to the randomization procedure proposed by Greig-Smith (1983). A system of coordinated X-Y axes was used, one being 400 m long (approximately in the E-W direction) and the other 200 m long - imaginary orthogonal straight lines originating along the principal axis, all directed approximately to the South. The northeastern vertex of each quadrat was obtained through the drafting of random X-Y number pairs (Fig. 2). Inside the quadrats, stems $\geq$ 5 cm DBH were tagged, identified, and counted. For all quadrats the same two inclusion and two exclusion sides were defined a priori, and individuals touching the quadrat limit at the inclusion sides were included, and the ones that touched the exclusion sides were excluded. Provisional tree identification was made in the field, based on vegetative and reproductive characters. Tree branches were collected for identification in the laboratory, using literature and comparison with identified material in the State University of Campinas Herbarium (UEC). Specialists confirmed definitive identifications. Voucher material was lodged in UEC collection.

Search for similar spatial structures of species composition and position on slope variables

To investigate spatial structure in species composition and position on slope we computed semi-variances, constructed sample semivariograms and fitted isotropic semivariogram models for variables representing species composition and position on slope (Legendre & Legendre 1998). The position on slope was represented by the elevation of each quadrat in relation to the lowest one. Quadrat elevation was obtained with the aid of a transparent hose almost completely filled with water. We started from the lowest quadrat on the slope and measured the differences of the water column height in each end of the hose, which was positioned in two nearest quadrats. Species composition was represented by axis-1 scores of a PCA applied to a secondary matrix of covariances. This matrix was obtained from the primary data matrix of the 81 species with more than one individual in the sample and the 100 quadrats. Cells of the primary matrix had the number i of individuals of each species per quadrat, and a logarithmic transformation ($\log i + 1$) was applied before calculation of the secondary matrix. *Almeidea lilacina* St.-Hil., an understory Rutaceae tree densely clumped in a few quadrats, was excluded in order to avoid this species dominating the analysis. PCA analysis was performed with the software Fitopac (Shepherd 1996).

The semivariogram models of axis-1 scores and elevation were used to create continuous surfaces of interpolated values of these variables through ordinary kriging

(Isaaks & Srivastava 1989). Thus, surfaces could be visually inspected in order to check for similar spatial structures. The quality of kriged surfaces was evaluated through cross-validation (Legendre & Legendre 1998). The co-variation between axis-1 scores and elevation was also evaluated through a cross-variogram between these variables following a linear model of co-regionalization (Isaaks & Srivastava 1989). A negative cross-variogram indicates that axis-1 scores are negatively related to elevation, and *vice-versa*. The computation of sample and model semivariograms and the construction of continuous surfaces of kriged values for axis-1 scores and elevation were done with the software GS+ (Robertson 2000).

To investigate the relationships between species composition and position on slope we correlated axis-1 scores and elevation distance matrices through simple and partial Mantel tests based on Pearson correlation coefficient (Legendre & Legendre 1998). Partial Mantel test was used to partial out the effect of common spatial structures on the correlation between species composition and position on slope. Axis-1 scores and elevation distance matrices used Euclidian distances computed from the respective data-vector matrix. A matrix of geographic distance among quadrats was computed from a matrix containing quadrat coordinates using Euclidian distance. Monte Carlo permutation test (1000 permutations) was used to evaluate statistical significance of the correlations. R-package software (package vegan) was used to compute distance matrices and to run Mantel tests.

Results

One thousand and eighty individuals belonging to 119 species of tree angiosperms were sampled. PCA axis 1 explained 13.7% of the total variance in the data matrix. This axis represented a floristic gradient in which abundance of species varied continuously among quadrats. The spatial dependency of species composition and position on slope was depicted by semivariograms of axis-1 scores and elevation, respectively (Fig. 3). A spherical model was used to fit semivariogram of axis-1 scores and explained the autocorrelation well, with $r^2 = 0.92$ (Fig. 3a, Table 1). Spatial dependence of axis-1 scores was apparent over a distance (Range) of 96 m. The spatially structured variance ((Sill – Nugget)/Sill) was 38% of the total variance of the data (Sill), thus indicating a relatively high nugget effect and a considerable proportion of the total variance not spatially structured or spatially structured at a scale finer than the sampling interval (Table 1). As expected for a smooth relief, a gaussian model fitted the sample semivariogram of elevation fairly well with $r^2 = 1$ and spatially structured variance of 99.7% (Fig. 3b, Table 1).

The negative cross-variogram showed a negative co-variation of axis-1 scores and elevation (Fig. 3c). A gaussian model fitted the cross-variogram with $r^2 = 0.99$ and spatially structured variance of 98.2% (Table 1). Accordingly, the continuous surfaces of kriged values of axis-1 scores and elevation were similar (Fig. 4). Elevation map (Fig. 4a) showed two valleys and a more elevated region between them, whereas axis-1 scores map (Fig. 4b) depicted a general trend to decrease values with elevation. This trend seems to conform to the relief as showed by the relatively high values of scores in the regions corresponding to the valleys (specially the left valley) and the relatively low values of scores in the central region, which corresponds to the plateau. Cross-validation analysis of these surfaces yielded regression coefficients of 0.866 ($r^2 = 0.19$) for axis-1 scores surface and 0.998 ($r^2 = 0.98$) for elevation surface. These figures indicate that the interpolation method accurately estimated the values for axis-1 scores and for elevation, though not so precisely for the first variable.

This way, we confirmed that species composition along axis 1 and position on slope show similar spatial structures in the studied area. A simple Mantel test also showed the correlation between axis-1 scores and elevation ($r_\mathrm{m} = 0.11$, $p < 0.001$). More interestingly, the partial Mantel test statistics remained significant after common spatial structure has been controlled for ($r_m = 0.09$, $p = 0.002$), thus indicating a causal relationship between species composition and position on slope.

Discussion

The local-scale spatial structure of species composition we found is consistent with the view of vegetation as a fractal, showing patterns at different scales (Palmer 1988). Such structure could be the result of spatially dependent processes, such as, for example, reproduction, without any environmental determinism. This is not the case, however, as indicated by the close agreement between axis-1 scores and elevation spatial structures and confirmed by the significant relationship found between the two variables after the spatial component has been partialled out. Thus, elevation seems to control species composition in the studied area through niche assembly organizing processes. According to the niche assembly model, different species would exhibit different habitat requirements (Leigh 1999; Wright 2002; Leigh et al. 2004). At small scales, species composition patterns have been associated mainly to chemical and physical soil characteristics (Lescure & Boulet 1985; Rodrigues et al. 1989; Oliveira-Filho 1994; Oliveira-Filho et al. 1997; Sabatier et al. 1997; Cardoso & Schiavini 2002; Martins et al. 2003; Valencia et al. 2004). Physical and chemical soil properties, including soil water regime, covary at small scales with elevation (Sollins 1998; van den Berg & Oliveira-Filho 1999). Therefore, the exact environmental correlates determining species composition still need to be elucidated, whereas elevation demonstrated to be a good easy-to-access indicator of potential species composition. These findings clearly show that niche assembly should be considered as part of the theoretical basis for environmental planning and ecological restoration models.

We think it is important to address the hypothesis of niche assembly at different scales and our work tested this hypothesis at a scale smaller than the scales used elsewhere (e.g. Tuomisto et al. 2003; Cannon & Leighton 2004; Valencia et al. 2004). If an ecological relation may be demonstrated to occur at different scales, this can increase the power of generalization of the resulting models. At local scales, stochastic variation in species composition is likely to be high relative to species responses to environmental factors. However, if even at a local scale correlations can be found between environmental and species gradients, then this reinforces the hypothesis of environmental determinism. The other reason to study community organization at local scales is a practical one. Deforested slopes associated with watercourses, such as the one studied here, are very common in tropical world. Restoration efforts in these situations will demand to know whether environmental determinism is shaping the community composition in the landscape units represented by those slopes.

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Table 1. Parameters of semivariogram models fitted to sample semivariograms and cross-variogram of axis 1 scores and elevation, along with their statistics. *SSV* is the spatially structured variance.

Variable	**Model**	**Range (m)**	**Nugget**	**Sill**	***SSV***	r^2
Axis-1 scores	Spherical	96	0.0665	0.1080	0.384	0.915
Elevation	Gaussian	203	0.5	138.8	0.996	1
Axis-1 scores x elevation	Gaussian	152	-0.027	-1.529	0.982	0.993

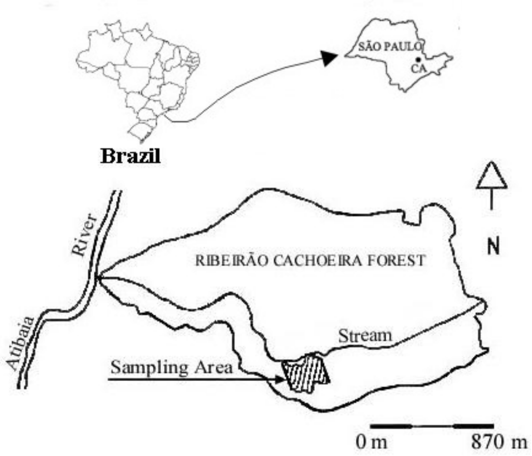


Fig. 1. Location of Campinas municipality (CA), SE Brazil and the 6.5-ha sampling area at Ribeirão Cachoeira forest.

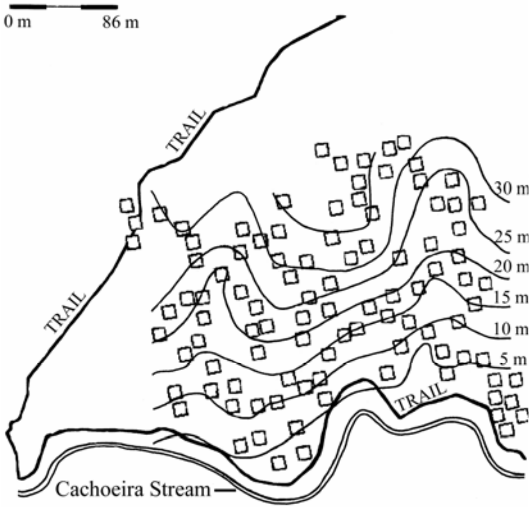


Fig. 2. Diagram showing the sampling design of the 100 10 x 10 m quadrats on a slope at Ribeirão Cachoeira forest.

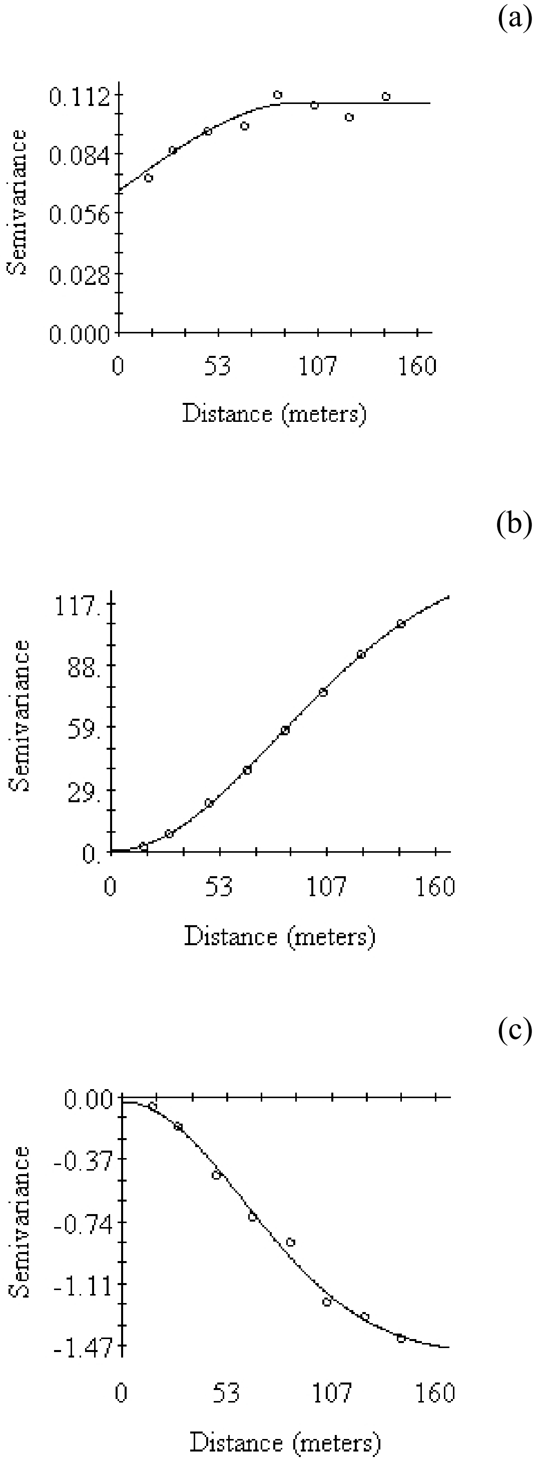
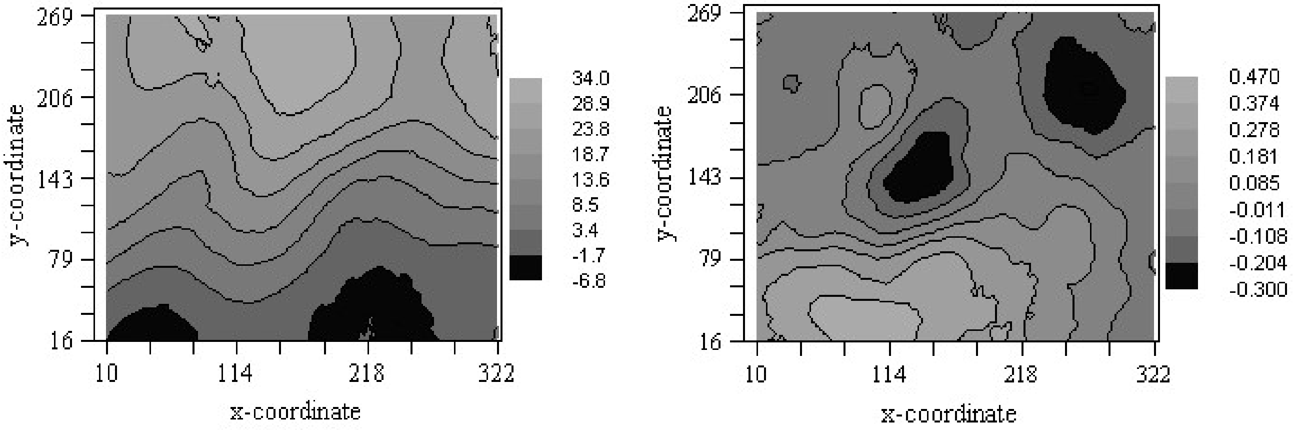


Fig. 3. Sample and fitted semivariograms of (a) axis-1 scores and (b) elevation; (c) cross-variogram between axis-1 scores and elevation.



(a)

(b)

Fig. 4. Continuous surfaces of interpolated (kriged) values of (a) elevation and (b) axis-1 scores.

CAPÍTULO 3

Precision and stability of the tree species abundance rank in Semideciduous Atlantic forest

Manuscrito formatado de acordo com as normas da revista *Community Ecology*.

Tabelas e figuras no final do capítulo.

Precision and stability of the tree species abundance rank in Semideciduous Atlantic forest

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Keywords: Brazil, Phytosociology, Resampling, Tropical forests, Vegetation data.

Abstract: Quantitative vegetation descriptions are usually aimed at comparing different forest samples, correlating the differences with environmental factors, and classifying vegetation. A tentative comparison among forests and between species by mean of visual inspection of the position held by species in abundance ranks is a common feature of quantitative vegetation description studies. Quantitative descriptors are, in general, estimated through sampling, but the estimate’s precision is not taken into account in such comparisons. In this paper we assess the precision and stability of the abundance rank obtained from a sample of 100 10 x 10 m plots randomly placed in a 6.5-ha tropical forest in Southeast Brazil. Parametric and bootstrap confidence intervals were calculated for density, frequency, basal area and the importance value index estimates. A resampling procedure was used to construct simulated abundance ranks for density at different sampling intensities. The simulated ranks were compared with the bootstrap rank and were used to assess the frequency and extent of rank displacement across resampling trials. We found little difference between parametric and bootstrap confidence intervals, which largely overlapped among species considering any one of the above descriptors. Abundance ranks showed high instability for sampling intensities of 25 and 50 plots and all species presented some degree of rank displacement across resampling trials for sampling intensity of 50 plots. Our results highlight the low statistical precision and stability of abundance ranks obtained through sampling in tropical forests and the unreliability of comparisons based on visual inspections of abundance ranks.

Abbreviations: IVI-importance value index.

Nomenclature follows: Judd et al. (2002)

Introduction

In the ancient attempts to classify vegetation, phytogeographers used physiognomic characters as descriptors to construct broad scale classification systems (e.g. Schimper 1903). Phytosociology arose as a natural legacy of phytogeography due to the need of finer scale classification systems (Mueller-Dombois and Ellenberg 1974, Anderson and Kikkawa 1986). The main phytosociological school developed in Europe was Braun-Blanquet's, which uses, as vegetation descriptors, the floristic composition and the species abundance on a semi quantitative scale combining coverage and density (Braun-Blanquet 1979).

In the past, due to difficulties in the analyses, the different schools of phytosociology had only marginal interest in quantitative descriptors (Mucina 1997). The application of numerical methods of analysis (Classification and Ordination) encouraged the use of quantitative data and promoted the development of new approaches in ecological studies of plant communities. This contributed to a better understanding of the structure and dynamics of the vegetation and impelled the theoretical development of community ecology (Fisher and Bemmerlein 1989). The main quantitative descriptors of the arboreal vegetation have been density, frequency, basal area, and the sum of their relative values, that is, the importance value index (IVI), commonly called phytosociological parameters (Curtis and McIntosh 1950, 1951, Mueller-Dombois and Ellenberg 1974).

In Brazil, numerical techniques had contributed to a more precise determination of plant formation geographical limits and allowed the formulation of working hypotheses on the factors and processes determining communities spatial distribution (Silva and Shepherd 1986, Salis et al. 1995, Torres et al. 1997, Pinder and Rosso 1998, Castro and Martins

1999, Ivanauskas et al. 2000, Oliveira-Filho and Fontes 2000, Oliveira and Nelson 2001, Scudeller et al. 2001, Ratter et al. 2003, Durigan et al. 2003, Oliveira 2006). Most of these phytosociological analyses applied multivariate analysis to matrices of binary data (presence or absence of species). Recently, some phytosociological analyses have applied numerical methods to matrices of quantitative data (Araújo et al. 1999, van den Berg and Oliveira-Filho 2000, Scudeller et al. 2001, Oliveira 2006). Such vegetation surveys require the quantitative description of several forests in a time-consuming collective effort involving many independent researches.

A common feature observed in those researches is the tentative comparison among different forests and between different species within the same forest through the visual inspection of the position held by species in an abundance rank. The abundance rank might be graphically represented plotting the species on the x-axis from the most abundant to the rarest, while the y-axis shows the abundance of each species. Quantitative descriptors are generally estimated by vegetation sampling, but such comparisons have not taken into account the consequences implied in vegetation description by estimating statistical parameters. Vegetation sampling cannot give us the real values of descriptors, but only its estimated values. If we repeat the same random sampling procedure several times, the estimated values will vary each time due to the interaction of random variation in the position of sampling units and the natural heterogeneity of vegetation. The lower the variation of estimated values across sampling trials, the greater would be the precision of a given estimated value. That stability of estimates may be reached by increasing sample size (Greig-Smith 1983, Pillar 1998). As sample size increases, the whole abundance rank also becomes more stable meaning that each species tend to hold the same position from one rank to another. However, it is not necessary to repeat the same sampling procedure several times to assess the precision of estimated values nor the stability of the abundance rank, since statistical inference and resampling techniques can be used to achieve that task. These statistical procedures are discussed in several textbooks (Greig-Smith 1983, Causton 1988, Dixon 1993, Hayek and Buzas 1997, Krebs 1999, Sokal and Rohlf 1999, Zar 1999), but attempts to gather and to apply them to phytosociological parameters are still lacking.

Considering a random sample taken from a tropical forest area, the objectives of this paper are: 1. To assess the precision and stability of the abundance rank gathered in a quantitative vegetation description research. 2. To evaluate the implications of the estimate precision and of the rank stability in investigation of variations within or among forests through the visual inspection of abundance ranks.

Materials and methods

Study site

This work was carried out in the Ribeirão Cachoeira forest, a 245-ha forest fragment located in the Environmental Protection Area of the municipality of Campinas, São Paulo state, at the coordinates 46º55' W and 22º50' S (Santin 1999). The regional climate is Koeppen’s Cwa, with a hot rainy season from October to March, with average temperatures between 22 ºC and 24 ºC and precipitation of 1057 mm; and a dry season from April to September, with average temperatures between 18 ºC and 22 ºC and precipitation of 325 mm (Ortolani et al. 1995). Altitude varies from 630 to 760 m above sea level, the relief is hilly with steepness varying from 12% to more than 45% (Instituto Geológico 1993). Soil is Haplic Lixisol (Prado 2003), with sandy texture and many rock fragments. The forest is crossed in the east-west direction by Cachoeira stream, a tributary of Atibaia River (**Fig. 1a**). The vegetation may be classified as Seasonal Semideciduous forest due to the prevalence of phanerophytes, climatic seasonality, and deciduousness observed in about 30% of the highest trees during the dry season (IBGE 1992).

The sampling area has 6.5 ha and is located in the southern portion of the forest, at the left margin of Cachoeira stream (Fig. 1a). It was selected with aid of an aerial photograph in 1:25,000 scale, and by walking in its interior. In choosing this area, we avoided great declivity variations and the presence of too large gaps. The vegetation of this area has a few small gaps as one physiognomical extreme and continuous canopy 15 to 18 m high with emergent trees of up to 30 m as the other. There are no signs of recent anthropogenic disturbances in the area, such as charcoal on the ground surface, soot on trunks, and presence of stumps or coppiced trees. The sampling area is located on a slope of approximately 270 m length with average steepness of 15%. The boundary of the sampling area at its lower portion corresponds to a trail alongside the Cachoeira stream, and does not undergo periodic flooding (**Fig. 1b**).

Sampling procedure

The sampling was made by the multiple plot method, with the plots arranged in accordance to the unrestricted randomization procedure (Greig-Smith 1983). A system of coordinated axes was used, one with 400 m length (the X axis, following the trail along

Cachoeira stream, approximately in the E-W direction) and the others with 200 m length (the Y axes, imaginary straight lines originating from the principal axis, all directed approximately to the South). The coordinates of each plot northeastern vertex were obtained by the drafting of random X-Y number pairs (Fig. 1b). A hundred 10 x 10 m plots were installed, with vertices demarcated by permanent PVC pipe stakes.

We sampled trees with trunk perimeter at 1.3 m above the soil, or breast height (PBH), ≥ 15.5 cm. We recorded the PBH and tagged each tree. Trees with multiple trunks were recorded, provided that at least one of the trunks had PBH ≥ 15.5 cm, and in this case all trunks were measured. We established *a priori* two inclusion and two exclusion sides for each plot: all individuals that touched the plot limit line at the inclusion sides were included in the sample, and those that touched the exclusion sides were excluded. Calculations of quantitative descriptors followed Mueller-Dombois and Ellenberg (1974). Provisional tree identification to species was made in the field, based on vegetative and reproductive characters. Vouchers in reproductive period were collected for identification in the laboratory by mean of identification keys and comparison with material lodged in the State University of Campinas Herbarium. Specialists confirmed definitive identifications.

Assessing the precision of the abundance rank

The precision of the estimates of species density, frequency, basal area, and IVI was obtained by calculating confidence intervals at a 95% probability level (Hayek and Buzas 1997, Zar 1999). These calculations took the *t*-Student distribution as the reference distribution (Hayek and Buzas 1997). The theoretical basis to use *t* distribution as reference in large sample sizes when setting confidence intervals comes from the Tchebycheff´s Inequality, Weak Law of Large Numbers, Central Limit Theorem and Slutzky´s Theorem (James 1981, Hayek and Buzas 1997). It is known that the mean of the distribution of the sample means equals the population mean and also that the mean of the distribution of the sample variances is the population variance. It is possible to demonstrate that the variances of both sample attributes – mean and variance – tend to zero when the sample size tends to infinity. As a consequence of these facts, by means of Tchebycheff´s Inequality and Weak Law of Large Numbers (Appendix 1), if the sample size is large enough, the sample mean and the sample variance are arbitrarily close to the population mean and variance, respectively, with arbitrarily high probability (Hayek and Buzas 1997, Sokal and Rohlf 1999, Zar 1999).

Furthermore, the Central Limit Theorem states that the distribution of the sample mean will tend to normality as sample size increases whichever the population distribution be (Morettin and Bussab 2004). Thus, by the Central Limit Theorem, the Weak Law of Large Numbers and Slutzky´s Theorem (Appendix 2), if the sample size is large enough it is possible to estimate a confidence interval from the Normal (*z*) distribution for the sample mean at a given confidence level using the square root of the sample variance divided by the sample size *n*, that is, the standard error of the mean. On the other hand, when sample size is not large enough, the standardized distribution of the sample mean will deviate from *z* and approximate the *t* distribution with *n*-1 degrees of freedom, and a shift of reference distribution from *z* to *t* is then required (Hayek and Buzas 1997). However, with small sample size (say less than 30), the reliability of the approximation of *t* distribution, as well as of the estimation of the distribution of the sample mean standard deviation from the estimated standard error of the mean, relies on the normality of the population distribution (Sokal and Rohlf 1999). Examining our data we saw reasons to reject normality for density (frequency histograms not shown here), especially for the less abundant species. In this case, distributions tend to Poisson and Negative Binomial for species with random and contagious distribution, respectively (Greig-Smith 1983, Krebs 1999). As these distributions approximate normality as the mean increases (Greig-Smith 1983), we arbitrarily defined a minimum number of ten individuals and set confidence intervals for estimated means (for density and other descriptors) of species that attained this criterion.

To calculate standard error and parametric confidence intervals of the different descriptor estimates, we follow the procedures described in (Zar 1999). For each species we estimated the averages of density, frequency, basal area and IVI. Then, we calculated variance, standard error and the 95% confidence intervals of these averages. All calculations considered the plot as the sampling unit, that is, the unit area of 100 m^2. To calculate the IVI average and variance, we used the method of fragmented relative values (Morais and Scheuber 1997), in which the IVI of each species in a plot is composed of the sum of its relative fragmented values for density, basal area and frequency in this plot. The relative fragmented density of a species in a plot is the ratio of the number of individuals of the species in that plot to the number of individuals of all species in all plots; the relative fragmented dominance of a species in a plot is the ratio of the species basal area in that plot to the total basal area in all plots; and the relative fragmented frequency of a species in a plot is the species presence or absence in that plot (1 or 0, respectively), divided by the sum of presences of all species in all plots (Morais and Scheuber 1997).

The analysis of the confidence intervals of abundance estimates for more-than-ten-individuals species was enough to evaluate the precision of the abundance rank. However, concerning the need of normality, Greig-Smith (1983) considerations would lead to the use of rather more abundant species, and Cochran (1977) third moment-based recommendation would allow confidence interval calculations for too few species. Aware that our decision could not be enough to control for lack of normality, we also estimated averages and confidence intervals through bootstrap resampling (Efron 1979, Efron and Tibshirani 1993, Dixon 1993, Pillar 1998). Bootstrap resampling allows estimating confidence intervals through bootstrap percentiles without assuming normality (Dixon 1993) based on the principle that, without better information, resampling from the sample could provide the best information about the population distribution (Efron 1979). Bootstrap percentiles confidence intervals were calculated through 10,000 iterations for each species using the software Multiv (Pillar 2006). Details on the algorithm of bootstrap resampling can be found in Efron (1979), Efron and Tibshirani (1993), Dixon (1993) and Pillar (1998). All the averages and confidence intervals were given in a 1-ha basis through the multiplication of the respective values by the factor 100. The results were plotted in graphics to allow visual inspection of the confidence interval overlaps.

Assessing the stability of the abundance rank

To assess the stability of abundance rank we used resampling without replacement to construct simulated abundance ranks for species density at different sampling intensities ($n = 25$, $n = 50$ and $n = 75$). For each sampling intensity, the plots were chosen at random from the entire sample of a hundred plots resulting in sub-samples of 25, 50 or 75 plots. From these sub-samples we calculated simulated abundance ranks for each species with 10 or more individuals in the sample. Because resampling was without replacement, each plot was allowed to integrate the sub-sample only once. This procedure is recommended when the sampling universe can be considered large enough for successive plot removals do not produce significantly changes in species proportions. For each sampling intensity ($n = 25$, $n = 50$ and $n = 75$) we obtained thirty sub-samples and calculated the respective simulated abundance rank. The simulated ranks were plotted in a graph along with a bootstrap rank obtained through bootstrap resampling (sampling intensity $n = 100$ plots, 10,000 iterations). The stability of the abundance rank could then be evaluated by comparing the simulated ranks with the reference bootstrap rank. Furthermore, we simulated 10,000 abundance ranks for $n = 50$ through bootstrap resampling and computed, for each simulated rank, the number of rank position displacements of each species in relation to the reference rank: sampling intensity $n = 100$ plots, 10,000 iterations. Then, for each species, we plotted, in a frequency histogram, the percentage of each class of rank displacement starting from the lower limit of rank displacement for that species; …; -3; -2; -1; 0; 1; 2; 3; …; until the upper limit. A negative number of positions displaced means that the species dropped in the simulated rank whereas a positive number means ascension of the species in the simulated rank. Zero means no displacement. In mathematical terms, number of rank displacements = position occupied in the reference rank – position occupied in the simulated rank. These histograms allowed us to assess the stability of the abundance rank and the contribution of each species to the lack of stability. Through bootstrap percentiles, applied to the vector of number of rank displacement, it was also possible to determine the amplitude of rank displacement of each species at a probability level of 10%. This amplitude shows the rank position limits that a species could reach in a given sample with n = 50 random plots with a probability of 10%. Simulated abundance ranks were obtained through resampling with and without replacement by the software RDSA (Martins and Cielo-Filho 2007) and EcoSim700 (Gotelli and Entsminger 2001), respectively.

Results

Precision of the abundance rank

One thousand and eighty live individuals comprising 119 species were sampled. Twenty four species had ten or more individuals (**Table 1**), and for these species confidence intervals were calculated. As expected, the bootstrap percentile confidence intervals were not symmetrical around the averages. Differences between bootstrap percentile and parametric solution confidence intervals were greater in the upper limits. There was also a general trend of bootstrap percentile upper limits to be greater than those of the parametric solution. Bias and skewness in bootstrap resampling are discussed by Dixon (1993). However, averages and confidence intervals obtained through bootstrap resampling and parametric solution presented little differences, and so were joint-analyzed in a conservative manner.

Esenbeckia leiocarpa was the species with highest abundance in the sampling area, being the only one that could confidently be distinguished from all others in the abundance rank. Confidence intervals of IVI and frequency estimates for this species did not overlap with the intervals of the other species, and the overlaps of confidence intervals for density and basal area were very small (**Fig. 2**). The species invariably following *E. leiocarpa* in the abundance rank were *Savia dictyocarpa*, *Astronium graveolens* and *Aspidosperma polyneuron*. The lowest limits of these species overlapped with the confidence intervals of 11 species for density, eight species for IVI and basal area, and four species for frequency, thus indicating that, especially for density, there is a great amount of uncertainty in considering the three species after *E. leiocarpa* as the most abundant in the forest (Fig. 2). It can also be concluded from the observation of the confidence interval overlaps that, except for *E. leiocarpa*, there is little sense in stating the exact rank position for any one species based on the visual inspection of the abundance rank.

Stability of the abundance rank

If we repeat the same random sampling procedure, it would be possible to obtain very different abundance ranks, especially for the lower sampling intensities of n = 25 and n = 50 (**Fig. 3**). For example, we can obtain abundance ranks in which *Almeidea lilacina* could occupy rank positions as different as the 3rd and the 21th most abundant species for n = 50, whereas it cannot even being present in ranks for n = 25 (Fig. 3). That amplitude of rank position displacement is not probabilistic and one can argue that it could rarely occur. However, it can be seen in Table 1 that, if we repeat the same random sampling procedure with n = 50 plots, *A. lilacina* may occupy rank positions as different as the 3rd and the 33th most abundant species for 10% of the time. Rank displacement of several positions is not an uncommon event for *A. lilacina* as can be seen in the frequency histogram of rank displacement (**Fig. 4**). Comparable with that species concerning variability of rank position are *Aegiphila sellowiana*, *Jacaratia spinosa* and *Rudgea jasminoides* (Fig. 4). These species also showed the greatest amplitude of rank position displacement, from the 5º to the 86º, from the 12º to the 60º and from the 15º to the 57º position, respectively (Table 1). Together, these four species contributed with a great portion of the instability of the abundance rank. For these species, spatial clumping at the 100 m^2 scale greatly decreased the precision of density estimates (R. Cielo-Filho, M.A. Gneri and F.R. Martins unpubl.) resulting in the low stability of the estimated values across resampling trials. However, all species showed some degree of rank displacement and there was no simulated rank equaling the bootstrap rank across the 10,000 resampling trials. In general, the frequency and extent of rank displacement increased towards the least abundant species (Fig. 4, Table 1). Accordingly, a positive relationship between the abundance and estimate precision was reported for these species (R. Cielo-Filho, M.A. Gneri and F.R. Martins unpubl.). *Esenbeckia leiocarpa* shows the greater stability (Fig. 4, Table 1) confirming the relation between stability and precision and the numerical dominance of this species in the forest.

In summary, quite different abundance ranks were found. Rank instability is very high with sampling intensity of $n = 25$ and remains quite high with $n = 50$. Only with $n = 75$ the abundance rank reached a reasonable level of stability. Sampling procedures applying less than 50 10 x 10 m-plots are not uncommon in quantitative vegetation descriptions of Atlantic forests (A. Caiafa and F.R. Martins unpubl.).

Discussion

In mega diverse countries, such as Brazil (Mittermeier et al. 1997), phytosociology may be an important tool for biodiversity conservation (Schaminée and Stortelder 1996, Pinder and Rosso 1998, Burke 2001, Zak and Cabido 2002, Ewald 2003, Biondi et al. 2004). Due to the continuous nature of vegetation, phytosociological units (syntaxa) must be delimited in a syntaxonomical space, in an analogous manner as species are delimited in a taxonomical space, through relative morphological differences and similarities (Mirkin 1989). Since continuity at smaller scales arises from individual species responses to environmental gradients that may manifest as abundance variation (Whittaker 1975), the syntaxonomical space would be defined by quantitative variation of species. This will be true even considering the restrictions that phytocoenoses impose on species individualistic performances (Moravec 1989). Thus, abundance structure remains as the most suitable attribute for forest descriptions with finer scale classification purposes.

Analysis and interpretation of quantitative vegetation data

A considerable portion of studies describing the abundance structure of forests has dealt with the ecological relationships among the species based on their position in a decreasing abundance rank. Thus, the abundance rank has been used to point out the species phytosociological importance in the forest. It has also been used to evaluate structural variation among forests through the comparison of the species position in the abundance rank, the observed differences being associated with particular environmental conditions. However, such procedures deserve some criticism. For instance, numerical dominance is a recurrent phenomenon in tropical forests, but given the long and complex gradients observed in these forests (Scudeller et al. 2001) associated with several environmental factors, it is unlikely that such approach reveals detailed and accurate patterns. In fact, the detection of numerical dominance patterns and related environmental variables relies on the use of more powerful analytical methods applied to numerous and well distributed forest samples. Furthermore, caution is needed in ecological interpretations of numerical dominance because it does not necessarily comes from ecological dominance, that is, the species that most affects presence and performance of the others and is less affected by them (Greig-Smith 1986). The correspondence between numerical and ecological dominance relies on the relative importance of bottom-up *versus* top-down mechanisms of plant community regulation (Pace et al. 1999). If the bottom-up mechanisms have greater relative importance, competition for nutrients, light and water greatly determines the biomass distribution among species and those with greater competitive ability will have higher abundances. In this case there will be agreement between numerical and ecological dominance. On the other hand, species abundance can also be regulated by herbivores (top-down mechanisms), favoring species with smaller competitive ability but with larger investment in defenses against herbivory (Terborgh et al. 2001). In tropical forests there is evidence suggesting that both types of mechanism may play a role (Rao et al. 2001, Terborgh et al. 2001). Thus, the abundance rank does not necessarily reflect the ecological relations among species.

The reliability of the few inferences resulting from visual inspection of abundance ranks can be jeopardized when the rank precision and stability are taken into account. In this study, except for *Esenbeckia leiocarpa*, it was not possible to distinguish among positions of species occupying the same region of the bootstrap abundance rank for n = 100. Furthermore, very different abundance ranks could have been obtained with less sampling intensity for the same forest. Considering the low statistical precision and stability of the abundance rank, subjective comparisons among forests based on visual inspection of the abundance rank would only be valid when they involve species occupying extreme regions in the abundance distribution curve, say the most abundant *versus* the rare species. The importance of these comparisons to detect patterns relies on the extent of the numerical responses of species to varying environmental factors. If the responses of species to environmental variation were enough to place them in different extremes of the rank in different forests, patterns could be described through visual inspection. However, this condition would hardly be satisfied at the finer scales in which the use of quantitative vegetation data would be required for pattern detection.

Finally, we should emphasize the strong dependency of the results reported here on the scale adopted in the sampling procedure. The choice of 10 x 10 m sampling units implies in a great amount of between plots variance (Greig-Smith 1983). In spite of this, because of practical constraints, the multiple plot method using 10 x 10 m plots is widely used in quantitative descriptions of tropical forests (Martins 1993). Furthermore, the plot size adopted here must be viewed in the context of the highly fragmented landscapes found today in the geographic range area of the Semideciduous Atlantic forest (Viana and Tabanez 1996, Viana et al. 1997, Oliveira-Filho and Fontes 2000). For instance, in the 800-km^2 region of the Campinas municipality, more than 50% of the remaining vegetation fragments have less than 10 ha (Santin 1999). Since sampling designs will generally avoid edges, the available sampling universe free from edge effects in those forest fragments will be something smaller than 10 ha (Laurance et al. 1998). Therefore, the small sampling universes available impose an upper limit in the amount of data that can be collected. Under such circumstances, the use of a greater number of smaller plots (larger *n*) will have a desirable impact on the standard error of the mean, as defined by $s_{\bar{x}} = \left(s^2/n\right)^{0.5}$, leading to a greater precision of parameter estimates (Kenkel et al. 1989). Furthermore, small sampling unit area is preferable in forest typification because it maximizes variation among plots allowing a better discrimination between vegetation types and, in a second stage, allows joining plots of each forest type at each sampling location in order to increase precision of vegetation type estimates (Kenkel et al. 1989). It is important to note that, despite their small areas, Semideciduous Atlantic forest remnants constitute a significant source of the information required to investigate patterns and processes at several scales in this forest type. Therefore, conservation and quantitative description of those forest fragments must be highly encouraged.

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Appendix 1

The Tchebycheff´s Inequality

In the following we give two equivalent versions of a classical result known as Tchebycheff´s Inequality.

1st Version: Let X be a random variable such that $E(X) = \mu$ and $0 < \sigma^2 = Var(X) < \infty$.

Let t>0. Then:

Probability $(\{|X-\mu| \geq t \times \sigma\}) \leq 1/t^2$,

where μ denotes Mean(X).

2nd Version: Let X be a random variable such that $E(X) = \mu$ and $0 < \sigma^2 = Var(X) < \infty$.

Let ε>0. Then:

Probability $(\{|X-\mu| \geq \varepsilon\}) \leq \sigma^2 / \varepsilon^2$.

Observation 1. This result provides upper bounds to the probability of the tails of the distributions or equivalently, lower bounds to the concentration of the distribution in some neighborhoods of the mean.

Observation 2. The first version gives useful information only if $t > 1$ and the second one only if $\varepsilon > \sigma$.

The weak law of large numbers and some consequences

Let X be a random variable such that $0 < \sigma^2 = \text{Variance}(X) < \infty$. Let μ denote Mean(X). Consider a simple random sample of the random variable X and denote by $\bar{x}$ the sample mean. It is well known that:

Mean $(\bar{x}) = \mu$ and Variance $(\bar{x}) = n^{-1} \times \sigma^2$

Let ε be any strictly positive number. Then, if we apply the Tchebycheff′s Inequality to the random variable $\bar{x}$, we obtain:

Probability $(\{|\bar{x} - \mu| \geq \varepsilon\}) \leq \sigma^2/(n \times \varepsilon^2)$.

Then we have the Weak Law of Large Numbers:

$\lim_{n\to\infty}$ Probability ($\{|\bar{x} - \mu| \geq \varepsilon\}$) = 0*.

Let $s^2 = \frac{\sum_{i=1}^{n}\left(x_i - \bar{x}\right)^2}{n-1}$ be the sample variance. If Mean $(X-\mu)^4 < \infty$, it is known that (see Mood et al. 1974):

Mean $(s^2) = \sigma^2$

and that:

Variance $(s^2) = n^{-1} \times [\text{Mean } (X-\mu)^4 - (n-3) \times \sigma^4/(n-1)]$

In an analogous way as in the case of $\bar{x}$ - by means of Tchebycheff′s Inequality – it is possible to show that:

$\lim_{n\to\infty}$ Probability ($\{|s^2 - \sigma^2| \geq \varepsilon\}$) = 0 for all strictly positive ε

and also:

$\lim_{n\to\infty}$ Probability ($\{|s/\sigma - 1| \geq \varepsilon\}$) = 0 for all strictly positive ε. (1)

Appendix 2

The limit distribution of $n^{1/2} \times (\bar{x} - \mu)/s$

The Central Limit Theorem states that the distribution of the sample mean tends to normality as sample size tends to infinity whichever the population distribution be. That is, we have:

the distribution of $n^{1/2} \times (\bar{x} - \mu)/\sigma$ tends to Normal(0,1). (2)

Slutzky´s Theorem states that:

If the distribution of U_n tends to some limit distribution U and the random variable V_n satisfies

$\lim_{n\to\infty}$ Probability($\{|V_n - c| \geq \varepsilon\}$) = 0 for all strictly positive number ε

(where c is a constant, $c \neq 0$), then: the distribution of U_n / V_n tends to the distribution of U/c. Now, applying Slutzky´s Theorem (see James 1981) to (1) and (2) and the central limit theorem we can assert that the distribution of

$$n^{1/2} \times (\bar{x} - \mu) / s = n^{1/2}\left(\frac{\bar{x} - \mu}{\sigma}\right) / (s / \sigma)$$

tends to Normal (0,1) as n tends to infinity.

The primitive version of this result, known as weak law of large numbers, is due to Jacques Bernoulli (Bernoulli 1713). His proof was not so simple because Tchebycheff´s Inequality was stated after 1850.

Table 1. Species with ten or more individuals found in a 6.5-ha sampling area of Ribeirão Cachoeira forest, in decreasing order for density (individuals/ha). PRR = position in the reference rank; ARD$_{(10\%)}$ = amplitude of rank displacement at a probability level of 10%.

Density	**Family**	**Species**	PRR	ARD$_{(10\%)}$
147	Rutaceae	*Esenbeckia leiocarpa* Engl.	1º	1º - 1º
88	Phyllanthaceae	*Savia dictyocarpa* Müll. Arg.	2º	1º - 4º
59	Anacardiaceae	*Astronium graveolens* Jacq.	3º	2º - 7º
49	Apocynaceae	*Aspidosperma polyneuron* Müll. Arg.	4º	3º - 9º
47	Euphorbiaceae	*Actinostemon communis* (Müll. Arg.) Pax	5º	3º - 12º
44	Meliaceae	*Trichilia catigua* A. Juss.	6º	3º - 11º
42	Rutaceae	*Metrodorea nigra* A. St.-Hil.	7º	4º - 11º
37	Rutaceae	*Almeidea lilacina* A. St.-Hil.	8º	3º - 33º
34	Fabaceae	*Holocalyx balansae* Micheli	9º	5º - 15º
30	Rutaceae	*Galipea multiflora* Schult.	10º	5º - 19º
29	Urticaceae	*Urera baccifera* (L.) Gaudich. ex Wedd.	11º	4º - 22º
25	Euphorbiaceae	*Croton floribundus* Spreng	12º	7º - 19º
24	Meliaceae	*Trichilia claussenii* C. DC.	13º	7º - 24º
23	Apocynaceae	*Aspidosperma ramiflorum* Müll. Arg.	14º	7º - 24º
22	Lauraceae	*Ocotea beulahiae* Baitello	15º	9º - 23º
20	Myrtaceae	*Myrciaria floribunda* (West ex Willd) O.Berg.	16º	9º - 25º
17	Lamiaceae	*Aegiphila sellowiana* Cham.	17º	5º - 86º
15	Euphorbiaceae	*Sebastiania edwalliana* Pax & Hoffm.	18º	12º - 30º

Table 1. Continued

Density	**Family**	**Species**	PRR	RDA$_{(10\%)}$
15	Phytolaccaceae	*Seguieria langsdorffii* Moq.	19º	12º - 31º
14	Myrsinaceae	*Rapanea balansae* Mez	20º	13º - 34º
13	Moraceae	*Brosimum glaziovii* Taub.	21º	13º - 38º
12	Lauraceae	*Ocotea indecora* (Schott) Mez	22º	14º - 41º
11	Caricaceae	*Jacaratia spinosa* (Aubl.) A. DC.	23º	12º - 60º
10	Rubiaceae	*Rudgea jasminoides* (Cham.) Müll. Arg.	24º	15º - 57º

Figure captions

Fig. 1. Location of the 6.5-ha sampling area at Ribeirão Cachoeira forest, Campinas, São Paulo, Brazil (a). Diagram showing the sampling design of the 100 10 m x 10 m-plots used to describe a 6.5-ha sampling area at Ribeirão Cachoeira forest (b).

Fig. 2. Estimated averages and confidence intervals for IVI, frequency, density and basal area (95% probability level) of species with 10 or more individuals sampled in a 6.5-ha sampling area at Ribeirão Cachoeira forest, Campinas, São Paulo, Brazil.

Fig. 3. Abundance ranks obtained through resampling without replacement (number o trials = 30), at three sampling intensities (*n* = 25, 50, 75), from the 100 10 x 10 m-plots and for species with 10 or more individuals in a 6.5-ha sampling area at Ribeirão Cachoeira forest. The thick line shows the reference bootstrap abundance rank (see text for details).

Fig. 4. Frequency histograms of rank displacement in relation to the reference rank, after 10,000 resampling trials with replacement (*n* = 50) of the 100 10 x 10 m-plots and for species with 10 or more individuals in a 6.5-ha sampling area at Ribeirão Cachoeira forest.

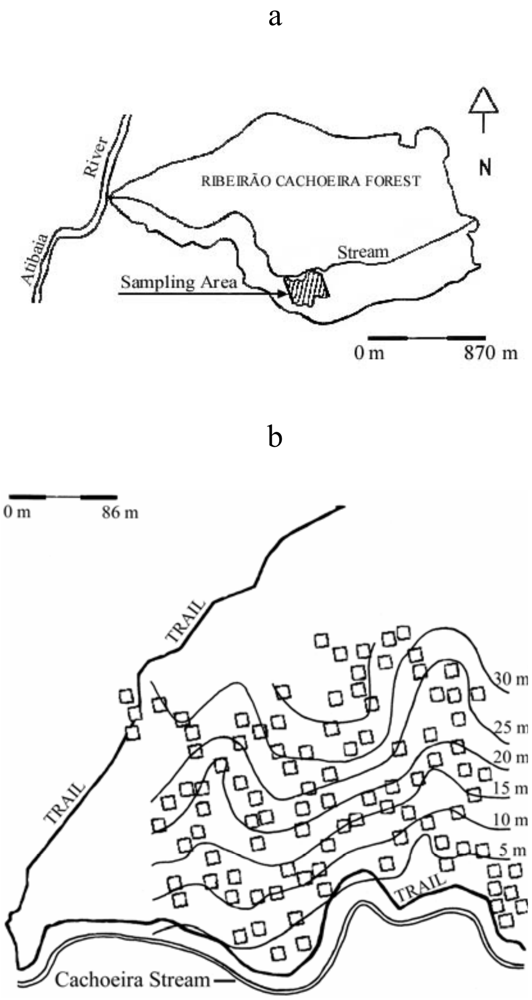
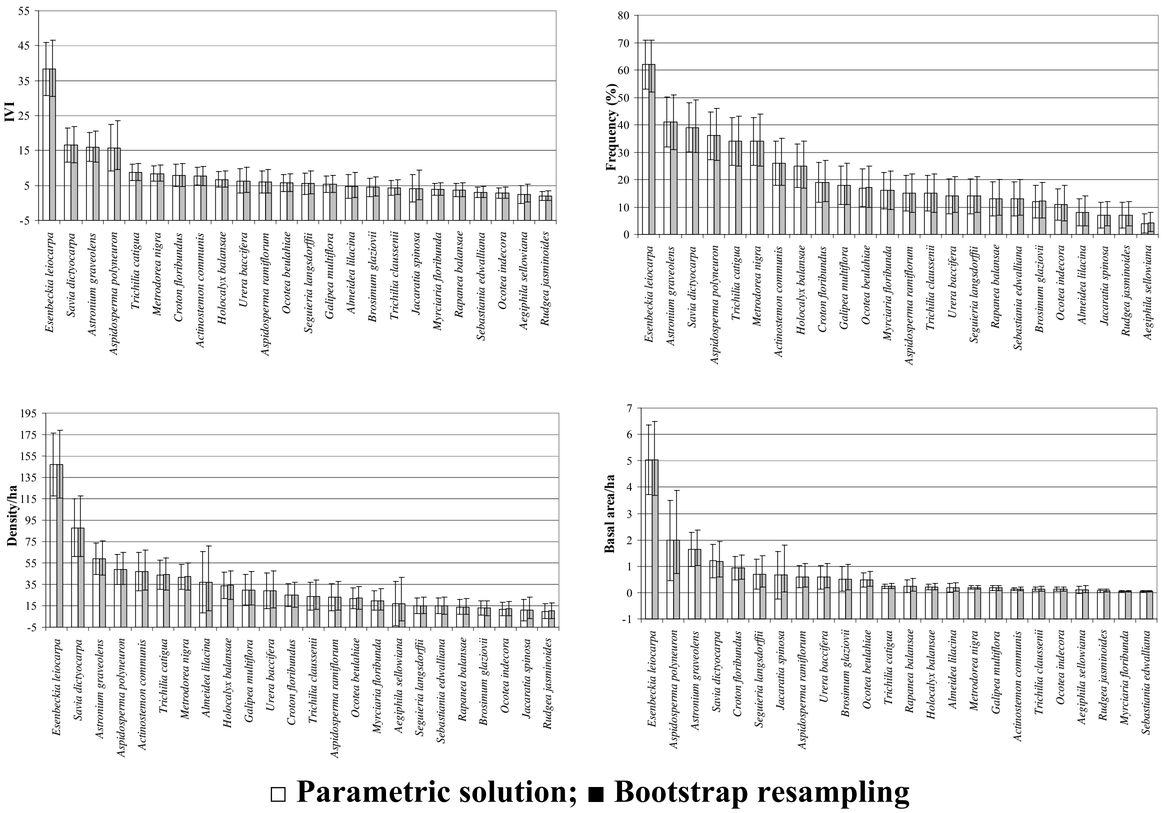
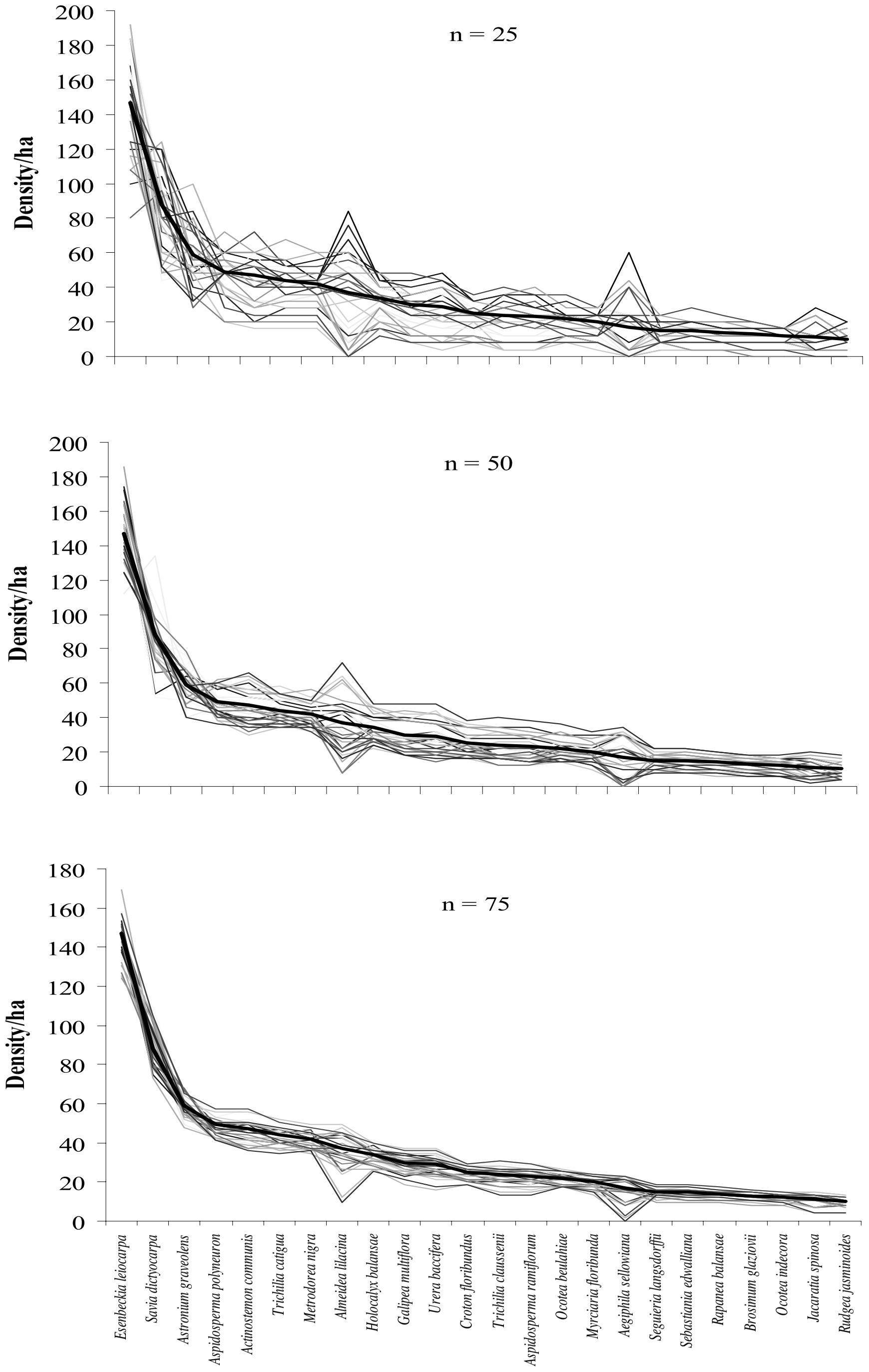

a
River
Atibaia
RIBEIRÃO CACHOEIRA FOREST
N
Stream
Sampling Area
0 m
870 m
b
0 m
86 m
TRAIL
TRAIL
30 m
25 m
20 m
15 m
10 m
5 m
TRAIL
Cachoeira Stream

Fig. 1.



□ Parametric solution; ■ Bootstrap resampling

Fig. 2.



Density/ha
n = 25
200
180
160
140
120
100
80
60
40
20
0
Density/ha
n = 50
200
180
160
140
120
100
80
60
40
20
0
Density/ha
n = 75
180
160
140
120
100
80
60
40
20
0
Esenbeckia leiocarpa
Savia dictyocarpa
Astronium graveolens
Aspidosperma polyneuron
Actinostemon communis
Trichilia catigua
Metrodorea nigra
Almeidea lilacina
Holocalyx balansae
Galipea multiflora
Urera baccifera
Croton floribundus
Trichilia claussenii
Aspidosperma ramiflorum
Ocotea beulahiae
Myrciaria floribunda
Aegiphila sellowiana
Seguieria langsdorffii
Sebastiania edwalliana
Rapanea balansae
Brosimum glaziovii
Ocotea indecora
Jacaratia spinosa
Rudgea jasminoides

Fig. 3.

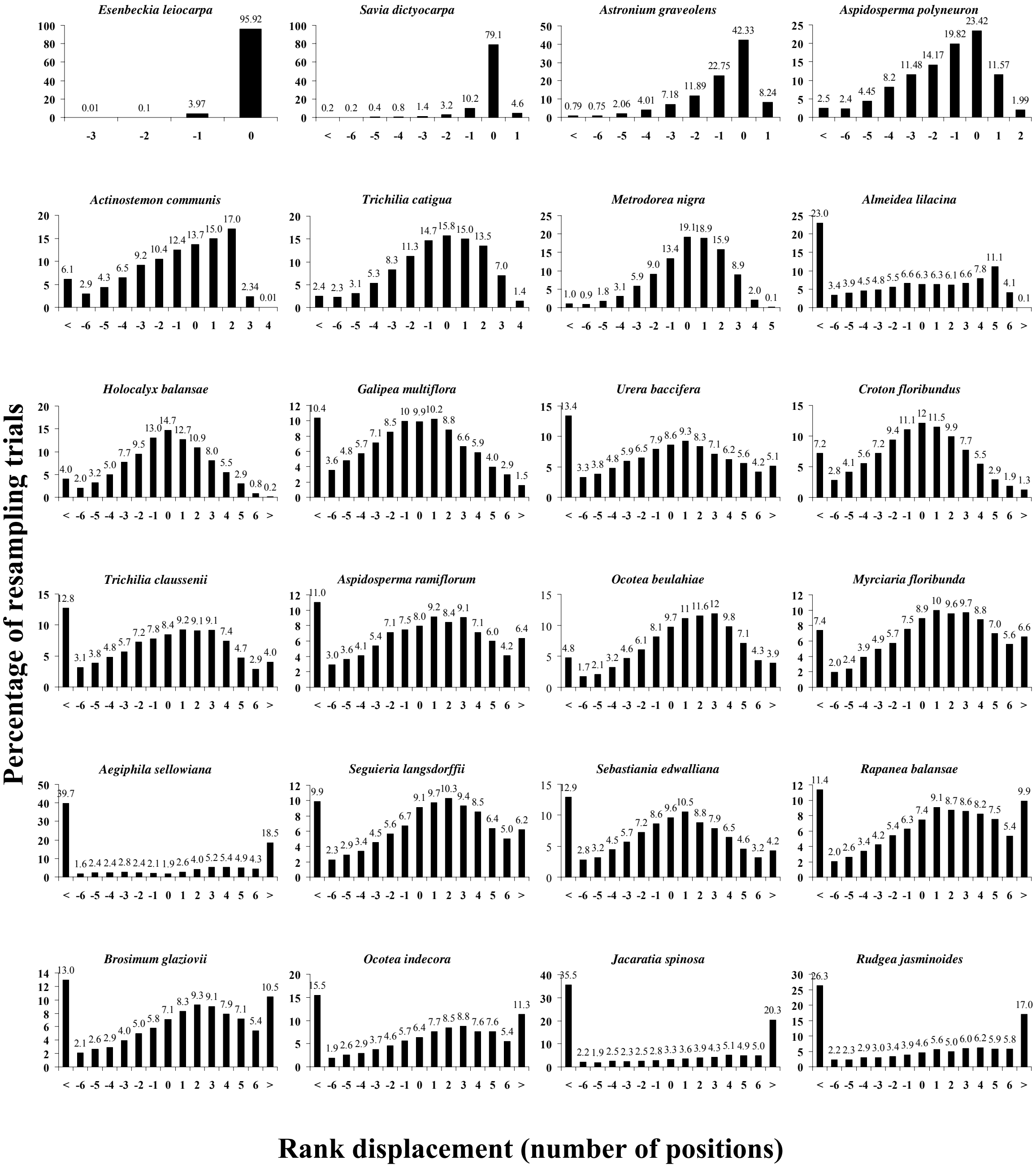
 Percentage of resampling trials
Rank displacement (number of positions)
Esenbeckia leiocarpa
0.01 0.1 3.97 95.92
-3 -2 -1 0
Savia dictyocarpa
0.2 0.2 0.4 0.8 1.4 3.2 10.2 79.1 4.6
< -6 -5 -4 -3 -2 -1 0 1
Astronium graveolens
0.79 0.75 2.06 4.01 7.18 11.89 22.75 42.33 8.24
< -6 -5 -4 -3 -2 -1 0 1
Aspidosperma polyneuron
2.5 2.4 4.45 8.2 11.48 14.17 19.82 23.42 11.57 1.99
< -6 -5 -4 -3 -2 -1 0 1 2
Actinostemon communis
6.1 2.9 4.3 6.5 9.2 10.4 12.4 13.7 15.0 17.0 2.34 0.01
< -6 -5 -4 -3 -2 -1 0 1 2 3 4
Trichilia catigua
2.4 2.3 3.1 5.3 8.3 11.3 14.7 15.8 15.0 13.5 7.0 1.4
< -6 -5 -4 -3 -2 -1 0 1 2 3 4
Metrodorea nigra
1.0 0.9 1.8 3.1 5.9 9.0 13.4 19.1 18.9 15.9 8.9 2.0 0.1
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5
Almeidea lilacina
23.0 3.4 3.9 4.5 4.8 5.5 6.6 6.3 6.3 6.1 6.6 7.8 11.1 4.1 0.1
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Holocalyx balansae
4.0 2.0 3.2 5.0 7.7 9.5 13.0 14.7 12.7 10.9 8.0 5.5 2.9 0.8 0.2
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Galipea multiflora
10.4 3.6 4.8 5.7 7.1 8.5 10 9.9 10.2 8.8 6.6 5.9 4.0 2.9 1.5
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Urera baccifera
13.4 3.3 3.8 4.8 5.9 6.5 7.9 8.6 9.3 8.3 7.1 6.2 5.6 4.2 5.1
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Croton floribundus
7.2 2.8 4.1 5.6 7.2 9.4 11.1 12 11.5 9.9 7.7 5.5 2.9 1.9 1.3
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Trichilia claussenii
12.8 3.1 3.8 4.8 5.7 7.2 7.8 8.4 9.2 9.1 9.1 7.4 4.7 2.9 4.0
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Aspidosperma ramiflorum
11.0 3.0 3.6 4.1 5.4 7.1 7.5 8.0 9.2 8.4 9.1 7.1 6.0 4.2 6.4
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Ocotea beulahiae
4.8 1.7 2.1 3.2 4.6 6.1 8.1 9.7 11 11.6 12 9.8 7.1 4.3 3.9
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Myrciaria floribunda
7.4 2.0 2.4 3.9 4.9 5.7 7.5 8.9 10 9.6 9.7 8.8 7.0 5.6 6.6
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Aegiphila sellowiana
39.7 1.6 2.4 2.4 2.8 2.4 2.1 1.9 2.6 4.0 5.2 5.4 4.9 4.3 18.5
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Seguieria langsdorffii
9.9 2.3 2.9 3.4 4.5 5.6 6.7 9.1 9.7 10.3 9.4 8.5 6.4 5.0 6.2
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Sebastiania edwalliana
12.9 2.8 3.2 4.5 5.7 7.2 8.6 9.6 10.5 8.8 7.9 6.5 4.6 3.2 4.2
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Rapanea balansae
11.4 2.0 2.6 3.4 4.2 5.4 6.3 7.4 9.1 8.7 8.6 8.2 7.5 5.4 9.9
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Brosimum glaziovii
13.0 2.1 2.6 2.9 4.0 5.0 5.8 7.1 8.3 9.3 9.1 7.9 7.1 5.4 10.5
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Ocotea indecora
15.5 1.9 2.6 2.9 3.7 4.6 5.7 6.4 7.7 8.5 8.8 7.6 7.6 5.4 11.3
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Jacaratia spinosa
35.5 2.2 1.9 2.5 2.3 2.5 2.8 3.3 3.6 3.9 4.3 5.1 4.9 5.0 20.3
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >
Rudgea jasminoides
26.3 2.2 2.3 2.9 3.0 3.4 3.9 4.6 5.6 5.0 6.0 6.2 5.9 5.8 17.0
< -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 >

Fig. 4.

CAPÍTULO 4

Sampling sufficiency analysis for stand recognition and estimation of conservation status indicator attributes in the Semideciduous Atlantic forest

Manuscrito formatado de acordo com as normas da revista *Forest Ecology & Management*.

Tabelas e figuras no final do capítulo.

Sampling sufficiency analysis for stand recognition and estimation of conservation status indicator attributes in the Semideciduous Atlantic forest

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Abstract

The lack of self-sustainability of Semideciduous Atlantic forest fragments and the need for ecological restoration of this ecosystem require studies related to two main objectives. Firstly, it is important to evaluate and monitor fragment conservation status through estimation of attributes such as total basal area and density, diversity and dominance. Secondly, the typification of vegetation cover at meso-scale will allow a more efficient management, environmental planning and restoration projects design. When sampling vegetation with meso-scale typification purpose, one must be able to discriminate between different stands along the common quite subtle environmental gradients found in Semideciduous forest fragments, a process known as entitation. In this study we investigate sampling sufficiency requirements for entitation and for estimation of conservation status indicator attributes in a 6.5-ha Semideciduous forest slope in SE, Brazil. In a previous work, an ordination of 100 10 m x 10 m sampling units randomly placed throughout this slope, revealed the existence of a variation in species composition unequivocally related to terrain elevation. Here, process sampling and bootstrap resampling were used to evaluate the stability of a significance measure of the ordination dimension describing that forest variation and of indicator attributes estimated through that sampling scheme. Sampling sufficiency for entitation was evaluated through the stabilization of the significance measure across progressively larger sample sizes. Analysis of indicator attributes sampling sufficiency took into account the stability of estimated values and/or of their confidence intervals. The stability curve of the ordination axis expressing the vegetation gradient showed that this dimension was the most consistent among the ordination axes monitored.

The curve did not reach stability, but increase in axis consistency was small beyond 65 sampling units. So, adopting a conservative approach, increase of axis consistence cannot justify the use of more than 80 sampling units. The stability curves of total basal area and density, diversity (Shannon) and dominance (Simpson) showed a sample size requirement of 50 sampling units. Dominance showed faster stabilization than diversity, but this behavior was counterweighted by the greater precision of diversity estimates (narrower confidence intervals). Thus, for purposes of entitation and estimation of conservation status indicator attributes, 80 and 50 sampling units, respectively, were adequate sample sizes. The conservation status indicator attributes evaluated seem to be equivalent concerning sampling efficiency. Further studies, however, should address the disturbance sensitivity of those attributes.

Keywords: Forest samples, Forest fragmentation, Vegetation typification, Tropical forest

1. Introduction

Typification studies in the Atlantic forest have used multivariate analysis to investigate floristic patterns, following the pioneer work of Silva and Shepherd (1986). Multivariate analysis applied to data sets of species-composition forest samples may allow the investigation of patterns at several scales and the mapping of communities and diversity distribution, thus aiding in environmental planning, conservation decisions, and restoration efforts (Yeo et al., 1998; Zak and Cabido, 2002; Hernandez-Stefanoni and Ponce-Hernandes, 2004). A prerequisite for typification studies is the existence of an adequate number of forest samples for the scale and complexity of the patterns to be investigated. Although the amount of vegetation data on Atlantic forest increased in the last decades, considering the great complexity of the vegetation (Scudeller et al, 2001) it is correct to assert that, for meso-scale (1-100 km^2, Vormisto et al, 2004) typification purposes, the number of forest samples is still limited. Increase in the number of data sets is particularly important to improve knowledge about the Semideciduous forest, which figures among the most fragmented physiognomic units of the Atlantic forest (Viana and Tabanez, 1996; Viana et al., 1997; Mittermeier et al., 1999). A remarkable feature of Semideciduous forests is the variation of species composition associated with terrain elevation at very local scales related to soil properties (Oliveira-Filho, 1994; Oliveira-Filho et al., 1997a; van den Berg and Oliveira-Filho 1999; Cardoso and Schiavini, 2002; Martins et al., 2003). This variation should be taken into account when sampling vegetation with meso-scale typification purposes. The process of recognizing different forest stands in a sampling area is known as entitation (Cain and Castro 1959; Mueller-Dombois and Ellenberg 1974).

Besides its importance for vegetation typification, species-composition forest samples can also provide reference values (standards) for forest attributes, such as total basal area and density, diversity and dominance. These standards may be obtained by compiling the information of several forest samples in order to provide the range of each attribute for well-conserved forests (e.g. Leitão-Filho, 1987; Martins, 1993). Then, the standards could be used for assessing conservation status of forest fragments in general. This kind of assessment is necessary because continued perturbation imposed by edge effects on Semideciduous forest fragments can cause species loss, increase in total density and decrease in total basal area (Viana and Tabanez, 1996; Oliveira-Filho et al., 1997b; Tabanez et al., 1997).

However, a methodological question that arises is how much sampling effort do we need to obtain forest samples for meso-scale typification surveys and for the estimation of conservation status indicator attributes? In the first case, it is important to consider the local-scale species-composition variation along subtle environmental gradients. This variation may implicate in the presence of more than one community type at a scale smaller than the area covered by an individual sample (in its concrete sense a community type is equivalent to a stand (Cain and Castro, 1959; Mueller-Dombois and Ellenberg, 1974, van der Maarel 2005)). Thus, an entitation is needed that allows taking one forest sample of each stand, improving meso-scale vegetation typification (Cain and Castro, 1959; Mueller-Dombois and Ellenberg, 1974, Greig-Smith, 1983; van der Maarel 2005). Because of the subtleness of the vegetation variation we are dealing with, this entitation cannot be accomplished subjectively, through visual assessment (e.g. Mueller-Dombois and Ellenberg, 1974). Based on sampling procedure recommendations of Kenkel et al. (1989), for typification purposes, one can start with small sampling units and, once different stands are recognized, sampling units of the same stand could be pooled to constitute an individual sample. The question is how many sampling units would be enough for this entitation? The kind of forest variation regarded here usually stands out in one of the first axes of an ordination of sampling units scattered throughout the sampling area (e.g. Oliveira-Filho et al., 1997a; van den Berg and Oliveira-Filho, 1999; Cielo-Filho et al. 2007), hence the significance of such axis could be used to assess the sampling intensity adequacy (Pillar, 1999). On the other hand, when the objective is to estimate conservation status indicator attributes such as diversity, dominance, total basal area and density, the interest lies in the fragment as a whole. Therefore, previous entitation is not required and the sampling intensity adequacy can be evaluated through the precision of the estimates in the whole sampling area or the forest fragment itself.

The present work aimed to investigate how much sampling effort is enough a) to an accurate description of species composition variation in order to allow entitation of the sampling area in Semideciduous Atlantic forest, and b) to adequately estimate conservation status indicator attributes.

2. Material and methods

2.1. Forest fragment and sampling area

This study was carried out in the Ribeirão Cachoeira forest, the second largest forest fragment (245 ha) in a region where forest cover was highly fragmented (Santin, 1999). It is located in the municipality of Campinas, Southeast Brazil with the coordinates 22º50'S and 46º55'W. The fragment is crossed east-west by the Cachoeira stream (Fig. 1A). The vegetation may be classified as Seasonal Semideciduous forest due to climatic seasonality, and deciduousness of about 30% of the highest trees during the dry season (IBGE, 1992). The climate is Koeppen's Cwa, with a hot rainy season from October to March, with monthly average temperatures between 22 ºC and 24 ºC, and average total precipitation of 1057 mm; and a dry season from April to September, with monthly average temperatures between 18 ºC and 22 ºC, and average total precipitation of 325 mm (Ortolani et al., 1995). Altitude varies from 630 m to 760 m a.s.l., the relief is hilly with steepness varying from 12% to more than 45% (Instituto Geológico, 1993). Soil is Haplic Lixisol (Prado, 2003), with sandy texture and many rock fragments.

The sampling area has 6.5 ha and is located in the south portion of the forest, at the left margin of the stream (Fig. 1A). This area was chosen by examination of an aerial photograph in 1:25,000 scale and visual inspection by walking in the forest. The choice criterion was the range of topography and vegetation physiognomy in order to avoid great declivity variations and the presence of too large gaps. The physiognomic extremes are a few, small gaps and continuous canopy to a height of 15-18 m, with emergent trees of up to 30 m. There are no signs of recent anthropogenic disturbances, such as charcoal on the ground surface, soot on trunks, and presence of stumps or coppiced trees. The area is located on a slope, approximately 270 m in length, with 40 m of difference in the altitudes of the lowest and highest points, and an average steepness of 15% (Fig. 1B). The choice of a relatively small sampling area in a slope associated with a stream was based on the commonness of these characteristics among Semideciduous Atlantic forest fragments

(Santin, 1999; Kronka et al. 2005), what may improve the generality of conclusions reached here.

2.2. Sampling scheme and data collection

One hundred 10 m x 10 m permanent sampling units were allocated in the sampling area in accordance to the randomization procedure proposed by Greig-Smith (1983). A system of X-Y coordinated axes was used. The northeastern vertex of each sampling unit was obtained through the drawing of random X-Y number pairs (Fig. 1B). Inside the sampling units, stems ≥ 5 cm dbh were tagged, identified, counted, and measured. Identification was made in the field, based on vegetative and reproductive characters. Branches were collected for laboratory identification, using literature and comparison with identified material of State University of Campinas Herbarium, where vouchers were lodged. Specialists confirmed definitive identification.

2.3. Data analysis

The vegetation attributes considered were total basal area and density, diversity and dominance. Total basal area and density refer to all species together and were expressed on a sampling unit basis. Diversity and dominance were respectively assessed through indices *H'* (Shannon, 1948) and *l* (Simpson 1949). Species composition variation was described in a previous study, by the first axis of a Principal Component Analysis (PCA) applied to a covariance matrix obtained from a data matrix containing the log-transformed density of non-singleton species in each of the 100 sampling units. The vegetation variation found strongly appeals for entitation, since sampling unit scores on that axis showed a significant negative correlation with terrain elevation even after spatial autocorrelation had been controlled for (Cielo-Filho et al. 2007; Chapter 2). These findings point to the operation of niche–assembly organizing process (Hubbell 1997; Wright 2002) reinforcing the need for entitation in sampling tropical forests with meso-scale typification purposes. The PCA axis 1 scores were used to separate two sets of sampling units with similar sizes pertaining to different stands (Chapter 5). As we run a centered PCA, the two sets were split by the scores signal, resulting in a 49-sampling units set with negative scores and in a 51-sampling units set with positive scores.

Sampling sufficiency was evaluated through a combination of process sampling (Greig-Smith, 1983) and bootstrap resampling (Efron, 1979; Efron and Tibshirani, 1993; Dixon, 1993) proposed by Pillar (1998), for evaluation of parameter estimates precision, and Pillar (1998; 1999), for evaluation of ordination axes significance. In the first case (Pillar, 1998), progressively larger sample sizes are obtained from the original data through random resampling of the sampling units with replacement. At each sample size n_k, the parameter of interest is calculated for a large number of resampling runs and an average and percentile confidence intervals are obtained. The method relies on the relation between stability and precision (Pillar, 1998). As n_k increases, the estimate becomes more stable across the resampling runs and also the confidence intervals of the averages become narrower, that is, the estimate becomes more precise. Therefore, sampling sufficiency can be regarded as the n_k at which the estimate reaches stability or at which the decrease of confidence interval amplitude slows down (Pillar, 1998). For total basal area and density, diversity and dominance, we constructed curves showing the average values and 95% bootstrap percentile confidence intervals at progressively larger sample sizes, starting from 5 sampling units. The criterion of sampling sufficiency for estimation of total basal area and density was the decreasing magnitude of the confidence interval amplitude with increasing sample size, so that the sample size (n_k) was considered large enough when the amplitude of the confidence interval becomes relatively stable across progressively larger values of n_k. For diversity and dominance estimates, the stability of the average estimated value across progressively larger values of n_k was also taken into account for the determination of sampling sufficiency. Construction of diversity and dominance curves was performed with the software RDSA (Martins and Cielo-Filho, 2007) whereas basal area and density curves were obtained with the software Multiv (Pillar, 2006). Ten thousand iterations were adopted in the resampling for all attributes and sample sizes (n_k).

The method devised for evaluation of ordination axes significance (Pillar, 1999), is also probabilistic. At each resampling run, for a defined n_k, the algorithm computes the correlation coefficient (θ^*) between reference scores, obtained through the ordination based on the original data matrix; and simulated scores, obtained through the ordination based on a data matrix with n_k sampling units. At the same resampling run, the algorithm also computes the correlation coefficient (θ^o) between reference scores, obtained through the ordination based on the original data matrix after a random permutation of values within variables; and simulated scores, obtained through the ordination based on the same unstructured data matrix with n_k sampling units. The method also involves a Procrustean adjustment in order to preserve the order of expression of intrinsic ordination dimensions (see Pillar, 1999, for details). The frequency $F(\theta^{\circ} \geq \theta^{*})$, after a large number of resampling runs, can be interpreted as a probability $P(\theta^{\circ} \geq \theta^{*})$, measuring the significance of the ordination axis being monitored. A low probability value means that the given ordination dimension is nontrivial and that the corresponding sample size (n_k) is large enough to reveal that dimension. The probability $P(\theta^{\circ} \geq \theta^{*})$ can be analyzed in the common statistical sense of a α significance level of 5%, so that if $P(\theta^{\circ} \geq \theta^{*}) \leq 0.05$, then the dimension can be considered nontrivial, with a probability ≤ 5% of being wrong. If a higher order, less important dimension, is considered significant, all other more important axes will also be, independently of their own values for $P(\theta^{\circ} \geq \theta^{*})$ (Pillar, 1999). On the other hand, we can consider the values of $P(\theta^{\circ} \geq \theta^{*})$ across progressively larger values of n_k as a gradient of the axis reliability (Pillar, 1999). In this case, the sample size n_k in which $P(\theta^{\circ} \geq \theta^{*})$ reaches stability points to the adequate sampling effort for revealing the given dimension. Thus, to define the adequate sample size to show the PCA dimension related to terrain elevation, we construct, for the first four ordination dimensions, stability curves of $P(\theta^{\circ} \geq \theta^{*})$ across progressively larger sample sizes (starting with $n_k = 30$), using the software Multiv (Pillar, 2006). Sampling sufficiency was evaluated starting from the more rigorous and then, considering the more flexible approach. Ten thousand iterations were used in the bootstrap resampling for all dimensions and sample sizes (n_k). This analysis was refined by elimination of the disturbed sampling units from the original data matrix. Tallest tree height was used as a measure of disturbance (Cielo-Filho et al. 2007). Furthermore, we also eliminated three pioneer species (*Urera baccifera* (L.) Gaudich. ex Wedd., *Aegiphila* *sellowiana* Cham. and *Croton floribundus* Spreng.), strongly correlated with PCA second axis; which expressed a disturbance vegetation gradient (Cielo-Filho et al. 2007). Thus, ten sampling units with the lowest tallest tree height were eliminated from the original data matrix.

3. Results

Sampling sufficiency for the description of species composition variation along the slope was not reached, taking into account that all the principal axes monitored presented probabilities $P(\theta^o \geq \theta^*) > 0.05$ (Fig. 2). Considering a more flexible approach, however, the axis expressing that vegetation variation (axis 1) showed the lowest values of $P(\theta^o \geq \theta^*)$ among the four axes monitored and a decreasing tendency for those values with increasing sample sizes, although the curve did not reached stability even near full samples (Fig. 2). This decreasing tendency, however, was not monotonic and it was possible to see a subtle inflection point at about 60 sampling units, from where the decreases of $P(\theta^o \geq \theta^*)$ are relatively small. This result suggests that there are little to gain in using a sample size greater than 65 sampling units to attain an accurate description of the main vegetation gradient in the sampling area. With elimination of disturbed sampling units a fourth pioneer species, *Trema micrantha* (L.) Blume was absent from the sample and so, also excluded. The curve of $P(\theta^o \geq \theta^*)$ against n_k then showed a pattern similar to that of the curve previously obtained, except for the low probability values and for a retraction of the inflection point to about 45 sampling units (Fig. 2). Thus, above 50 sampling units there was comparatively little decay in $P(\theta^{o} \geq \theta^{*})$. A conservative sampling scheme would, therefore, employ 75 and 60 sampling units for description of the vegetation gradient associated with terrain elevation, with and without including disturbance regime, respectively.

The sample size of 100 sampling units allows for sampling sufficiency to be reached for the estimation of total basal area and density, diversity and dominance (Fig. 3A-D). Indeed, much less sampling effort could have been applied to estimate these attributes. Above approximately 50 sampling units, there was a considerable decline in the ratio of confidence intervals amplitude decrease for total basal area and density (Fig. 3A-B). The estimated values for diversity did not stabilized even quite above 50 sampling units, however, its confidence intervals narrowness at this sample size, compensated for the lack of stability/accuracy (Fig. 3C). Dominance showed an opposite behavior, with comparatively wider confidence intervals at a sample size of 50 sampling units, compensated by the remarkable stability of estimated values well below that sampling intensity (Fig. 3D).

4. Discussion

Were the 100 sampling units a good enough sampling effort for revealing the quite interpretable species composition variation expressed by the PCA axis 1? In other words, if we repeat the same random sampling procedure, using 100 sampling units, should we expect the PCA axis 1 to reveal that vegetation gradient? Considering the corresponding probability $P(\theta^{\circ} \geq \theta^{*})$ as a relative measure for the axis reliability (Pillar 1999), the observed decreasing tendency of $P(\theta^{\circ} \geq \theta^{*})$ values with increasing sample sizes means a parallel increase in axis consistency. However, although the trend becomes less pronounced near full samples, stability was not reached. This fact allows the interpretation of the stability curve of PCA axis 1 as indicating that only with about 100 sampling units should a sample be considered appropriate enough to describe the species composition variation along the slope. It is worth to note that the use of 100 sampling units and the split of the sampling area into two stands will result in one forest sample for each stand with approximately 0.5 ha, a sample size inside the range of minimal area (0.4 – 1 ha) recommended by van der Maarel (2005) for sampling of tropical rain forest stands. However, the inflection point in the curve of $P(\theta^{\circ} \geq \theta^{*})$ against n_k reveal a threshold in sampling intensity above which the gain in axis reliability would not justify the use of more than 75 sampling units. The removal of disturbed sampling units and pioneer species, with the corresponding decrease in the data matrix dimensionality, produced an increase of axis 1 consistency with lower values of $P(\theta^{\circ} \geq \theta^{*})$. This occurs because vegetation gradient associated with terrain elevation, and expressed by PCA axis 1, was not related to disturbance (Cielo-Filho et al. 2007). The stability curve then obtained reinforces the idea of a sampling intensity threshold and reveals the possibility of a further reduction in sampling intensity if disturbed sites are excluded from the sample, although such procedure should only be applied in specific situations when estimation of diversity or description of disturbance-related vegetation gradients are not required. To reconcile these findings with the literature recommendation (van der Maarel, 2005), a sampling intensity of 80 sampling units could thus be suggested for sampling of forests with similar sizes and environmental heterogeneity. Thus, it would be possible to obtain two samples of approximately 0.4 ha, one for each of the stands defined by the soil catena related to the terrain elevation.

Significance of ordination dimensions describing vegetation variation among stands, seems to be a quite appropriate criterion for sampling sufficiency evaluation whenever sampling forest fragments with meso-scale typification purposes. Another criterion, based on the general sampling error of dominant species quantity estimates in the same forest fragment, resulted in a sample size requirement of 100 sampling units (Cielo-Filho et al. unpublished). Rather than the need for entitation, this criterion is justified by the great influence that dominant species will exert on stands ordination configuration in typification surveys. However, the analysis of ordination dimension significance (Pillar 1999) used here can be scaled up allowing an alternative approach in those surveys, so that sample size adequacy will be expressed by the number of stands, rather than the number of sampling units used.

Sampling sufficiency is a relative matter, related to the objectives of the study (Kenkel et al. 1989; Pillar 1998). In agreement with this reasoning, the results concerning sampling sufficiency showed different levels of sampling intensity requirements for description of species composition variation through ordination and for estimation of conservation status indicator attributes. The basic difference between these two kinds of estimation is that the first is multivariate while the second is univariate (Kenkel et al. 1989). In the multivariate estimation for ordination of sampling units, the associations among all species are computed simultaneously from the matrix of species abundances per sampling units. The subsequent calculations are all based on that association matrix, so the sampling intensity might be enough to show an accurate picture of the correlation structure for the species growing in the sampling area. Because the subtleness of the environmental gradient, stochastic factors can play an important role in species space occupation (Cielo-Filho et al. 2007), what introduces a considerable noise in interspecific associations, especially for the less abundant species. Therefore, the correlation structure becomes weak, demanding a greater sampling effort. On the other hand, estimation of total basal area and density deals with all species together rather than with individual species, whereas the estimation of forest diversity and dominance deals with species density in the whole sample rather than within individual sampling units. In these cases, stochastic factors become less important and less sampling effort will be required.

A conspicuous difference was found between diversity and dominance stability curves. The curve of *l* against sample size flattens off at a sampling intensity well below the corresponding point in the *H'* curve, but at a given sample size, precision of *l* was always smaller than *H'*. *H'* is more sensitive to species number and so, more dependent of sample size than *l* (Magurran, 1988). For instance, the addition of singletons with increase of sample size will cause an increase in *H'*, whereas *l* will remain constant. Because of this attribute *H'* curve did not reach stability even near full samples. On the other hand, *H'* does not give disproportional importance to the most abundant species, as *l* does, and this may improve the extent to which the super estimation of one species could be counterweighted by the underestimation of another, resulting in greater precision of *H'* estimates. So, concerning sampling efficiency, *H'* and *l* can be considered equivalents, the greater precision of the former counteracting the faster stabilization of the later.

Consequently, total basal area and density, diversity and dominance all seem to be good attributes for conservation status assessment. Further studies, however, should address the relative sensitivity of each attribute to disturbance. For instance, the Simpson dominance index showed a greater ability to discriminate between communities submitted to different levels of disturbance than abundance distribution models (Cielo-Filho et al. 2002).

The figures for sampling sufficiency presented here were obtained for a specific sampling scheme concerning sampling unit's distribution, size and shape. In general terms, it is possible to assert that larger rectangular sampling units and systematic distribution would result in smaller variances and allow a decrease of sampling effort for estimation of conservation status indicator attributes (Greig-Smith, 1983). Nevertheless, for description of species composition variation, the only change in sampling scheme that could be expected to improve sampling efficiency is systematic distribution of sampling units, because a more uniform covering of the sampling area is obtained then, if compared with random distribution. A larger, more elongated, sampling unit can make entitation difficult, since there will be a greater number of sampling units crossing boundaries between different stands.

5. Conclusion

Sampling sufficiency analysis showed that around 80 10 m x 10 m sampling units is a suitable sample size to discriminate between different stands in a typical Semideciduous Atlantic forest fragment. About 50 sampling units can be used to give an accurate picture of total basal area and density, diversity and dominance.

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Figure captions

Fig. 1. (A) Location of the 6.5-ha sampling area (hatched polygon) in Ribeirão Cachoeira forest, SE, Brazil; (B) Diagram showing the sampling design with 100 10 m x 10 m sampling units.

Fig. 2. Stability curves of the first four axes of a PCA applied to the vegetation matrix gathered in the Ribeirão Cachoeira forest sampling area (solid symbols). The curves were obtained through bootstrap resampling across progressively larger sample sizes. Probability $P(\theta^{o} \geq \theta^{*})$ measures the significance of ordination axes. Open diamonds refers to the stability curve of the first axis after removal of disturbed sampling units (dsu) from the matrix.

Fig. 3. (A-D) Stability curves of total basal area and density, Shannon diversity and Simpson dominance indices estimates along with the 95% confidence intervals. The curves were obtained through bootstrap resampling across progressively larger sample sizes.

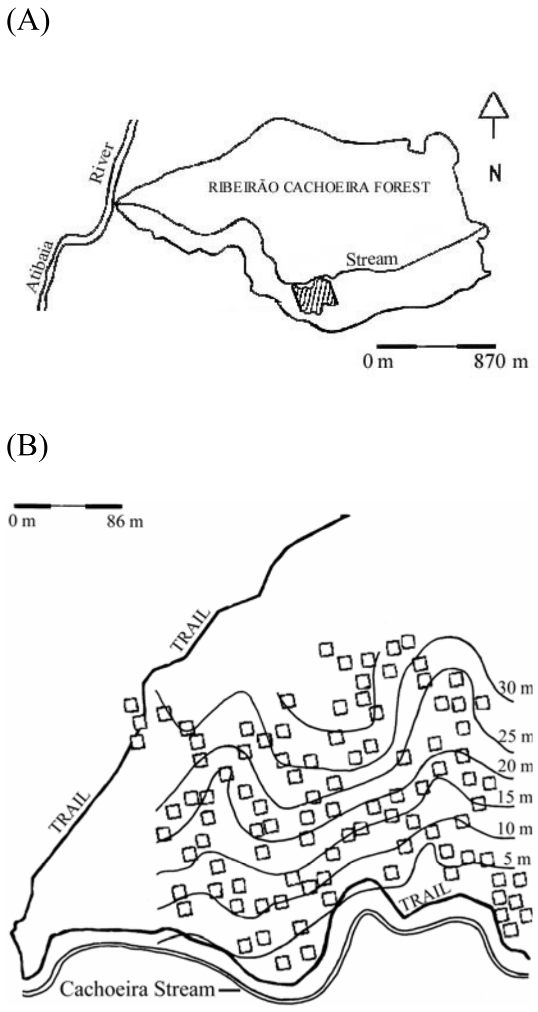
(A)
River
Atibaia
RIBEIRÃO CACHOEIRA FOREST
N
Stream
0 m
870 m
(B)
0 m
86 m
TRAIL
TRAIL
30 m
25 m
20 m
15 m
10 m
5 m
TRAIL
Cachoeira Stream

Fig. 1.

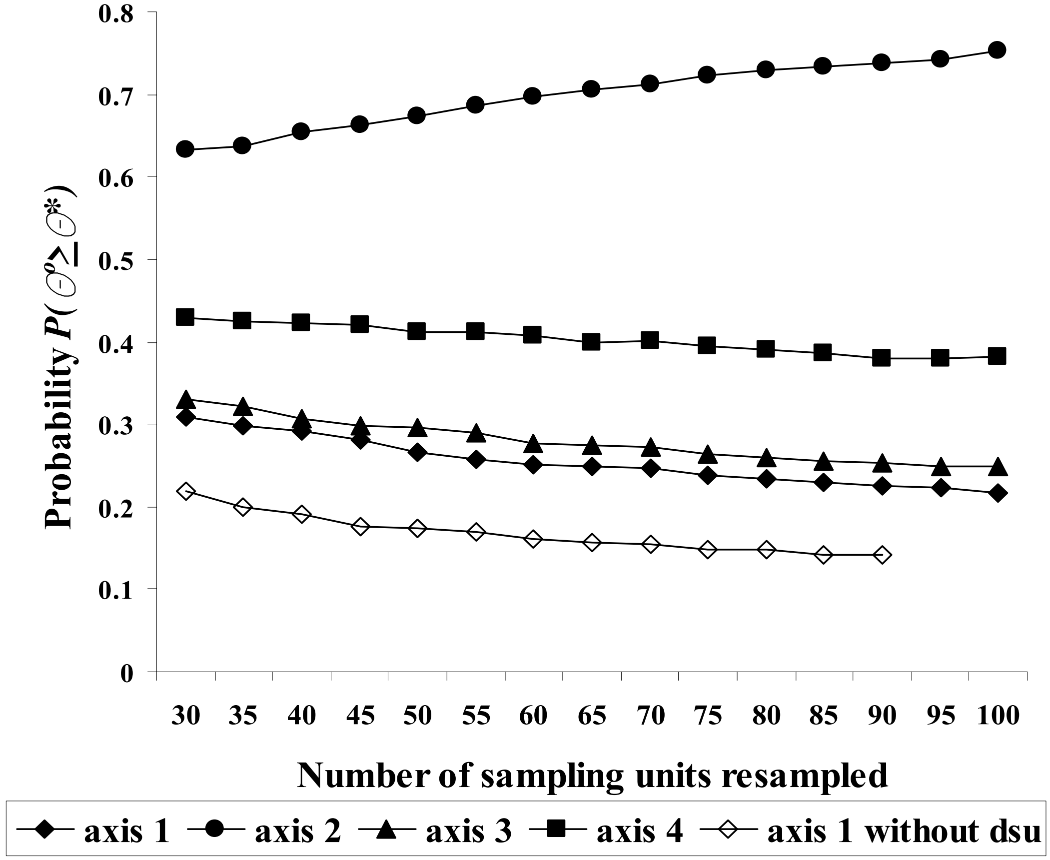
Probability $P(\Theta^o \geq \Theta^*)$
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
Number of sampling units resampled
axis 1
axis 2
axis 3
axis 4
axis 1 without dsu

Fig. 2.

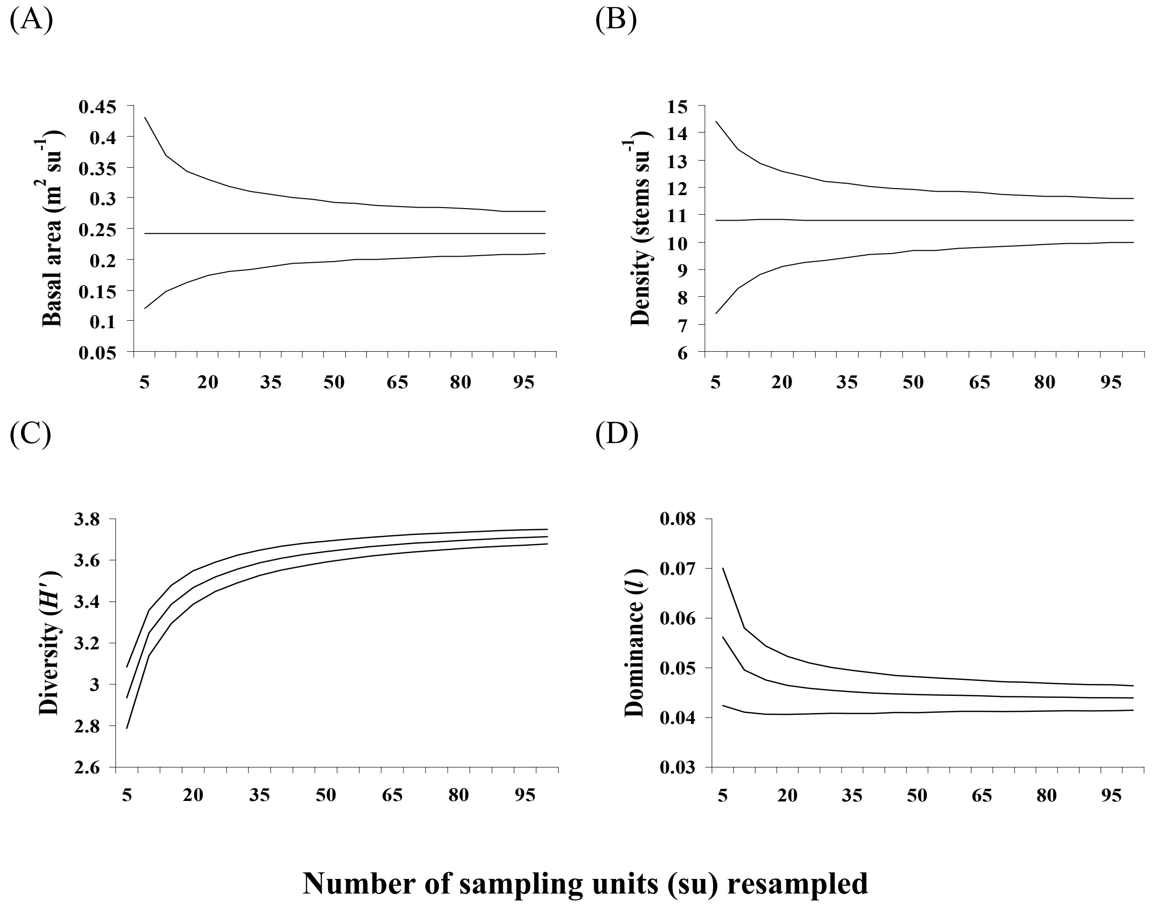
(A)
Basal area (m^2 su^{-1})
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
5
20
35
50
65
80
95
(B)
Density (stems su^{-1})
15
14
13
12
11
10
9
8
7
6
5
20
35
50
65
80
95
(C)
Diversity (*H'*)
3.8
3.6
3.4
3.2
3
2.8
2.6
5
20
35
50
65
80
95
(D)
Dominance (*l*)
0.08
0.07
0.06
0.05
0.04
0.03
5
20
35
50
65
80
95
Number of sampling units (su) resampled

Fig. 3.

CAPÍTULO 5

Describing forest stands outlined through objective entitation and assessing classification and conservation status in the Semideciduous Atlantic forest

Manuscrito formatado de acordo com as normas da revista *Plant Ecology*.

Tabelas e figuras no final do capítulo.

Describing forest stands outlined through objective entitation and assessing classification and conservation status in the Semideciduous Atlantic forest

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Key words: Forest assessment, Forest description, Forest fragmentation, Tropical forest

Abstract

In Brazil, a currently growing branch of phytosociology is synchorology. As the investigation of floristic patterns scales down, a refinement in the sampling procedure becomes necessary to recognize different stands (to make an entitation) along subtle environmental gradients. Forest samples also provide useful information for classification and conservation status assessment of tropical forest fragments. In this paper, we described species composition and assessed classification and conservation status of a 6.5-ha Semideciduous Atlantic forest slope in SE Brazil. One hundred 10 x 10 m random sampling units were split into two stands according to their scores on a PCA axis obtained in a previous study. This axis describes the main floristic gradient in the forest slope. Stands A and B showed remarkable differences in species composition. Of the total 119 species found, 21 and 35 were exclusive to stands A and B, respectively. The dominant species in stand A, with a relative density of 26.6%, comprises only 2.7% of the stems in stand B. The corresponding figures for the dominant species in stand B were 13.4% and 1.8%, respectively. Bray-Curtis dissimilarity between stands was 51%. This composition difference was statistically significant according to the Multi-response Permutation Procedure ($T = -33.26$, $p < 10^{-8}$). Previous studies have demonstrated that such fine-scale variation in species composition is a common and non-trivial feature of Semideciduous forest areas. Thus, entitation is a strongly recommended sampling procedure in meso-scale vegetation surveys. The richest families were Fabaceae, Lauraceae, Myrtaceae, Meliaceae,

Rubiaceae, Euphorbiaceae and Rutaceae. Shannon diversity index was 3.79 nats stem^{-1}, whereas 31% of the total species found were considered rare (density = 1 stem ha^{-1}). Comparison of the above figures with standards available in the literature reveals that the area can be considered a typical well-conserved Semideciduous Atlantic forest. The high proportion of rare species, however, implies the possibility of a significant diversity loss. Species richness distribution among families, diversity and percentage of rare species are useful attributes for assessing classification and conservation status in Semideciduous forests, but standards for these attributes should be updated and complemented with figures for dominance, total basal area and density.

Introduction

In Brazil, most of the extra-Amazonian forests classified as Deciduous and Semideciduous forests, and Ombrophilous Open, Dense and Mixed forests compose a tree species distribution continuum generically known as Atlantic forest (Oliveira-Filho and Fontes 2000). The Atlantic forest encompasses physiognomies occurring east and south of the dry corridor formed by “Cerrado” (Brazilian savanna) and “Caatinga” (thorn woodland/shrubland). This corridor ranges from northeast to southwest of the country and reaches western Paraguay and northwestern Argentina (Oliveira-Filho and Fontes 2000). In São Paulo state, the Semideciduous forest gradually shifts into the eastern Ombrophilous Dense forest at the Atlantic Plateau (Oliveira 2006). It extends to the west intertwining with areas of “Cerrado” and enters Mato Grosso do Sul state (Leitão Filho 1982; 1987). The Semideciduous forest is characterized by high species richness of Fabaceae, Meliaceae, Rutaceae, Euphorbiaceae, Lauraceae, Myrtaceae and Rubiaceae, thus differing from the Ombrophilous Dense Atlantic forest, where Sapotaceae, Melastomataceae and Chrysobalanaceae also play an important role (Leitão Filho 1982; 1987). The species composition differences between Semideciduous and Ombrophilous forests increases with the distance from the coast, and is related to the increasing climatic seasonality towards the interior (Salis et al. 1995; Torres et al. 1997; Oliveira Filho and Fontes 2000). Furthermore, the Semideciduous forest may be divided into high-altitudinal and low-altitudinal floristic blocks. The limits between blocks lay around 700 to 750 m a.s.l., the increase of humidity and frost frequency with altitude being the main climatic conditioners (Salis et al. 1995; Torres et al. 1997; van den Berg and Oliveira-Filho 2000).

Those vegetation surveys have addressed one of the phytosociological branches, namely synchorology, that is concerned with geographical distribution of plant communities (Braun-Blanquet 1972). The methodological background of these studies was given by Silva and Shepherd (1986), who introduced multivariate analysis for the study of Brazilian forests. Since that study, much effort has been made in order to sample forest areas and to build databases of forest samples such as FITOGEO (Scudeller and Martins 2003), that has been used as metadata in synchorology (e.g. Oliveira 2006). However, to scale down floristic patterns investigations of the Atlantic forest, a refinement on sampling procedures is required. The process of recognizing different forest stands in a sampling area is known as entitation and must be applied when obtaining forest samples for meso-scale (1-100 km^2, Vormisto et al. 2004) floristic patterns investigations (Cain and Castro 1959; Mueller-Dombois and Ellenberg 1974, van der Maarel 2005). On the other hand, such discrimination is of little utility when relating samples at broader scales.

Forest samples can also provide information for assessing classification and conservation status of forest fragments. For instance, in spite of the intense fragmentation of the Semideciduous forest (Viana and Tabanez 1996; Viana et al. 1997; Mittermeier et al. 1999), well-conserved fragments suitable for sampling can still be found (Santin 1999; Santos 2003). The objective assessment of the classification and conservation status of these fragments should be an important task to be attained in monitoring programs of fragmented landscapes and environmental impact studies. In order to accomplish that task, forest attributes indicating classification and conservation status may be compared with reference values (standards) obtained from the compilation of several forest samples with well established classification and conservation status.

In this work we described the species composition of a 6.5-ha Semideciduous Atlantic forest sampling area, with and without entitation, and assessed the classification and conservation status of the vegetation.

Material and methods

Study area

This work was carried out in the Ribeirão Cachoeira forest, São Paulo state, Southeast Brazil (22º50'S, 46º55'W). It is located in the Campinas Environmental Protection Area in a region where forest cover was very fragmented (Santin 1999) (Fig. 1a). The fragment is crossed east-west by the Ribeirão Cachoeira stream, a tributary of Atibaia River (Fig. 1b). According to IBGE (1992) criteria, the vegetation may be classified as Seasonal Semideciduous forest due to the prevalence of phanerophytes, climatic seasonality, and deciduousness of about 30% of the highest trees during the dry season. However, IBGE (1995) map classifies Ribeirão Cachoeira vegetation as Ombrophilous Dense forest. The climate is Koeppen's Cwa, with a hot rainy season from October to March, with monthly average temperatures between 22 ºC and 24 ºC, and average total rainfall of 1057 mm; and a dry season from April to September, with monthly average temperatures between 18 ºC and 22 ºC, and average total rainfall of 325 mm (Ortolani et al. 1995). Soil is Haplic Lixisol (Prado 2003), with sandy texture and many rock fragments.

The sampling area is 6.5 ha, located in the south portion of the forest, at the left margin of Cachoeira stream (Fig. 1b). This area was chosen by examination of an aerial photograph in 1:25,000 scale and visual inspection by walking in the forest. The physiognomic extremes of the area are a few, small gaps and continuous canopy to a height of 15-18 m with emergent trees of up to 30 m. There are no signs of recent anthropogenic disturbances, such as charcoal on the ground surface, soot on trunks, and presence of stumps. The area is located on a slope of approximately 270 m length with 40 m of difference in the altitudes of the lowest and highest points, and an average steepness of 15% (Fig. 1c).

Sampling design and data collection

One hundred 10 x 10 m permanent sampling units were allocated in the 6.5-ha area in accordance to the randomization procedure proposed by Greig-Smith (1983). A system of X-Y coordinated axes was used and the northeastern vertex of each sampling unit was obtained through the drawing of random X-Y number pairs (Fig. 1c). Inside the sampling units, stems ≥ 5 cm dbh were tagged, identified, counted, and measured. For all sampling units the same two inclusion and two exclusion sides were defined a priori, and stems touching the sampling unit limit at the inclusion sides were included, and the ones that touched the exclusion sides were excluded. Tree identification was made in the field and laboratory, using literature and comparison with material in the State University of Campinas Herbarium, where vouchers were lodged. Specialists confirmed definitive identifications.

The forest attributes considered were species composition, species richness distribution among families, species diversity and percentage of rare species. Species composition was assessed through density, frequency, basal area and IVI, commonly called phytosociological characters (Curtis and McIntosh 1950; Mueller-Dombois and Ellenberg 1974). Richness of families was summarized by the distribution of species among the families, according to Judd et al. (2002). Diversity was assessed through the calculation of Shannon index (*H'*) (Magurran 1988). Following Hubbell and Foster (1983), species with density = 1 stem ha^{-1} were considered for the calculation of the proportion of rare species.

Data analysis

The entitation of the sampling area took into account the species composition variation along the slope described in a previous study, by the first axis of a Principal Component Analysis (PCA) applied to a covariance matrix obtained from a data matrix containing the log-transformed number of non-singleton species stems in each of the 100 sampling units (Cielo-Filho et al. 2007). The sampling unit scores on that axis showed a significant negative correlation with terrain elevation (Cielo-Filho et al. 2007; Chapter 2) and were used here to separate two sets of sampling units with similar sizes pertaining to different stands: a 49-sampling units set with negative scores (stand A), and a 51-sampling units set with positive scores (stand B). Thus, species composition was presented for the two stands and for the whole sampling area. Dissimilarity between stands was quantified through the calculation of Bray-Curtis coefficient (Greig-Smith 1983). To test the hypothesis of composition differences between stands the Multi-response Permutation Procedure (MRPP) was used (McCune and Grace 2002). The test statistic (*T*) measures the tightness of the groups, being more negative when groups are sharper. The chance-corrected within group agreement (*A*) measures the *effect size*, being higher as smaller the heterogeneity within groups. As the groups were outlined through a PCA, the distance measure used in MRPP was Euclidean, since PCA preserves the Euclidean distance among objects (Legendre and Legendre 1998). Number of stems of each species in each sampling unit was log-transformed before running the MRPP analysis using the software PC-ORD (McCune and Mefford 1999).

The species richness distribution among families, the estimated values of *H'* and percentage of rare species, considering the whole sampling area, were compared with the standards obtained by Leitão Filho (1987) and Martins (1993) through the compilation of the respective descriptor values in several forest samples. These comparisons aid in assessing classification and conservation status of the vegetation.

Results

In the whole sampling area 1080 living trees were sampled belonging to 119 angiosperm species (Table 1). The corresponding figures for stands A and B were 492 trees and 84 species, and 588 trees and 98 species, respectively (Table 1). The two stands showed remarkable differences. From the 119 species identified in the sampling area, 21 only occurred in stand A and 35 were exclusive of stand B. Thus, 47% of the species were stand-exclusive. The species phytosociological characters also showed strong dissimilarity (Table

1), resulting in quite different abundance ranks and in a Bray-Curtis dissimilarity of 51%. The dominant species in stands A and B, respectively, *Esenbeckia leiocarpa* Engl. and *Savia dictyocarpa* Müll. Arg., showed quite different figures for relative density in each stand. The former species comprises 26.6% of the total abundance in stand A and only 2.7% in stand B. For the later, relative density was 13.4% in stand B and only 1.8% in stand A. The hypothesis of composition differences between stands was supported by the MRPP test (T = -33.26, $p < 10^{-8}$). Effect size was low (A = 0.05), however, values of A below 0.1 are common in community data (McCune and Grace 2002).

Among the 38 families found, the richest ones were Fabaceae (with 17 species), followed by Lauraceae (11); Myrtaceae (10); Meliaceae and Rubiaceae (8); Euphorbiaceae and Rutaceae (6). There was a strong accordance between these families and those listed by Leitão-Filho (1982; 1987) as the richest families in Semideciduous Atlantic forest areas of São Paulo state, corroborating the classification status of the forest we studied, according to IBGE (1992) criteria. Diversity estimated by H' was 3.79 nats stem^{-1}. Thirty-seven species had only one stem ha^{-1}, that is, 31% of the species found were rare (Table 1). For samples of Semideciduous forests in São Paulo state, Martins (1993) and Leitão-Filho (1987) found values of H' varying from 3.50 to 4.29 nats stem^{-1}, whereas Martins (1993) recorded percentages of rare species ranging from 26% to 30%.

Discussion

There were conspicuous qualitative and quantitative composition differences between stands A and B. Variation in species composition at very local scales was reported by different authors in different localities (Oliveira-Filho 1994; Oliveira-Filho et al. 1997a; van den Berg and Oliveira-Filho 1999; Cardoso and Schiavini 2002; Martins et al. 2003; Cielo-Filho et al. 2007). These vegetation gradients constitute the basis for the need of entitation when sampling Semideciduous forest areas for meso-scale floristic patterns investigations. Evidences of underlining niche–assembly organizing process related to environmental heterogeneity (Hubbell 1997; Wright 2002) reinforce the need for entitation (Cielo-Filho et al. 2007; Chapter 2). Although some authors have argued for subjective entitation (e.g. Mueller-Dombois and Ellenberg 1974), it is very hard to distinguish subjectively between different stands along subtle environmental gradients of complex Atlantic forests (Scudeller et al. 2001). In such situations, objective entitation may be a more appropriate approach (Mueller-Dombois and Ellenberg 1974).

When the species richness distribution among families of Ribeirão Cachoeira forest is compared with standards available in the literature, the vegetation may be considered a typical Semideciduous Atlantic forest. Thus, family composition can be useful to check the physiognomic class to which the forest belongs and to detect possible faults in the physiognomic map. For example, IBGE (1995) mapped Ribeirão Cachoeira forest in the region of the Ombrophilous Dense Atlantic forest, which has a different distribution of species richness among families (Leitão-Filho 1982; 1987).

Comparison of the value of *H'* found here with the standard range obtained from literature confirms the well-conserved status of Ribeirão Cachoeira forest. In agreement with this conclusion, Ribeirão Cachoeira forest showed the smallest canopy openness among forest fragments of the region (Santos 2003). On the other hand, the relatively high proportion of rare species poses the question of how effectively the forest fragment can maintain its plant diversity. Diversity decline in tropical forest fragments is a well-documented fact (Bierregaard et al. 1992; Terborgh 1992; Turner 1996). Plant species loss may arise especially from continued perturbation imposed by edge effects that cause increased tree mortality and substitution of old growth forest by successional trees and lianas (Laurance et al. 1998, 2000, 2001, 2006). Furthermore, populations in isolated fragments will also suffer demographic declines owing to pollen and seed dispersal limitation and, especially, the rare species can became locally extinct (Ghazoul 2005; Knight et al. 2005; Vamosi et al. 2006). Thus, in spite of a good conservation status, a fragment like Ribeirão Cachoeira may not be able to sustain its diversity for longer. In order to assess this issue, further studies need to address key aspects of forest dynamics in fragmented landscapes, such as reproductive plant biology and pervasiveness of matrix types. Different species experience different degrees of isolation in fragmented landscapes depending on their mechanisms of pollination and seed dispersal, the foraging ranges and behavior of pollinators and seed dispersers and on the characteristics of the surrounding matrix (Pulliam and Dunning 1997; Noss and Csuti 1997; Ghazoul 2005). Comprehension of reproductive biology of rare species and evaluation of the pervasiveness of different matrix types is a key step to evaluate the degree of threaten to these species and to outline management actions.

Species richness distribution among families, diversity and percentage of rare species can be interpreted as classification and conservation status indicators. On the other hand, the standards presented by Leitão-Filho (1982; 1987) and Martins (1993) should be updated, considering the new forest samples accumulated since their publication.

Furthermore, reference values for dominance, total basal area and density can also aid in conservation status assessment given the sensitivity of these attributes to forest disturbance (Oliveira-Filho et al. 1997b; Cielo-Filho et al. 2002). Ideally, a set of forest attributes should be used in conservation status assessment.

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Figure legend

Figure 1. (a) location of the Ribeirão Cachoeira forest (RCF) and other remaining forest fragments in Campinas municipality (CA), SE Brazil; (b) location of the 6.5-ha sampling area (hatched polygon) in Ribeirão Cachoeira forest; (c) diagram showing the sampling design of the one hundred 10 x 10 m sampling units used to describe the forest attributes.

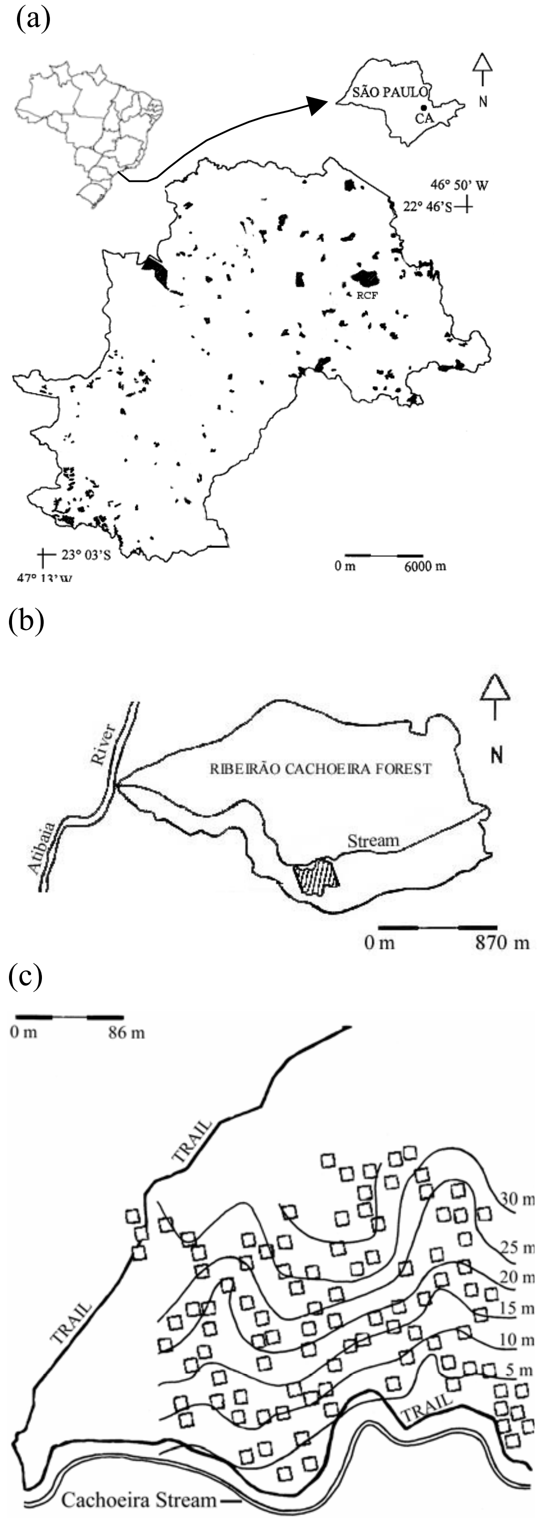
(a)
SÃO PAULO
CA
N
46° 50' W
22° 46'S
RCF
23° 03'S
47° 13' W
0 m
6000 m
(b)
River
Atibaia
RIBEIRÃO CACHOEIRA FOREST
Stream
N
0 m
870 m
(c)
0 m
86 m
TRAIL
TRAIL
TRAIL
30 m
25 m
20 m
15 m
10 m
5 m
Cachoeira Stream

Figure 1.

Table 1. Species composition in a 6.5-ha Semideciduous forest slope of SE Brazil and in stands A and B in the same slope. AD = absolute density in stems ha^{-1}; ABA = absolute basal area in m^{2} ha^{-1}; AF = absolute frequency in percentage; IVI = Importance Value Index; N = number of stems in the sample.

	Forest slope				**Stand A**					**Stand B**				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Anacardiaceae														
Astronium graveolens Jacq.	59	1.643	41	17.791	36	73.47	2.0703	48.98	22.587	23	45.1	1.2324	33.33	13.5
Annonaceae														
Annona cacans Warm.	2	0.0117	2	0.503	1	2.04	0.0141	2.04	0.559	1	1.96	0.0094	1.96	0.456
Guatteria nigrescens Mart.	1	0.0118	1	0.276	1	2.04	0.0241	2.04	0.597	-	-	-	-	-
Rollinia sylvatica (A. St.-Hil.) Mart.	4	0.1859	4	1.679	-	-	-	-	-	4	7.84	0.3644	7.84	3.264
Apocynaceae														
Aspidosperma polyneuron Müll. Arg.	49	1.9795	36	17.585	23	46.94	1.2138	36.73	14.807	26	50.98	2.7151	35.29	20.789
Aspidosperma ramiflorum Müll. Arg.	23	0.5966	15	6.621	12	24.49	0.586	14.29	6.823	11	21.57	0.6067	15.69	6.501
Rauvolfia sellowii Müll. Arg.	1	0.2873	1	1.417	-	-	-	-	-	1	1.96	0.5633	1.96	2.897

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Arecaceae														
Syagrus oleracea (Mart.) Becc.	1	0.0151	1	0.29	1	2.04	0.0307	2.04	0.623	-	-	-	-	-
Syagrus romanzoffiana (Cham.) Glassman	4	0.1264	4	1.433	1	2.04	0.0676	2.04	0.767	3	5.88	0.183	5.88	2.05
Asteraceae														
Piptocarpha sellowii (Sch. Bip.) Baker	1	0.0088	1	0.264	-	-	-	-	-	1	1.96	0.0172	1.96	0.491
Vernonia diffusa Less.	1	0.0131	1	0.282	1	2.04	0.0266	2.04	0.607	-	-	-	-	-
Bignoniaceae														
Zeyheria tuberculosa (Vell.) Bureau	1	0.0081	1	0.261	-	-	-	-	-	1	1.96	0.016	1.96	0.485
Boraginaceae														
Cordia ecalyculata Vell.	2	0.0651	2	0.724	-	-	-	-	-	2	3.92	0.1277	3.92	1.392
Cordia sellowiana Cham.	1	0.0115	1	0.275	-	-	-	-	-	1	1.96	0.0225	1.96	0.514
Cannabaceae														
Celtis tala Gillies ex Planch.	4	0.18	4	1.655	2	4.08	0.3528	4.08	2.381	2	3.92	0.014	3.92	0.891

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Trema micrantha (L.) Blume	3	0.0181	1	0.487	-	-	-	-	-	3	5.88	0.0356	1.96	0.911
Caricaceae														
Jacaratia spinosa (Aubl.) A. DC.	11	0.6607	7	4.698	8	16.33	1.3248	8.16	7.986	3	5.88	0.0227	5.88	1.344
Celastraceae														
Maytenus robusta Reissek	1	0.0062	1	0.253	1	2.04	0.0127	2.04	0.553	-	-	-	-	-
Chrysobalanaceae														
Hirtella hebeclada Moric. ex DC.	1	0.0282	1	0.344	-	-	-	-	-	1	1.96	0.0552	1.96	0.658
Elaeocarpaceae														
Sloanea monosperma Vell.	1	0.006	1	0.252	-	-	-	-	-	1	1.96	0.0118	1.96	0.467
Euphorbiaceae														
Actinostemon communis (Müll. Arg.) Pax	47	0.14	26	8.436	9	18.37	0.0528	16.33	4.437	38	74.51	0.2237	35.29	11.85
Actinostemon concolor (Spreng.) Müll. Arg.	4	0.0146	3	0.835	-	-	-	-	-	4	7.84	0.0287	5.88	1.54
Alchornea glandulosa Poepp.	4	0.8884	4	4.588	1	2.04	0.3752	2.04	1.965	3	5.88	1.3814	5.88	7.332

Table 1. Continued

	Forest slope				**Stand A**					**Stand B**				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Croton floribundus Spreng.	25	0.9354	19	8.748	10	20.41	0.7015	14.29	6.866	15	29.41	1.1601	23.53	10.598
Philyra brasiliensis Klotzsch	1	0.0045	1	0.246	1	2.04	0.0091	2.04	0.539	-	-	-	-	-
Sebastiania edwalliana Pax & K. Hoffm.	15	0.0479	13	3.339	5	10.2	0.0288	10.2	2.63	10	19.61	0.0663	15.69	3.949
Fabaceae-Caesalpinioideae														
Copaifera langsdorffii Desf.	1	0.0211	1	0.315	-	-	-	-	-	1	1.96	0.0414	1.96	0.597
Holocalyx balansae Micheli	34	0.2166	25	7.414	16	32.65	0.1514	26.53	7.746	18	35.29	0.2794	23.53	7.226
Hymenaea courbaril L.	5	0.468	5	3.075	3	6.12	0.8504	6.12	4.822	2	3.92	0.1007	3.92	1.273
Tachigali multijuga Benth.	2	0.3423	2	1.872	-	-	-	-	-	2	3.92	0.6711	3.92	3.787
Fabaceae-Faboideae														
Andira fraxinifolia Benth.	1	0.018	1	0.302	-	-	-	-	-	1	1.96	0.0352	1.96	0.57
Centrolobium tomentosum Guill. ex Benth.	6	0.3347	6	2.75	3	6.12	0.416	6.12	3.131	3	5.88	0.2567	5.88	2.375
Lonchocarpus muehlbergianus Hassl.	5	0.3209	4	2.331	1	2.04	0.0072	2.04	0.531	4	7.84	0.6223	5.88	4.156
Luetzelburgia guaissara Toledo	2	0.019	2	0.533	-	-	-	-	-	2	3.92	0.0372	3.92	0.993

Table 1. Continued

	Forest slope				**Stand A**					**Stand B**				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Machaerium nyctitans (Vell.) Benth.	4	0.192	4	1.704	1	2.04	0.2873	2.04	1.622	3	5.88	0.1004	5.88	1.686
Machaerium stipitatum (DC.) Vogel	3	0.0084	2	0.582	-	-	-	-	-	3	5.88	0.0165	3.92	1.072
Ormosia arborea (Vell.) Harms	4	0.0332	4	1.047	3	6.12	0.0442	6.12	1.683	1	1.96	0.0225	1.96	0.514
Fabaceae-Mimosoideae														
Acacia langsdorfii Benth.	4	0.0237	4	1.008	-	-	-	-	-	4	7.84	0.0465	7.84	1.863
Acacia polyphylla DC.	3	0.0151	3	0.745	2	4.08	0.0218	4.08	1.092	1	1.96	0.0086	1.96	0.453
Albizia cf. *niopoides* (Spr. ex Benth.) Burkart	2	0.0076	2	0.486	1	2.04	0.0042	2.04	0.52	1	1.96	0.011	1.96	0.463
Calliandra foliolosa Benth.	4	0.0145	3	0.835	2	4.08	0.0177	2.04	0.776	2	3.92	0.0115	3.92	0.88
Inga luschnathiana Benth.	3	0.0948	3	1.075	1	2.04	0.0101	2.04	0.543	2	3.92	0.1762	3.92	1.606
Piptadenia gonoacantha J.F. Macbr.	7	0.3637	7	3.097	3	6.12	0.0296	6.12	1.626	4	7.84	0.6847	7.84	4.676
Lamiaceae														
Aegiphila sellowiana Cham.	17	0.1124	4	2.579	1	2.04	0.0044	2.04	0.521	16	31.37	0.2162	5.88	4.407
Lauraceae														

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Aniba firmula (Nees & C. Mart.) Mez	1	0.0219	1	0.318	-	-	-	-	-	1	1.96	0.043	1.96	0.604
Cryptocarya moschata Nees & C. Mart.	5	0.0355	5	1.284	2	4.08	0.02	4.08	1.085	3	5.88	0.0504	5.88	1.466
Endlicheria paniculata (Spreng.) J.F. Macbr.	2	0.0151	2	0.517	1	2.04	0.0166	2.04	0.568	1	1.96	0.0136	1.96	0.474
Lauraceae 1	1	0.1169	1	0.711	1	2.04	0.2386	2.04	1.433	-	-	-	-	-
Nectandra oppositifolia Nees & Mart.	2	0.0537	2	0.677	-	-	-	-	-	2	3.92	0.1053	3.92	1.293
Ocotea beulahiae Baitello	22	0.4885	17	6.351	4	8.16	0.0663	8.16	2.272	18	35.29	0.8941	25.49	10.18
Ocotea bicolor Vattimo	1	0.0696	1	0.516	1	2.04	0.142	2.04	1.056	-	-	-	-	-
Ocotea corymbosa (Meisn.) Mez	4	0.1494	4	1.528	2	4.08	0.1402	4.08	1.553	2	3.92	0.1582	3.92	1.526
Ocotea elegans Mez	1	0.0147	1	0.288	-	-	-	-	-	1	1.96	0.0289	1.96	0.542
Ocotea indecora (Schott) Mez	12	0.1219	11	3.098	8	16.33	0.1502	14.29	4.313	4	7.84	0.0947	7.84	2.075
Ocotea odorifera (Vell.) Rohwer	4	0.0819	3	1.114	2	4.08	0.0256	2.04	0.807	2	3.92	0.1359	3.92	1.428
Lecythidaceae														
Cariniana estrellensis (Raddi) Kuntze	5	0.1051	5	1.572	2	4.08	0.1686	4.08	1.664	3	5.88	0.044	5.88	1.437

Table 1. Continued

	Forest slope				**Stand A**					**Stand B**				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Cariniana legalis (Mart.) Kuntze	6	0.0462	6	1.555	1	2.04	0.0068	2.04	0.53	5	9.8	0.084	9.8	2.443
Malvaceae														
Chorisia speciosa A. St.-Hil.	8	0.6939	8	4.692	8	16.33	1.4162	16.33	9.543	-	-	-	-	-
Eriotheca candolleana (Schum.) A. Robyns	1	0.0089	1	0.264	1	2.04	0.0182	2.04	0.575	-	-	-	-	-
Pseudobombax grandiflorum A. Robyns	3	0.0315	3	0.813	2	4.08	0.0125	4.08	1.056	1	1.96	0.0498	1.96	0.634
Melastomataceae														
Miconia pusilliflora (DC.) Naudin	1	0.0033	1	0.241	1	2.04	0.0068	2.04	0.53	-	-	-	-	-
Mouriri glazioviana Cogn.	6	0.0315	6	1.495	1	2.04	0.0059	2.04	0.526	5	9.8	0.056	9.8	2.32
Meliaceae														
Cabralea canjerana (Vell.) Mart.	4	0.1333	3	1.327	1	2.04	0.1014	2.04	0.898	3	5.88	0.164	3.92	1.722
Cedrela fissilis Vell.	1	0.0413	1	0.398	1	2.04	0.0842	2.04	0.831	-	-	-	-	-
Guarea macrophylla Vahl	1	0.0048	1	0.247	1	2.04	0.0097	2.04	0.542	-	-	-	-	-
Trichilia casaretti C. DC.	1	0.0042	1	0.245	-	-	-	-	-	1	1.96	0.0083	1.96	0.451

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Trichilia catigua A. Juss.	44	0.2372	34	9.638	29	59.18	0.2584	40.82	12.907	15	29.41	0.2169	27.45	6.93
Trichilia claussenii C. DC.	24	0.1364	15	4.809	16	32.65	0.1815	20.41	6.962	8	15.69	0.093	9.8	2.993
Trichilia elegans A. Juss	4	0.0131	3	0.829	2	4.08	0.0156	4.08	1.068	2	3.92	0.0108	1.96	0.632
Trichilia pallida Sw.	5	0.0475	5	1.333	1	2.04	0.0322	2.04	0.629	4	7.84	0.0622	7.84	1.932
Moraceae														
Brosimum glaziovii Taub.	13	0.5134	12	4.947	6	12.24	0.5058	10.2	4.691	7	13.73	0.5206	13.73	5.197
Ficus guaranitica Chodat	3	0.0534	2	0.768	-	-	-	-	-	3	5.88	0.1048	3.92	1.461
Maclura tinctoria (L.) D. Don ex Steud	6	0.2636	6	2.456	4	8.16	0.3801	8.16	3.494	2	3.92	0.1518	3.92	1.498
Myrsinaceae														
Rapanea balansae Mez	14	0.2356	13	4.024	8	16.33	0.1235	16.33	4.51	6	11.76	0.3432	9.8	3.756
Rapanea loefgrenii Mez	2	0.0069	2	0.483	2	4.08	0.014	4.08	1.062	-	-	-	-	-
Myrtaceae														
Calycorectes acutatus (Miq.) Toledo	5	0.044	5	1.319	1	2.04	0.0141	2.04	0.559	4	7.84	0.0728	7.84	1.979

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Eugenia glazioviana Kiaersk.	4	0.0214	4	0.998	3	6.12	0.0354	6.12	1.649	1	1.96	0.0079	1.96	0.449
Eugenia leptoclada O. Berg	1	0.0069	1	0.256	-	-	-	-	-	1	1.96	0.0136	1.96	0.474
Eugenia pyriformis Cambess.	1	0.0027	1	0.239	1	2.04	0.0056	2.04	0.525	-	-	-	-	-
Eugenia sp 1	3	0.0078	3	0.714	2	4.08	0.0103	4.08	1.047	1	1.96	0.0053	1.96	0.438
Eugenia sp 2	5	0.0473	5	1.333	4	8.16	0.0754	8.16	2.308	1	1.96	0.0202	1.96	0.504
Eugenia stenophylla O. Berg.	1	0.0046	1	0.246	1	2.04	0.0094	2.04	0.54	-	-	-	-	-
Myrcia fallax (Rich.) DC.	2	0.0214	2	0.543	-	-	-	-	-	2	3.92	0.0421	3.92	1.014
Myrcia richardiana (O. Berg) Kiaersk.	1	0.0022	1	0.236	-	-	-	-	-	1	1.96	0.0042	1.96	0.433
Myrciaria floribunda O. Berg.	20	0.0572	16	4.245	4	8.16	0.0247	8.16	2.11	16	31.37	0.0885	23.53	6.045
Nyctaginaceae														
Guapira opposita (Vell.) Reitz	1	0.0044	1	0.246	-	-	-	-	-	1	1.96	0.0086	1.96	0.453
Pisonia ambigua Heimerl	1	0.014	1	0.285	-	-	-	-	-	1	1.96	0.0275	1.96	0.536
Olacaceae														

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Schoepfia brasiliensis A. DC.	1	0.0286	1	0.346	-	-	-	-	-	1	1.96	0.0562	1.96	0.662
Oleaceae														
Chionanthus filiformis (Vell.) P.S. Green	2	0.0233	2	0.551	-	-	-	-	-	2	3.92	0.0456	3.92	1.03
Phyllanthaceae														
Savia dictyocarpa Müll. Arg.	88	1.1969	39	18.36	9	18.37	0.5005	14.29	5.88	79	154.9	1.8659	62.75	29.483
Phytolaccaceae														
Gallesia integrifolia (Spreng.) Harms	3	0.5299	3	2.876	2	4.08	1.0641	4.08	5.151	1	1.96	0.0167	1.96	0.488
Seguieria langsdorffii Moq.	15	0.6937	14	6.148	5	10.2	0.2765	10.2	3.594	10	19.61	1.0946	17.65	8.725
Piperaceae														
Piper amalago L.	2	0.0052	2	0.476	2	4.08	0.0106	4.08	1.048	-	-	-	-	-
Polygonaceae														
Polygonaceae 1	1	0.006	1	0.252	-	-	-	-	-	1	1.96	0.0118	1.96	0.467
Rosaceae														

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Prunus myrtifolia (L.) Urb.	1	0.0033	1	0.241	-	-	-	-	-	1	1.96	0.0066	1.96	0.443
Rubiaceae														
Alseis floribunda Schott	6	0.0855	6	1.718	2	4.08	0.0825	4.08	1.328	4	7.84	0.0885	7.84	2.048
Amaioua intermedia Mart.	4	0.0192	4	0.989	3	6.12	0.0255	6.12	1.61	1	1.96	0.0131	1.96	0.472
Guettarda uruguensis Cham. & Schltdl.	1	0.0064	1	0.254	1	2.04	0.013	2.04	0.554	-	-	-	-	-
Guettarda viburnoides Cham. & Schltdl.	1	0.006	1	0.252	-	-	-	-	-	1	1.96	0.0118	1.96	0.467
Ixora gardneriana Benth.	2	0.033	2	0.591	-	-	-	-	-	2	3.92	0.0647	3.92	1.114
Ixora venulosa Benth.	1	0.0032	1	0.241	1	2.04	0.0065	2.04	0.529	-	-	-	-	-
Rudgea jasminoides (Cham.) Müll. Arg.	10	0.0665	7	2.145	1	2.04	0.0042	2.04	0.52	9	17.65	0.1265	11.76	3.555
Simira sampaioana (Standl.) Steyerm.	3	0.0203	3	0.766	2	4.08	0.0193	4.08	1.082	1	1.96	0.0214	1.96	0.509
Rutaceae														
Almeidea lilacina A. St.-Hil.	37	0.1915	8	5.297	10	20.41	0.0901	6.12	3.284	27	52.94	0.289	9.8	7.088
Esenbeckia leiocarpa Engl.	147	5.0455	62	42.858	131	267.35	9.4567	100	78.169	16	31.37	0.8072	25.49	9.457

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Galipea multiflora Schult.	30	0.1749	18	5.928	19	38.78	0.2358	18.37	7.483	11	21.57	0.1163	17.65	4.584
Metrodorea nigra A. St.-Hil.	42	0.1889	34	9.253	9	18.37	0.074	16.33	4.52	33	64.71	0.2992	50.98	13.288
Zanthoxylum hyemale A. St.-Hil.	2	0.0405	2	0.622	1	2.04	0.0784	2.04	0.809	1	1.96	0.004	1.96	0.432
Zanthoxylum minutiflorum Tul.	2	0.0292	2	0.576	-	-	-	-	-	2	3.92	0.0572	3.92	1.081
Salicaceae														
Casearia gossypiosperma Briq.	3	0.2534	3	1.731	1	2.04	0.0094	2.04	0.54	2	3.92	0.4878	3.92	2.979
Casearia sylvestris Sw.	2	0.0327	2	0.59	1	2.04	0.0565	2.04	0.724	1	1.96	0.0098	1.96	0.458
Prockia crucis P. Browne ex L.	1	0.0097	1	0.268	1	2.04	0.0199	2.04	0.581	-	-	-	-	-
Sapindaceae														
Allophylus edulis Radlk. ex Warm.	2	0.0335	1	0.459	2	4.08	0.0684	2.04	0.973	-	-	-	-	-
Cupania vernalis Cambess.	1	0.0032	1	0.241	1	2.04	0.0065	2.04	0.529	-	-	-	-	-
Matayba elaeagnoides Radlk.	3	0.0303	3	0.808	-	-	-	-	-	3	5.88	0.0594	5.88	1.505
Sapotaceae														

Table 1. Continued

	Forest slope				Stand A					Stand B				
Family/Species	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**	**N**	**AD**	**ABA**	**AF**	**IVI**
Chrysophyllum gonocarpum Engl.	8	0.0355	8	1.966	4	8.16	0.0375	8.16	2.16	4	7.84	0.0336	7.84	1.806
Siparunaceae														
Siparuna guianensis Aubl.	1	0.013	1	0.281	-	-	-	-	-	1	1.96	0.0255	1.96	0.527
Urticaceae														
Cecropia hololeuca Miq.	3	0.2529	3	1.729	2	4.08	0.0274	4.08	1.114	1	1.96	0.4697	1.96	2.485
Urera baccifera (L.) Gaudich. ex Wedd.	29	0.579	14	6.969	8	16.33	0.4654	8.16	4.64	21	41.18	0.6882	19.61	9.049
Total	**1080**	**24.155**	**742**	**300**	**492**	**1004**	**25.679**	**679.5**	**300**	**588**	**1153**	**22.689**	**801.8**	**300**

CONCLUSÃO GERAL

Este estudo revelou que o regime natural de perturbação da floresta e a elevação do terreno influenciam a estrutura comunitária. Essa influência provavelmente se dá através da interação entre a vegetação e fatores abióticos relacionados àquelas variáveis. A elevação do terreno condiciona uma variação contínua na estrutura florestal, que pode ser percebida na forma de manchas com estruturas distintas. Além disso, a variação estrutural associada à elevação do terreno é acompanhada por uma variação particular na diversidade conhecida como desvio de dominância ecológica. Esses resultados indicam que as espécies não são equivalentes do ponto de vista ecológico, como postula a Teoria Neutra, e corroboram um modelo de organização comunitária baseado em diferenciação de nicho. Segundo esse modelo, a heterogeneidade ambiental é um dos fatores que contribuem para a coexistência de espécies que apresentam habilidades competitivas diferentes sob condições ambientais distintas. O ajuste ao modelo de montagem por diferenciação de nicho é notório em se tratando de transições ambientais abruptas, mesmo nas complexas florestas tropicais. Contudo, ao longo do gradiente ambiental sutil investigado aqui, boa parte da variação estrutural da floresta permaneceu sem explicação. Disso se infere que a variação comunitária na escala local não é determinada apenas pelo ambiente, mas também por fatores históricos e eventos estocásticos. A implicação prática para a conservação e recuperação de áreas degradadas, consiste em se reconhecer a necessidade de respeitar as preferências ou tolerâncias ecológicas das espécies, mesmo em áreas relativamente pequenas, que exibem variações ambientais sutis e graduais. Por outro lado, fica claro que não basta conservar e recuperar estreitas faixas de vegetação ao longo dos cursos de água, uma vez que a comunidade vegetal muda nas porções mais elevadas do terreno, apresentando características próprias, que também merecem ser conservadas.

A elevada diversidade e variação estrutural fizeram com que a floresta estudada constituísse um universo amostral bastante heterogêneo. Isso resultou numa baixa precisão das estimativas de abundância das espécies e em pouca estabilidade do rank de abundância. Esses resultados corroboram a informação reportada por outros autores de que a estimativa de abundância de espécies em comunidades vegetais envolve uma boa parcela de incerteza. Assim, a prática comum de comparação das espécies quanto à abundância, dentro de uma mesma floresta ou entre florestas distintas, com base na inspeção visual do rank de abundância deve ser evitada.

A comprovação de um gradiente vegetacional determinístico resultou na possibilidade de se estratificar o universo amostral para a tomada de amostras de composição de espécies. A análise de suficiência amostral para o reconhecimento de estandes distintos, feito por meio de ordenação, indicou a necessidade de amostras com oitenta parcelas de 10 x 10 m. Por outro lado, as estimativas da diversidade (Shannon), dominância (Simpson), área basal e densidade total na floresta como um todo apresentaram um nível razoável de precisão e acurácia com cinqüenta parcelas.

Os dois estandes reconhecidos na floresta apresentaram uma significativa diferenciação quanto à estrutura comunitária, reforçando a importância da estratificação do universo amostral na tomada de amostras de composição de espécies visando à investigação de padrões comunitários em pequenas escalas espaciais (meso escala). A descrição de atributos indicadores de status de classificação e conservação revelou que a mata estudada pode ser considerada uma típica e bem conservada floresta Estacional Semidecídua.

Algumas ressalvas

Neste trabalho utilizou-se a variável altura máxima na parcela como medida de perturbação (Capítulo 1). O uso dessa variável está apoiado no conceito de ecounidades (Oldeman 1990). De acordo com esse modelo conceitual, as ecounidades são fases arquiteturais observadas em uma unidade silvática, que se sucedem ao longo de uma cronosseqüência em florestas submetidas a perturbações (Oldeman 1990). Após um evento de perturbação com a destruição da biomassa aérea, ecounidades em reorganização são sucedidas por ecounidades em construção e posteriormente por ecounidades em bioestasia. A altura da vegetação é um atributo arquitetural importante para a definição de ecounidades e tende a aumentar ao longo da cronosseqüência. A utilidade da variável altura máxima na parcela como medida de perturbação depende do quanto os parâmetros do regime natural de perturbação da floresta se ajustam ao modelo conceitual. Um parâmetro importante é a escala da perturbação. Perturbações em pequena escala, representadas pela queda de galhos ou pela morte de árvores do dossel que permanecem em pé, não causam destruição da biomassa aérea que seja detectável em parcelas de 10 x 10 m através da avaliação da altura máxima na parcela. Por outro lado, tais perturbações podem alterar o microambiente o suficiente para provocar mudanças distinguíveis na estrutura da vegetação na parcela. Neste caso, a variável altura máxima na parcela, como medida de perturbação, não seria um bom previsor da estrutura comunitária. A mesma situação pode ser esperada se o tempo pós-perturbação for suficientemente longo para permitir o estabelecimento de ecounidades em construção com altura máximas comparáveis às verificadas em ecounidades em bioestasia. Assim, a variável altura máxima na parcela pode não ser muito sensível a perturbações mais antigas ou em pequena escala espacial. No presente estudo, com base no conhecimento prévio da área de amostragem na Mata Ribeirão Cachoeira (Cielo-Filho 2001), verificamos que a proporção de perturbações em escalas inferiores a 10 x 10 m e de ecounidades em fases sucessionais intermediárias não seria incompatível com o uso da variável altura máxima na parcela como previsor da estrutura comunitária. No entanto, este uso deve ser avaliado em cada caso frente às peculiaridades do regime natural de perturbação em diferentes florestas.

O Capítulo 4 tratou de um assunto muito pouco debatido na literatura ecológica, que é a suficiência amostral para descrições quantitativas de vegetação. A avaliação da suficiência amostral não pode desconsiderar os objetivos do estudo (Kenkel et al. 1989). A modelagem matemática da curva do coletor, por exemplo, é recomendada em situações em que é empregada amostragem preferencial para a investigação de padrões de vegetação perceptíveis subjetivamente (Pillar 1998). No entanto, as variações locais em florestas tropicais freqüentemente não são óbvias, e a amostragem preferencial não é adequada. Neste caso, uma estratificação estatística a posteriori poderá ser feita, e o primeiro objetivo do Capítulo 4 trata especificamente deste problema. O segundo objetivo está voltado para a investigação da suficiência amostral em estimativas de descritores de atributos indicadores de status de conservação de fragmentos da floresta Estacional Semidecídua. Para ambos os objetivos, as recomendações quanto à suficiência amostral possuem caráter de orientação. A aplicabilidade dessas recomendações irá depender do quanto o universo amostral em análise se aproxima daquele investigado na Mata Ribeirão Cachoeira em termos de tamanho e heterogeneidade ambiental. Por outro lado, o procedimento metodológico utilizado para avaliar a suficiência amostral (amostragem iterativa integrada ao método

Bootstrap, ver Pillar 2004) pode ser empregado em qualquer situação com os objetivos estabelecidos para o Capítulo 4.

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