MARKUS GASTAUER

SPECIES RICHNESS AND DIVERSITY IN THE ATLANTIC RAINFOREST AND ASSOCIATED ECOSYSTEMS: NICHE ASSEMBLY THEORIES AND NEUTRAL FORCES

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

VIÇOSA
MINAS GERAIS – BRASIL
2012

Ficha catalográfica preparada pela Seção de Catalogação e Classificação da Biblioteca Central da UFV

T
G25s
2012

Gastauer, Markus, 1976-
Species richness and diversity in the Atlantic Rainforest and associated ecosystems : niche assembly theories and neutral forces / Markus Gastauer. – Viçosa, MG, 2012.
ix, 166f. : il. ; 29cm.

Orientador: João Augusto Alves Meira Neto.
Tese (doutorado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1.Parque Estadual do Itacolomi (MG). 2. Ecologia das montanhas. 3. Ecologia Vegetal. 4. Espécies em extinção. 5. Desmatamento. 6. Biodiversidade. 7. Paisagens fragmentadas. 8. Ecologia das florestas tropicais. 9. Nicho (Ecologia). 10. Filogenia. I. Universidade Federal de Viçosa. II. Título.

CDD 22. ed. 581.7

MARKUS GASTAUER

SPECIES RICHNESS AND DIVERSITY IN THE ATLANTIC RAINFOREST AND ASSOCIATED ECOSYSTEMS: NICHE ASSEMBLY THEORIES AND NEUTRAL FORCES

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

APROVADA: 13 de abril de 2012.

Flávia Monteiro Coelho Ferreira

Flávia Maria da Silva Carmo

Ana Paula Santos Gonçalves

José Henrique Schoereder

João Augusto Alves Meira Neto
(Orientador)

Delight itself, however, is a weak term to express
the feelings of a naturalis who, for the first time,
has wandered by himself in a
Brazilian forest.
Charles Darwin, Feb. 29th, 1832

À Patrícia e Emmily,

dedico...

AGRADECIMENTOS

À minha esposa Patrícia por ser um ótimo cônjuge, mas também pela convivência de todas as decepções e dificuldades, bem como as conquistas e descobertas enfrentadas durante esse doutoramento, pela correção da minha produção textual e pelo preparo de um coquetel delicioso e inesquecível para comemorar a conclusão do meu curso.

À minha filha Emmily, que indica o que realmente importa na vida quando fala "Papai, brincar!".

Aos meus pais, por tudo que me ofereceram na vida e pela formação excelente que me habilitou concluir esse curso num pais que não é o meu.

Aos orientadores, professores, colegas dos diversos programas que cursei, estagiários, ajudantes de campo e os amigos que contribuíram para esse tese e para minha formação.

Sumário

RESUMO

GASTAUER, Markus, D.Sc., Universidade Federal de Viçosa, abril de 2012. **Riqueza das espécies e diversidade na Mata Atlântica e ecossistemas associados: Teorias de nichos e forças neutras.** Orientador: João Augusto Alves Meira Neto. Coorientadora: Andreza Viana Neri.

Na primeira parte desta tese, dois levantamentos fitossociológicos realizados em vegetação de*campo rupestre* são apresentados e comparados. A primeira área de estudo fica bem protegida dentro do Parque Estadual do Itacolomi. Asegunda área é afetada por agropecuária, fogo, e demais atividades de urbanização. Como a área impactada mostra maior riqueza e diversidade, outros indicadores para a avaliação dessa vegetação são apresentados como o número de espécies invasoras, endêmicas ou ameaçadas de extinção. A partir desses dois estudos fitossociológicos, o número de espécies de plantas de todo *campo rupestre* do Parque Estadual do Itacolomi é concordante estimado para 1100 por meio de três abordagens diferentes. As três abordagens aplicadas são (i) extrapolação da curva espécie-área com a inclinação de 0,25, que é geralmente bem aceito para plantas terrestres, (ii) o modelo de Krishnamani e (iii) o modelo de relação dos táxons. Na segunda parte da tese, uma comunidade arbórea de um hectare da Floresta de Seu Nico (FSN) é apresentado. Segundo seus proprietários, este fragmento florestal nunca foi cortado e sofreu somente extração seletiva de madeira. Portanto, a hipótese é testada que a FSN ainda apresenta características de floresta primária, como são percentuais elevados de espécies não-pioneiras, espécies dispersas por animais, espécies de sub-bosque e espécies endêmicas. A FSN cumpre todas essas premissas, especialmente a sua riqueza de espécies é notável para a região. No entanto, a dinâmica desta comunidade arbórea mostra uma perda de espécies alarmante e aumento do número de indivíduos bem como a biomassa. Perda de espécies poderia ser uma resposta retardada ao desmatamento do redor e o alto grau de fragmentação da paisagem que reduz a imigração de propágulos de espécies novas para a FSN. O aumento

da biomassa e do número de indivíduos indica aumento de disponibilidade de recursos, talvez devido às mudanças climáticas. Na terceira parte dessa tese, os mecanismos neutros e não-neutros são testados para explicar a distribuição espacial das espécies. Na FSN, as variáveis de solo e disponibilidade de luz no sub-bosque explicam pouco da distribuição espacial das espécies. A distribuição de abundância das espécies é ajustada melhor pelos modelos derivados de pressupostos neutros. A análise filogenética da comunidadena FSN, no entanto, indica sobredistribuição filogenética significativa devido à força alta de nichos, competição interespecífica e fatores de dependenciade densidade negativa. Como variáveis edáficas mostram um gradientepequeno e explicam apenas pouca variação na distribuição espacial das espécies, fatores bióticos como formuladas na hipótese de Janzen-Connell devem responder por essa distribuição formando um mosaico de diferentes nichos ecológicos.

ABSTRACT

GASTAUER, Markus, D.Sc., Universidade Federal de Viçosa, April, 2012. **Species richness and diversity in the Atlantic Rainforest and associated ecosystems: Niche assembly theories and neutral forces.** Adviser: João Augusto Alves Meira Neto. Co-adviser: Andreza Viana Neri.

In the first part of this thesis, two phytosociological surveys carried out in *campo rupestre* vegetation are presented and compared. One study site lies well-protected within the Itacolomi State Park. The other one is impacted by extensive pasture, fire, and settling activities. As the impacted area shows higher species richness and diversity, further indicators for the intactness of this vegetation are presented like number of invasive, endemic or endangered species. From both surveys, the number of plant species from the Itacolomi State Park´s *campos rupestre* is concordantly estimated to 1100 using three different approaches, the species-area realtionship with the generally accepted slope of 0.25 for terrestrial plants, the Krishnamani model and the taxon ratio model. In the second part, a one hectare tree community from the Forest of Seu Nico (FSN) is presented. According to its owners, this forest fragment never has been logged. Therefore, the hypothesis was tested that the FSN still shows characteristics as a primary forest, as they are elevated percentages of non-pioneer, animal-dispersed, understory and endemic species. The FSN fulfills all requirements, especially its species richness is outstanding for the region. Nevertheless, the dynamics of this tree community show an alarming loss of species and increase of number of individuals as well as biomass. Species loss might be a time-delayed answer to comprehensive logging and high degree of fragmentation and isolation in the landscape reducing immigration of propagules from new species to the FSN. Increase of biomass and number of individuals is a hint for increased resource availability, perhaps due to climate change. In the third part, neutral and non-neutral mechanisms are tested to explain spatial species distributions. In the FSN, soil variables and understory light availability explain little spatial species distribution, species abundance distribution is

furthermore best fit by models derived from neutral assumptions. A phylogenetic analysis of the community nevertheless indicates significant phylogenetic clustering due to niche assembly, interspecific competition and negative density-dependence factors. As edaphic variables show a short gradient only and explain little variance, biotic factors as formulated in the Connell-Janzen hypothesis should account for spatial species distribution forming a small-scaled mosaic of different ecological niches.

General Introduction

Nevertheless species richness and diversity from all over the world are threatened and influenced by climate change (IPCC 2007), habitat loss and landscape´s fragmentation (Wright 2010), the discussion about what maintains species richness and diversity is still not at end. This lack of knowledge comprises especially the underlying – ecological – mechanisms like neutrality (Hubbell 2001), environmental sorting (Carvender-Bares *et al*. 2004) or niche assembly due to environmental heterogeneity (Hutchinson 1957) and negative density-dependant factors (Janzen 1971, Connell 1971) that may form and maintain species rich and diverse ecosystems.

Before the Europeans arrived in South America, the Atlantic Rainforest, once classified as a *hotspot* of biodiversity (Myers *et al.* 2001) due to high species richness and a high degree of endemism (Stehmann *et al.* 2010), covered between 1.300.000 and 1.500.000 km^2 (Câmara 2005). Much of that has been logged and until today only 11 to 16 % of the original vegetation cover remainedin isolated fragments (Ribeiro *et al.* 2009). Most of these fragments are secondary forests smaller than 100 ha.

In the Espinhaço Mountain Range, these forests are displaced by rocky outcrop vegetation types above certain altitudes (usally above 900 m).These *campos rupestres* (literally rockfields) are species-rich ecosystems containing many endemic species (Giulietti *et al.* 1987, Conceição & Giulietti 2002; Caiafa & Silva 2005) over sandstones and shallow sandy soils.

Because most natural ecosystems are influenced by direct or indirect anthropogenic impacts, it is a great challenge to find out which part of natural ecosystems is pristine, which part is altered due to anthropogenic activities and how to evaluate intactness of a natural ecosystem. For whom is interested in these aspects of biodiversity and species richness, chapters 1 and 3 are recommended. In the first chapter, the importance of alternative indicators for intactness of *campo rupestre* vegetation like invasive, endemic or endangered species is discussed. In the third chapter, the hypothesis is tested that the Forest of Seu Nico (FSN), which never has been logged, still shows characteristics of a primary, pristine Atlantic Rainforest patch.

Another challenge is to answer the question about how many species are there in a forest fragment, a park or another spatial entity.Such extent of species

distribution is necessary to predict extinction rates caused by human impacts (Lewis 2006), declare biological hotspots (Myers *et al.* 2000) and learn more about ecosystem function. Departing from two phytosociological surveys, the author tried to estimate the number of plant species from the Itacolomi State Park in the second chapter.

By forest dynamic studies, alterations within natural communities can be detected and – taken ecological theory in account (e.g. MacArthur & Wilson 1967, Hubbell 2001, Ernest et al. 2009) – assigned to major environmental alterations due to economic activities of humans. Like that, the role of habitat loss, landscape´s fragmentation and climate change on species richness, diversity and accumulation of biomass in the FSN are highlighted in the forth chapter.

Finally, in the fifth chapter of this thesis, different theory – neutral and non-neutral ones – competingin explaining spatial species distribution patterns are tested by different methods (Leibold *et al.* 2004, Chave 2008). Looking for species-environment correlations, fitting species abundance distributions, comparing similarity between different tree communities and revealing the phylogenetic community structure, neutral models (Hubbell 2001) are tested versus non-neutral ones (Hutchinson 1957, Carvender-Bares *et al.* 2004). From that, the author hopes to answer questions about the factors that guarantee the co-existence of a high variety of species in tropical forests and associated ecosystems.

References

CAIAFA, N. A. AND A. F. SILVA. 2005. Composição floristica e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais – Brasil. Rodriguésia 56: 163-173.

CÂMARA, I. G. 2005. Breve história da conservação da Mata Atlântica. In: GALINDO-LEAL, C. AND CÂMARA, I. G. (Eds.), Mata Atlântica: biodiversidade,

ameaças e perspectivas, pp. 31-42. Fundação SOS Mata Atlântica/Conservação Internacional, São Paulo/Belo Horizonte, BR.

CARVENDER-BARES , J., D. D. ACKERLEY, D. A. BAUM, AND F. A. BAZZAZ. 2004. Phylogenetic overdispersion in Floridian oak communities. Am Naturalist 163: 823-843.

CHAVE, J. 2009. Competition, Neutrality, and Community Organization. In: LEVIN, S. A. (Ed.). The Princeton Guide to Ecology, pp. 264-273. Princeton University Press, Princeton, UK.

CONCEIÇÃO, A. A. AND A. M. GIULIETTI, 2002. Composição florística e aspectos estruturais de campo rupestre em dois platôs do Morro do Pai Inácio, Chapada Diamantina, Bahia, Brasil. Hoehnea 29:37-48.

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain Forest trees. In: BOER, P. J. AND GRADWELL, G. R. (Eds.). Dynamics of Populations, pp 198-310. Center for Agricultural Publishing and Documentation, Wageningen, BE.

ERNEST K. M., E. P. WHITE AND J. H. BROWN. 2009. Changes in a tropical forest support metabolic zero-sum dynamics. Ecol Lett 12: 507–515.

GIULIETTI A. M., N. L. MENEZES, J. R. PIRANI, M. MEGURO, AND M. G. L. WANDERLEY. 1987. Flora da Serra do Cipó, Minas Gerais: Caracterização e lista das espécies. Bol Bot Univers São Paulo 9:1-151.

HUBBEL, S. P. 2001. The Unified Theory of Biodiversity and Biogeography.Princeton University Press, Princeton, UK.

HUTCHINSON, G. E. 1957. Concluding remarks.Cold Spring Harbor Symposia on Quantitative Biology22: 415–427.

IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE) 2007. Climate Change 2007 – The Physical Science Basis. Contribution of Working Group I to the Forth Assessent Report of the IPCC. Cambridge University Press,Cambridge, UK.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. Am Naturalist 104: 501-528.

LEWIS, O. T. 2006. Climate change, species-area curves and the extinction crisis. PhilTrans R Soc B 361:163-171.

LEIBOLD, M. A., M. HOLYOAK, N. MOUQUET, P. AMARASEKARE, ET AL. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601-613. doi: 10.1111/j.1461-0248.2004.00608.x

MACARTHUR, R., AND E. O. WILSON. 1967.The Theory of Island Biogeography. Princeton University Press, Princeton, 203 p.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. FONSECA, AND J. KENT.2000. Biodiversity hotspots for conservation priorities. Nature 403:453-458.

RIBEIRO, M.C., J. P. METZGER, A. C. MARTENSEN, F. J. PONZONI, AND M. M. HIROTA. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. BiolConserv 142: 1141–1153.

STEHMANN, J. R., R. C. FORZZA, A. SALINO, M. SOBRAL, D. P. COSTA, AND L. H. Y.KAMINO (Org.) 2009. Plantas da Floresta Atlântica. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, BR.

WRIGHT, S. J. 2010. The future of tropical forests.Annals of the New York Academy of Sciences 1195: 1-27.

CHAPTER 1*

Floristic Composition, Species Richness and Diversity of campo rupestre vegetation from the Itacolomi State Park, Minas Gerais, Brazil

* This chapter will soon be submitted to **Revista Árvore**.

Floristic Composition, Species Richness and Diversity of *campo rupestre* vegetation from the Itacolomi State Park, Minas Gerais, Brazil

Markus Gastauer[1], Maria Cristina Teixeira Braga Messias[2] & João Augsuto Alves Meira Neto[1*]

[1] Plant Ecology Laboratory, Plant Biology Department, Federal University of Viçosa, Viçosa, 36570-000, Minas Gerais, Brazil

[2] Department of Biodiversity, Evolution and the Environment. Federal University of Ouro Preto, 35400-000, Ouro Preto, Minas Gerais, Brazil.
e-mail: cristina@iceb.ufop.br

[*] Corresponding author: j.meira@ufv.br

Abstract

Nevertheless *campos rupestres* are considered species rich and diverse vegetation formations, phytosociological surveys from the Itacolomi State Park, Minas Gerais, Brazil are lacking in scientific literature. To close this gap, we compared floristic composition, species richness and diversity from two sites, Lagoa Seca and Calais, situated within the park. Calais is moderately impacted by extensive pasture, fire, and settling activities. Both surveys contained 15 plots of 10 x 10 m, cardinality of each species was estimated. Beside species-richness, the indexes of Shannon-Wiener, Fisher's α, the community richness estimator Jackknife 1 and the numbers of endemic, endangered and invasive species were compared. With 107 species, the moderately impacted Calais showed higher species richness than Lagoa Seca (76 species). The indices of Shannon-Wiener and Fisher's α, the community richness estimator, as well as point diversity and spatial turnover derived from the species-area relationship (SAR) indicated higher diversity for Calais. From Lagoa Seca, 30% of all species are endemic to the Atlantic Rainforest or to Cerrado, and four species are endangered, not any species found in Lagoa Seca is described as an invasive one. On the other hand, 23 species found in Calais are invasive species, only one from all 107 species is endangered. Only 19% of all species found in Calais are endemic. Nevertheless species richness and diversity differ between both study sites, they are exceptionally high compared to similar vegetation formations from further regions. This justifies the declaration of the park as a local hotspot of biodiversity. Furthermore, our results prove that species richness or diversity measures are inappropriate criteria to evaluate the intactness of *campo rupestre* vegetation. More weight should be put on criteria like numbers of invasive, endemic or endangered species.

Keywords: endemism, endangered species, invasive species, conservation, species-area relationship, spatial turnover.

Resumo

Mesmo que campos rupestres são considerados ecossistemas ricos em espécies e extremamente diversas, levantamentos fitossociológicos do Parque Estadual do Itacolomi, Minas Gerais, Brasil, faltam na literatura cientifica. Para fechar essa lacuna, foram comparadas a composição florística, a riqueza e a diversidade de duas áreas, Lagoa Seca e Calais, ambas localizadas no entorno do parque. Calais é moderadamente impactado por agropecuária, fogo, e atividades de urbanização. Durante os levantamentos fitossociologicas, a cardinalidade de todas as espécies ocorrendo em 15 parcelas de 10x10m foi estimada. Além da riqueza de espécies, os índices de Shannon-Wiener e de Fisher´s α, o estimador da riqueza da comunidade Jackknife 1 e os números de espécies endêmicas, ameaçadas e invasoras foram comparados. Calais, mesmo sendo moderadamente impactado, mostrou com 107 espécies maior riqueza do que Lagoa Seca (apenas 76 espécies). Além disso, os índices de Shannon-Wiener e de Fisher´s α, o estimador de riqueza da comunidade, bem como a diversidade pontual e o *turnover* espacial derivada da relação espécie-área indicou maior diversidade para Calais. 30% de todas as espécies encontradas em Lagoa Seca são endêmicas da Mata Atlântica ou de Cerrado, e quatro espécies estão ameaçadas. Nenhuma das espécies encontradas em Lagoa Seca é descrito como invasiva. Por outro lado, 23 das espécies encontradas em Calais são espécies invasoras e apenas uma das 107 espécies está ameaçada. Apenas 19% de todas as espécies encontradas em Calais são endêmicas. Mesmo que a riqueza de espécies e a diversidade diferem entre as duas áreas de estudo, eles são excepcionalmente elevados em comparação com formações vegetais similares de outras regiões. Isso justifica a classificação do Parque Estadual do Itacolomi como *hotspot* local da biodiversidade. Além disso, nossos resultados mostram que as medidas de riqueza de espécies ou diversidade são critérios inadequados para avaliar a integridade de vegetação de campo rupestre. Na sua avaliação, mais peso deve ser colocado em critérios como número de espécies invasoras, endêmicas ou ameaçadas de extinção.

Palavras chave: endemismo, espécies ameaçadas, espécies invasoras, conservação, relação espécie-área, *turnover* espacial.

1. Introduction

In the Brazilian Mountain Ranges, forests are displaced by rocky outcrop vegetation types above certain altitudes (usually 900 m, SCOLFORO; CARVALHO, 2006). These rock fields are species-rich ecosystems containing many endemics (CAIAFA; SILVA, 2005; CONCEIÇÃO; GIULIETTI, 2002; GIULIETTI et al., 1987; JACOBI et al., 2008; MESSIAS et al., 2011; PIRANI et al., 1994; ROMERO; NAKAJIMA, 1999). Although endangered due to the intensification of grazing, fire clearing, continued urbanization, dispersion of invasive plant species, collection of endangered (medical) plants, mining activities and nutrient input from industry and traffic (PIRANI et al., 2003), still little is known about species composition and diversity of these ecosystems (ALMEIDA, 2008; MESSIAS et al., 2011; MOURÃO; STEHMANN, 2007).

Due to the geological underground, three different types of rocky outcrop vegetation can be distinguished, but differentiation is not unambiguous (ALVES; KOLBECK, 2009). We adapt the Alves and Kolbeck (2009) system, where *campo de altitude* (MARTINELLI et al., 1989), a term synonym for Brazilian *páramos* (SAFFORD, 2007), is restricted to granite and nephelin-syenite soils. *Canga* (sometimes missleadingly called *campo rupestre ferruginoso*) is bound to ironstone outcrops or lateric crusts (JACOBI et al., 2007). Finally, *campo rupestre* are found on quartzite outcrops or white sand only.

The Espinhaço Mountain Range forms the transition zone between the Atlantic Rainforest and the Cerrado biome (IBGE 2004). In the Iron Quadrangle, the Southern part of the Espinhaço Mountain Range where the Itacolomi State Park is located, a mosaic of *campo rupestre*, *canga*, Seasonal Semideciduous Mountain Forests and associated vegetation forms (DUTRA et al., 2009; PERON, 1989), forms an extremely species-rich and diverse landscape (FUNDAÇÃO BIODIVERSITAS, 2005).

With at least two species endemic to the park (BATISTA et al., 2004, DUTRA et al., 2008), the Itacolomi State Park contributes exceedingly to the diversity and species richness of the Iron Quadrangle. Nevertheless, botanical research activities are limited to compile voluminous plant lists (ALMEIDA

2008), but systematic phytosociological surveys measuring and comparing biological diversity are widely lacking for this region.

The aim of this paper is to close this gap presenting phytosociological surveys from two study sites within and nearby the Itacolomi State Park focusing on two topics: It is first tested, if the species richness and diversity found within and around the park is above average as described from literature. As both study sites differ in their disturbance regime, different indicators to measure and evaluate the intactness, i.e. the absence of impairments, of *campo rupestre* vegetation.

2. Material and Methods

2.1. Study Sites

The first study site, Lagoa Seca (dry pond in English), is situated near a periodically inundated area at the coordinates 20°26’ S and 43°29’ W, 1600 m above sea level. The second area, joining the margin of the park and the Ouro Preto urban district of Calais, is located at 20°25’ S and 43°30’ W at an altitude of 1270 m above sea level. Distance between both study sites is about three kilometres.

Both areas show a homogeneous, small-scaled mosaic of gramineous vegetation, small shrubs and rocky outcrops. While Lagoa Seca is well protected from anthropogenic impacts within the Itacolomi State Park, Calais is moderately disturbed by extensive grazing and burning. Settlement activities such as construction and waste deposits also threaten the area.

The climate of the region corresponds to Köppen’s climatic type Cwb (PEEL et al., 2007), i.e. mesothermic, with a rainy summer concentrated from November-March and a dry winter (NIMER, 1989). The average temperature ranges from 17 to 18.5° C, with an annual precipitation between 1450 and 1800 mm (WERNECK et al., 2000). According to Harley and Simmons (1986), the climate is moderated by moisture-laden clouds providing humidity as rain or dew throughout most of the year at high altitudes.

2.2. Data collection

The phytosociological survey was carried out in February 2009 using the plot method (MUELLER-DOMBOIS; ELLENBERG, 1974; NEWTON, 2007). In each study site, fifteen plots of 10 x 10 m were arranged in three rows. The distance between plots, both within and between rows, was 10 m.

All species within plots were collected, identified and grouped according to the Angiosperm Phylogeny Group (APG III 2009). The cardinality of each species was estimated using a combination of abundance (i.e. number of individuals or shoots) and vegetation cover as proposed by Reichelt and Wilmanns (1973, Table 1). All the collected specimens were herborized and deposited in the “Professor José Badini Herbarium” (OUPR) of the Federal University of Ouro Preto.

2.3. Floristic composition

The presence of invasive, endemic and threatened species was verified. Invasive species are exotic species, i.e. species which do not naturally occur in the studied area, as well as ruderal species indicating disturbances or impacts according to Aranha et al. (1982), Bacchi et al. (1984) and Leitão Filho et al. (1982). Endemic species are species endemic to the Cerrado or to the Atlantic rainforest biomes or species occurring in both biomes, but lacking in others. The species endemism data were taken from Stehmann et al. (2009) and Forzza et al. (2010). We consulted COPAM (2008) for information about threatened species. This is the most recent, but still unofficial red list of Minas Gerais.

2.4. Species richness and diversity measures

The number of species (i.e. species richness) was compared between both study sites.

The biodiversity indices of Shannon-Wiener and Fisher´s α were calculated for each study site with the software EstimateS (COLWELL; CODDINGTON, 1994). For that, vegetation cover of each species, derived from its cardinality as shown in Table 1, was used as a measure for abundance.

Based on presence-absence data only, the community richness for each study site was estimated by Jackknife 1. This estimator was calculated with EstimateS (Colwell; Coddington 1994).

The Sørensen similarity has been calculated between all 15 plots from each study site with the software EstimateS. Furthermore, Sørensen and Jaccard similarity has been computed between both study sites, using the same computer package.

Table 1 – Categories of species cardinality, defined according to Reichelt & Wilmanns (1973) and transformation to vegetation cover, an indirect measure for abundance

Tabela 1 – Categorias de cardinalidade das espécies, definidas de acordo com Reichelt & Wilmanns (1973) e sua transformação para cobertura vegetal, uma medida indireta de abundância

Category	Definition	Transformed vegetation cover [%]
r	Species with only one individual and less than 5% of vegetation cover	1
+	Species with two to five individuals and covering less than 5%	2
1	Species with six to 50 individuals and less than 5% of vegetation cover	3
2m	Species with more than 50 individuals and less than 5% of vegetation cover	4
2a	Species covering 6 to 15%	10
2b	Species covering 16 to 25%	20
3	Species covering 26 to 50%	38
4	Species covering 51 to 75%	63
5	Species covering 76 to 100%	88

2.5. Species-area relationships (SAR)

The species-accumulation curve from both areas was fitted by the power model proposed by Arrhenius (1921). For that, we calculated the average number of species of groups of two, four, seven, and finally all the 15 plots of each survey. Only neighbouring plots were grouped. Linearized after log-

transformation, the intercept of the SAR with the y-axis is a proxy of point or α-diversity, while the slope describes the difference between plots and might therefore be interpreted as a proxy for spatial turnover, or β-diversity (CONDIT et al., 1996).

3. Results

3.1. Floristic composition

In Lagoa Seca, 76 species from 55 genera and 25 families were found. In Calais the species richness was higher, with 107 species from 82 genera and 33 families (Table 2). The number of species per plot varied between 16 and 33 (on average 23.3 ±4.98) in Lagoa Seca and from 21 to 43 (on average 31.9 ±7.74) in Calais. Twenty two species occurred in both surveys.

The most abundant families in both surveys were Asteraceae, Poaceae, Cyperaceae and Melastomataceae. The family Fabaceae, well-represented in Calais, was absent in Lagoa Seca. Orchidaceae showed a greater richness in the Lagoa Seca area (6 species) compared with Calais (1 species).

From the total of 161 collected species in both study sites, four are considered as endangered according to COPAM (2008): *Richterago amplexifolia*, *Coppensia warmingii* and *Stachytarpheta commutata,* which occurred only in the Lagoa Seca area, while the fourth, *Sporobolus metallicolus,* was found in both study sites.

Twenty two species occurring in Calais, but none of those from the Lagoa Seca area, were considered invasive species (Table 2). Three of them, *Melinis minutiflora*, *Poa annua*, and *Urochloa decumbens,* are species introduced to South America by humans.

From all 161 collected species, 36 were restricted to the Atlantic Rainforest or the Brazilian Cerrado biomes. Twenty three of all endemic species were found in the Lagoa Seca area (30% of all species from this survey), while the Calais survey contained only 20 species endemic to the Atlantic Rainforest or the Cerrado biome (19% of species found within this survey, Figure 1).

Table 2 – Species list from two phytosociological surveys of *campo rupestre* vegetation at Lagoa Seca and Calais, Itacolomi State Park, Minas Gerais, Brazil, with endemism to the Cerrado or Atlantic Rainforest biomes, and further information about endangerment and their invasive character. ARF is species endemic to the Atlantic Rainforest biome; CE is endemic to the Cerrado biome, CE-ARF is endemic to Cerrado and Atlantic Rainforest biomes, EX is exotic species, CR is critically endangered, IP is invasive species, VU is vulnerable threatened according to COPAM (2008). * Information from Stehmann et al. (2009), ** information from Forzza et al. (2010)

Tabela 2 – Lista de espécies de dois levantamentos fitossociológicos de vegetação de *campo rupestre* em Lagoa Seca e Calais, Parque Estadual do Itacolomi, Minas Gerais, Brasil, com endemismo para os biomas Cerrado e Mata Atlântica, e informações sobre sua vulnerabilidade e seu caráter invasivo. ARF é espécie endêmica ao bioma Mata Atlântica; CE é espécie endêmica ao bioma Cerrado, CE-ARF é espécie endêmica nos dois biomas Cerrado e Mata Atlântica, EX é espécie exótica, CR é espécies criticamente ameaçada, IP é espécie invasora, VU é espécie vulnerável. * informações segundo Stehmann et al. (2009), ** informações segundo Forzza (2010)

Family/Species	**Lagoa Seca**	**Calais**	**Endemism**	**Endangerment / invasive character**
		LYCOPODIOPHYTA		
Selaginellaceae				
Selaginella sp.	X			
		PTERIDOPHYTA		
Anemiaceae				
Anemia ferruginea Humb. & Bonpl. *ex* Kunth		X		
Blechnaceae				
Blechnum schomburgkii (Klotzsch) C.Chr.		X	CE-ARF**	
Dennstaedtiaceae				
Pteridium arachnoideum (Kaulf.) Maxon		X		
Doryopteridaceae				
Doryopteris ornithopus (Hook. & Baker) J.Sm	X			

Continued...

Table 2. Continued.

Family/Species	Lagoa Seca	Calais	Endemism	Endangerment / invasive character
Gleicheniaceae				
Dicranopteris flexuosa (Schrad.) Underw.		X		IP
Polypodiaceae				
Pecluma pectinata (L.) M.G.Price		X		
ANGIOSPERMS - MAGNOLIIDS				
Annonaceae				
Guatteria villosissima A.St.-Hil.		X	ARF**	
Aristolochiaceae				
Aristolochia sp.	X			
ANGIOSPERMS - MONOCOTS				
Bromeliaceae				
Cryptanthus schwackeanus Mez	X		CE-ARF**	
Cyperaceae				
Fimbristylis sp.	X			
Rhynchospora consanguinea (Kunth) Boeckeler	X			
Rhychnospora corymbosa (L.) Britton		X		IP
Rhychnospora cf. *tenuis* Link		X		IP
Rhynchospora sp.1	X			
Rhynchospora sp.2	X			
Rhynchospora sp.3		X		
Scleria hirtella Sw.	X	X		
Scleria sp.		X		
Trilepis microstachya (C.B.Clarke) H.Pfeiff.	X	X	ARF*	
Cyperaceae sp.1	X	X		
Cyperaceae sp.2	X			
Cyperaceae sp.3	X	X		
Cyperaceae sp.4		X		
Commelinaceae				
Dichorisandra thyrsiflora J.C.Mikan		X	ARF*	
Tradescantia ambigua Mart.		X		
Dioscoreaceae				
Dioscorea sp.		X		
Hypoxidaceae				
Hypoxis decumbens L.		X		
Iridaceae				
Neomarica cf. *glauca* (Seub. *ex* Klatt) Sprague	X		CE-ARF**	

Continued...

Table 2. Continued.

Family/Species	Lagoa Seca	Calais	Endemism	Endangerment / invasive character
Sisyrinchium vaginatum Spreng.		X		
Orchidaceae				
Coppensia blanchetii (Rchb.f.) Campacci	X			
Coppensia warmingii (Rchb.f.) Campacci	X			VU
Epidendrum denticulatum Barb.Rodr.	X			
Habenaria cf. *rupicola* Barb.Rodr.	X		CE-ARF**	
Habenaria sp.	X			
Sacoila lanceolata (Aubl.) Garay		X		
Sophronitis sp.	X			
Poaceae				
Andropogon leucostachyus Kunth		X		IP
Apochloa poliophylla (Renvoize & Zuloaga) Zuloaga & Morrone		X	CE-ARF**	
Aristida sp.	X			
Axonopus siccus (Nees)Kuhlm.		X		
Chloris sp.		X		
Eragrostis maypurensis (Kunth)Steud.		X		IP
Ichnanthus bambusiflorus (Trin.)Döll	X	X		
Melinis minutiflora P.Beauv.		X	EX	IP
Otachyrium versicolor (Döll)Henrard	X			
Panicum pseudisachne Mez	X	X		
Panicum wettsteinii Hack.	X	X		
Paspalum coryphaeum Trin.	X			
Paspalum hyalinum Nees *ex* Trin.		X		
Paspalum multicaule Poir.	X			
Paspalum notatum Flüggé		X		IP
Paspalum plicatulum Michx.		X		
Pennisetum setosum (Sw.)Rich.		X		IP
Poa cf. *annua* L.		X	EX	IP
Schizachyrium sanguineum (Retz.) Alston	X	X		
Sporobolus metallicolus Longhi-Wagner & Boechat	X	X	CE**	VU

Continued...

Table 2. Continued.

Family/Species	Lagoa Seca	Calais	Endemism	Endangerment / invasive character
Urochloa decumbens (Stapf) R.D.Webster		X	EX	IP
Poaceae sp.1	X			
Poaceae sp.2	X	X		
Poaceae sp.3		X		
Smilaceae				
Smilax oblongifolia Pohl *ex* Grieseb.	X		CE**	
Velloziaceae				
Vellozia compacta Mart. *ex* Schult. & Schult. f.	X		CE**	
Xyridaceae				
Xyris cf. *plantaginea* Mart.	X		CE**	
Xyris sp.1	X			
Xyris sp.2	X			
ANGIOSPERMS - EUDICOTS				
Acanthaceae				
Ruellia macrantha (Nees) Lindau		X		
Amaranthaceae				
Amaranthaceae sp.		X		
Apiaceae				
Eryngium paniculatum Cav. & Dombey *ex* F.Delaroche	X			
Apocynaceae				
Oxypetalum appendiculatum Mart.		X		
Araliaceae				
Hydrocotyle quinqueloba Ruiz & Pav.	X			
Asteraceae				
Acanthospermum australe (Loefl.) Kuntze		X		IP
Achyrocline satureioides (Lam.) DC	X	X		
Baccharis aphylla (Vell.) DC	X			
Baccharis sessiliflora Vahl		X		
Baccharis dracunculifolia DC.		X		IP
Baccharis platypoda DC.	X			
Baccharis reticularia DC.	X			
Baccharis serrulata (Lam.) Pers.	X	X		

Continued...

Table 2. Continued.

Family/Species	Lagoa Seca	Calais	Endemism	Endangerment / invasive character
Baccharis sp.	X	X		
Chaptalia nutans (L.) Pol.		X		IP
Cyrtocymura scorpioides (Lam.) H.Rob.		X		IP
Eremanthus crotonoides (DC.) Sch.Bip.		X	CE-ARF**	
Eremanthus erythropappus (DC.) MacLeish	X	X	CE-ARF**	
Eremanthus incanus (Less.) Less.	X	X		
Eupatorium sp.		X		
Koanophyllon adamantium (Gardner) R.M.King & H.Rob.	X			
Mikania nummularia DC.	X	X	CE-ARF**	
Mikania sp.	X			
Pterocaulon lanatum Kuntze		X	CE**	
Richterago amplexifolia (Gardner) Kuntze	X		CE**	VU
Senecio adamantinus Bong.	X	X	CE-ARF**	
Stenocline sp.	X			
Stevia clausseni Sch.Bip. *ex* Baker		X	CE**	
Trichogonia sp.		X		
Vernonia sp.1		X		
Vernonia sp.2		X		
Boraginaceae				
Varronia curassavica Jacq.		X		
Campanulaceae				
Lobelia camporum Pohl	X		CE-ARF**	
Droseraceae				
Drosera montana A.St.-Hil.	X			
Fabaceae				
Aeschynomene elegans Schltdl. & Cham.		X		
Chamaecrista flexuosa (L.) Greene		X		
Chamaecrista rotundifolia (Pers.) Greene		X		
Crotalaria sp.		X		
Dalbergia brasiliensis Vogel		X	ARF*	
Desmodium adscendens (Sw.) DC.		X		IP
Desmodium barbatum (L.) Benth.		X		IP
Inga sessilis (Vell.) Mart.		X		

Continued...

Table 2. Continued.

Family/Species	Lagoa Seca	Calais	Endemism	Endangerment / invasive character
Mimosoideae sp.		X		
Periandra mediterranea (Vell.) Taub.		X		
Senna reniformis (G.Don) H.S.Irwin & Barneby		X		
Stylosanthes viscosa (L.) Sw.		X		
Zornia reticulata Sm.		X		
Lamiaceae				
Hyptis homolophylla Pohl *ex* Benth.	X	X	CE**	
Hyptis monticola Mart. *ex* Benth.	X		CE-ARF**	
Lentibulariaceae				
Genlisea repens Benj.	X			
Utricularia amethystina Salzm. ex A.St.-Hil. & Girard	X			
Lythraceae				
Cuphea carthagenensis (Jacq.) J.Macbr.		X		
Cuphea sp.		X		
Diplusodon buxifolius (Cham. & Schltdl.) A.DC.		X	CE**	
Malpighiaceae				
Banisteriopsis campestris (A.Juss.) Little		X		
Byrsonima variabilis A.Juss.	X	X		
*Heteropterys s*p.		X		
Malvaceae				
Sida linifolia Cav.		X		
Wissadula sp.		X		
Melastomataceae				
Cambessedesia hilariana (Kunth) DC.	X	X	CE-ARF**	
Lavoisiera sp.	X			
Leandra cf. *australis* (Cham.) Cogn.	X		ARF*	
Miconia pepericarpa DC.		X	CE**	
Miconia sp.1		X		
Miconia sp.2		X		
Microlicia crenulata Mart.	X		CE-ARF**	
Microlicia sp.1	X			
Microlicia sp.2	X			
Microlicia sp.3		X		
Tibouchina cardinalis (Humb. & Bonpl.) Cogn.	X		CE**	

Continued...

Table 2. Continued.

Family/Species	Lagoa Seca	Calais	Endemism	Endangerment / invasive character
Tibouchina heteromalla (D.Don) Cogn.		X	CE-ARF**	
Myrsinaceae				
Ardisia sp.	X			
Myrsine umbellata Mart.	X		ARF**	
Myrtaceae				
Myrcia amazonica DC.		X		
Myrcia eryocalix DC.	X			
Myrcia splendens (Sw.) DC.	X	X		
Myrcia subcordata DC.	X		ARF**	
Polygalaceae				
Polygala paniculata L.	X	X		
Polygala violaceae Aubl.		X		
Proteaceae				
Roupala montana Aubl.	X			
Rosaceae				
Rubus brasiliensis Mart.		X		IP
Rubiaceae				
Diodella teres (Walter) Small		X		IP
Borreria verticillata (L.) G.Mey		X		IP
Rutaceae				
Dictyoloma vandellianum A.Juss.		X		
Salicaceae				
Casearia sylvestris Sw.		X		
Sapindaceae				
Matayba marginata Radlk.		X	CE-ARF**	
Solanaceae				
Brunfelsia brasiliensis (Spreng.) L.B.Sm. & Downs	X		CE-ARF**	
Schwenckia americana Rooyen *ex* L.		X		
Solanum americanum Mill.		X		IP
Solanum cf. *granulosoleprosum* Dunal	X	X	-	
Verbenaceae				
Lantana camara L.		X		IP
Lantana fucata Lindl.		X		IP
Lippia hermannioides Cham.		X	CE**	
Stachytarpheta commutata Schauer	X		CE**	CR
161 species	**76**	**107**		

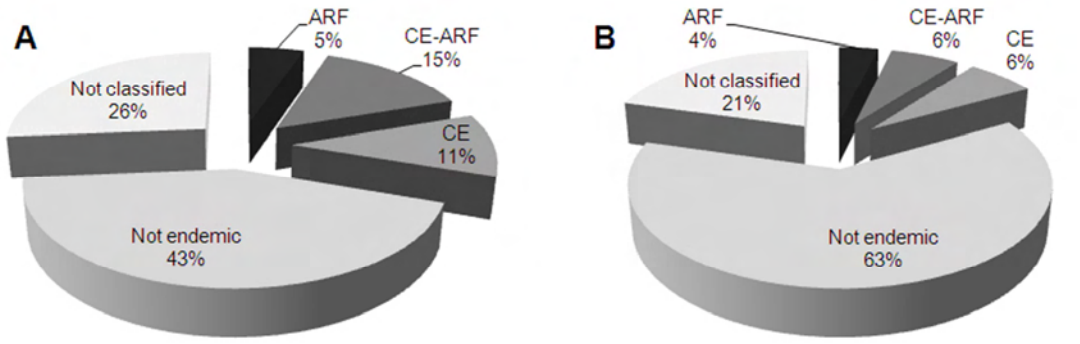


Figure 1 – Percentage of species endemic to the Atlantic Rainforest or the Cerrado biome found in Lagoa Seca (A) and Calais (B), two phytosociological surveys of *campo rupestre* vegetation, Itacolomi State Park, Minas Gerais, Brazil. ARF is the percentage of species occurring only in the Atlantic Rainforest biome, CE is the percentage of species occurring only in the Cerrado biome, and CE-ARF is the percentage of species endemic to both biomes.

Figura 1 – Percentagem de espécies endêmicas nos biomas Mata Atlântica e Cerrado encontradas em Lagoa Seca (A) e Calais (B), dois levantamentos fitossociológicos de vegetação de campo rupestre, Parque Estadual do Itacolomi, Minas Gerais, Brasil. ARF é a percentagem das espécies ocorrendo somente dentro do bioma Mata Atlântica, CE é a percentagem das espécies ocorrendo somente dentro do bioma Cerrado, e CE-ARF são espécies endêmicas para ambos os biomas.

3.2. Biodiversity measures

Due to the dominance of *Melinis minutiflora* in Calais, the indexes of Shannon-Wiener, Simpson, Berger-Parker and evenness indicated higher biodiversity in the Lagoa Seca study site (Table 3). On the other hand, Fisher's α suggested higher biodiversity for the Calais area. The estimator Jackknife 1 indicated lower community richness for the Lagoa Seca area (Figure 2).

Measured using Sørensen similarity, the floristic composition of plots is more homogeneous within the Lagoa Seca survey (0.550 ±0.129) than in Calais (0.453 ±0.123).

The Sørensen similarity between both surveys is 0.240, the Jaccard similarity 0.158.

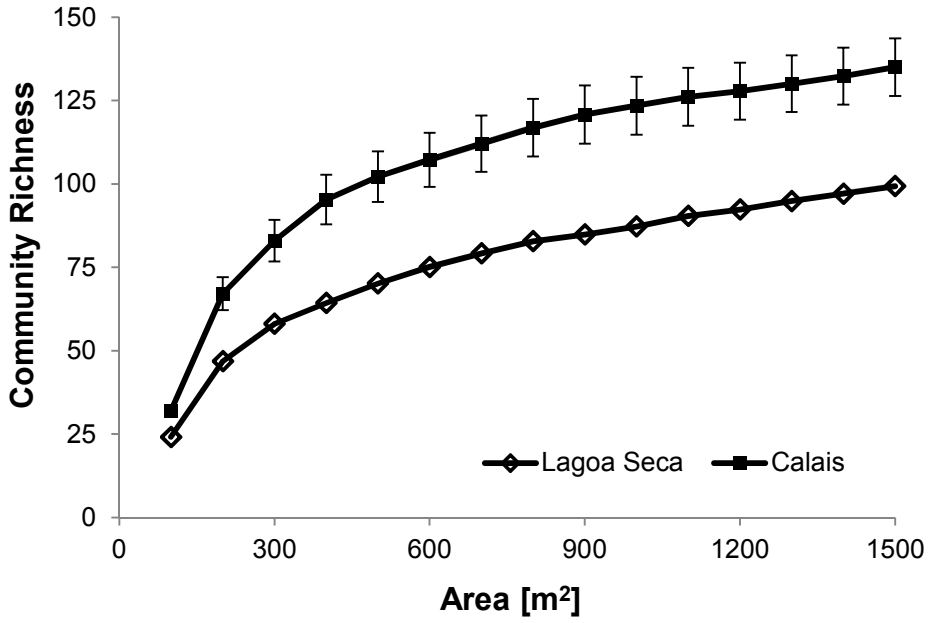


Figure 2 – Community richness estimators Jackknife 1 for Lagoa Seca and Calais, two phytosociological surveys from campo rupestre vegetation, Itacolomi State Park, Minas Gerais, Brazil.

Figura 2 – Jackknife 1, um estimador de riqueza da comunidade para Lagoa Seca e Calais, dois levantamentos fitossociológicos de vegetação de *campo rupestre*, Parque Estadual do Itacolomi, Minas Gerais, Brasil.

3.3. SAR

The species-accumulation curves of both study sites did not stabilize within the area analysed in both surveys (Figure 3). Their fittings with the power model show strong correlation coefficients (Lagoa Seca: Number of species = $3.308\ \text{area}^{0.434}$, $r^2 = 0.9915$; Calais: Number of species = $4.156\ \text{area}^{0.4519}$, $r^2 = 0.9908$). Linearized after logarithmic transformation, both regressions showed high significance (Lagoa Seca: $F_{1;3} = 350.9$, $p < 0.001$; Calais: $F_{1;3} = 302.8$, $p < 0.001$). This linear regression indicated slightly higher point diversity and spatial turnover for the Calais area (intercept, i.e. point diversity:

0.6187 ±0.0679, slope, i.e. spatial turnover 0.4519 ±0.0259) than for Lagoa Seca (intercept 0.5197 ±0.0607, slope 0.4343 ±0.0232).

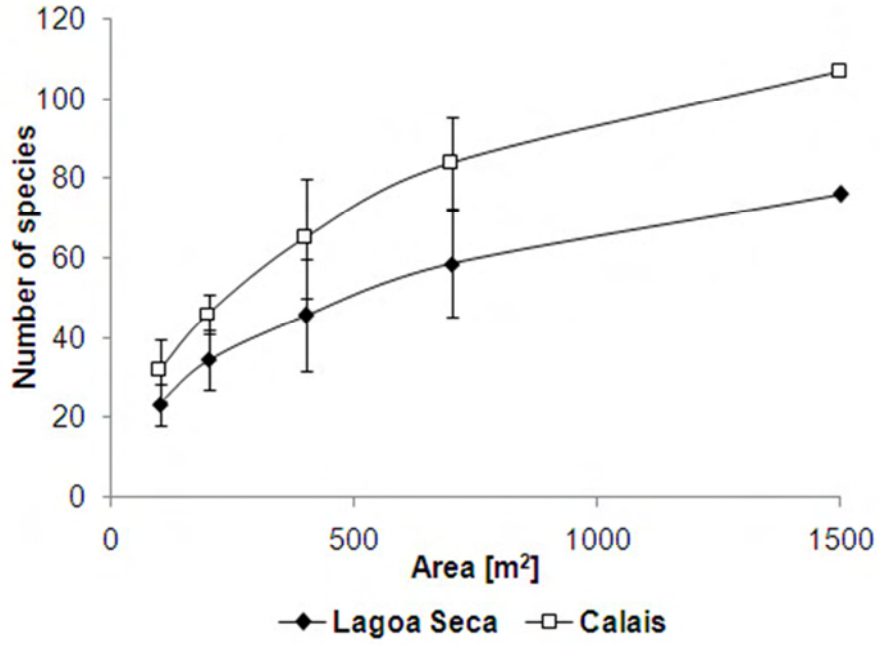


Figure 3 – Species-accumulation curves from Lagoa Seca and Calais, two phytosociological surveys in *campo rupestre* vegetation, Itacolomi State Park, Minas Gerais, Brazil. Vertical bars indicate standard deviation.
Figura 3 – Curva de acumulação de espécies em Lagoa Seca e Calais, dois levantamentos fitossociológicos em vegetação de campo rupestre, Parque Estadual do Itacolomi, Minas Gerais, Brasil. As barras verticais indicam o desvio padrão.

Table 3 – Biodiversity indices of Lagoa Seca and Calais, two areas of *campo rupestre* vegetation, Itacolomi State Park, Minas Gerais, Brazil, derived from phytosociological surveys. H' is Shannon-Wiener index and α is Fisher's α
Tabela 3 – Índices de biodiversidade de Lagoa Seca e Calais, duas áreas de vegetação de campo rupestre, Parque Estadual do Itacolomi, Minas Gerais, Brasil, derivado de levantamentos fitossociológicos. H' é o índice de Shannon-Wiener e α é Fisher´s α

	Lagoa Seca	**Calais**
H'	3.49	3.58
α	17.20 ±0.99	24.23 ±1.18

4. Discussion

Both study sites showed high levels of species richness compared to other phytosociological studies of *campo rupestre* and similar vegetation forms (CONCEIÇÃO; GIULETTI, 2002; JACOBI et al., 2008; LEMES 2009). The Shannon-Wiener index showed higher diversity for both study sites in and around Itacolomi State Park than for quartzite-sandstone *campos rupestres* in the Pai Inácio Mountains, in Chapada Diamantina, Bahia, Brazil (CONCEIÇÃO et al., 2007). These comparisons give further evidences to the high species richness and diversity already related for the park (ALMEIDA, 2008) and the Iron Quadrangle (FUNDAÇÃO BIODIVERSITAS, 2005) and justify the park´s classification as a local hotspot of biodiversity.

The inclination of the linearized SAR is around 0.25 for terrestrial plants (ROSENZWEIG, 1995). Within our surveys this value is nearly doubled, with 0.43 (Lagoa Seca) and 0.45 (Calais). This might be a consequence of a small sampling area (DOLNIK; BREUER 2008) and non-contiguous plot design (DENGLER, 2008). Nevertheless, the SAR's high slope values indicated high spatial turnover or beta diversity for the Itacolomi State Park, which have already been described for rock fields in general (JACOBI et al., 2007).

Low similarities between both study sites reinforce the affirmation of *campos rupestres* being species-rich ecosystems with a high degree of endemism (GIULIETTI et al., 1987; MENINI NETO et al., 2007; NAKAJIMA; SEMIR, 2001) and highlight once more the importance of the Itacolomi State Park.

Similar Shannon-Wiener diversity index values were found for Cerrado vegetation (NERI et al., 2007), while Atlantic Rainforest sites – either evergreen or deciduous – of nearby regions are more diverse (SILVA et al., 2004; WERNECK et al., 2000).

Fisher's α ranges from 25 to 195.1 for tropical forests (LOSOS; LEIGH JR., 2004) and from 12.60 (±0.73, ANDRADE et al., 2002) to 19.83 (±1.84, MARIMON; HARIDASAN, 2005) for Cerrado vegetation. Congruently with the index of Shannon-Wiener, Fisher´s α indicates diversity for *campo rupestre* vegetation between that from Cerrado vegetation and that from tropical

forests. Its ranking between savannah and forest vegetation highlights the localization of the *campos rupestres* from the Espinhaço Mountain Range in the ecotone between the Cerrado and the Atlantic Rainforest biome.

Nevertheless both study sites show high levels of species richness and diversity, those of Calais are even higher than that of Lagoa Seca. This is an unexpected result, because Lagoa Seca is the better protected area, while evidences for anthropogenic impacts were found during survey.
Although these impacts were not quantified, more registered species, higher community richness, higher biodiversity indices of Shannon-Wiener and Fisher´s α, lower similarity between plots as well as higher point diversity and spatial turnover in Calais support the intermediate disturbance hypothesis (CONNELL, 1978). According to this well accepted hypothesis (i.e. MOLINO; SABATIER, 2001), species richness and diversity are at maximum when disturbances are neither too rare nor too frequent because in this case ruderal, invasive or pioneer species are able to coexist with competitive ones. The presence of 22 invasive species contributed to the higher species richness in Calais and supports the hypothesis because anthropogenic disturbances prevent competitive exclusion of these species (HUGHES, 2010; SAX et al., 2002; SAX; GAINES 2003).
However, as outlined by Hughes (2010), the relationship between disturbance and diversity operates in both directions, since disturbances influence diversity, changing the response to future disturbances (HUGHES et al. 2007; LYONS et al., 2005). This and the lack of true replicates within our research impede generalizations. Further surveys are necessary to test the pattern before its final acceptance.

Although there are no true replicates, this study shows that species richness and diversity are poor predictors of the intactness of *campo rupestre* vegetation. Therefore, further parameters should be consulted for their evaluation (USHER, 1980).
High number of exotic and invasive species decrease the intactness of the species-richer Calais. On the other hand, Lagoa Seca holds more

endangered species than Calais. Furthermore, there are fewer orchid species in the better-accessible Calais. Some of them, especially *Coppensia* spp. and *Epidendrum denticulatum*, are popular ornamental plants with market values. Collecting activities in the less protected Calais area might explain the lack of most orchids in this study site.

Recent studies (i.e. LIEBSCH et al., 2008, GASTAUER et al., unpublished data) highlight the presence of endemic species as indicators for habitat intactness. As *campo rupestre* vegetation from the Espinhaço Mountain Range is situated on the ecotone between the Cerrado and Atlantic Rainforest biome, endemics from both biomes are expected emphasising the transitional character of this vegetation between both biomes (BENITES et al., 2003).

The absolute number of species endemic to the Atlantic Rainforest and the Cerrado biome does not differ between both study sites. But due to higher species richness, the percentage of endemic species is hence lesser in the impacted Calais than in Lagoa Seca.

We are aware that reduced percentages of endemic species might be due to a dilution effect because of the presence of invasive species increasing overall species richness as observed in Calais. But we can also imagine that endemic species as well as endangered ones show higher risk to go extinct under regimes of high disturbances. Therfore, we suggest the criterion “percentage of endemic species” as an indicator to evaluate the intactness of *campo rupestre* vegetation in further research activities. The presence of around one third of all species endemic to the biomes Atlantic Rainforest and Cerrado should be used as a reference for further surveys in *campos rupestres*.

5. Conclusions

Our study highlights the exceptional species richness and diversity found in the *campo rupestre* vegetation from the Itacolomi State Park. Intermediate diversity as well as the presence of species endemic to the Atlantic Rainforest and the Cerrado biome underline the transitional character of

campo rupestre vegetation from the Espinhaço Mountain Range between both biomes.

We showed that species richness and diversity are poor indicators for the intactness of *campo rupestre* vegetation and suggest further parameters like number of endangered, exotic or invasive species, pauperization of ornamental or medical plants as well as percentage of endemic species as more robust indicators. We suggest a magnitude of 30 % of species endemic to the Atlantic Rainforest and the Cerrado biome for intact *campos rupestres* patches.

6. References

ALMEIDA, G. S. S. **Asteraceae Dumort. nos campos rupestres do Parque Estadual do Itacolomi, Minas Gerais, Brasil.** 2008. Tese (Doutorado em Botânica). – Universidade Federal de Vicosa, Viçosa, 2008.

ALVES, R. J. V.; KOLBECK, J. Can campo rupestre vegetation be floristically delimited based on vascular plant genera? **Plant Ecology**, v. 207, p. 67–79, 2009.

ANDRADE, L. A. Z.; FELFILI, J. M.; VIOLATTI, L. Fitossociologia de uma área de cerrado denso na RECOR-IBGE, Brasília-DF. **Acta Botanica Brasilica**, v. 16, n. 2, p. 225-240, 2002.

APG III (ANGIOSPERM PHYLOGENY GROUP). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. **Botanical Journal of the Linnean Society**, n. 161, p.105–121, 2009

ARANHA, C.; BACCHI, O.; LEITÃO FILHO, H. F. **Plantas Invasoras de Culturas, volume 2***.* São Paulo: HUCITEC, 1982, 294p.

ARRHENIUS, O. Species and area. **Journal of Ecology,** v. 9, p. 95-99, 1921.

BACCHI, O.; LEITÃO FILHO, H. F.; ARANHA, C. **Plantas Invasoras de culturas, volumes 3.** São Paulo: HUCITEC, 1984, 308p.

BATISTA, J. A. N.; BIANCHETTI, L. B.; NOGUEIRA, R. E.; PELLIZZARO, K. F.; FERREIRA, F. E. The genus *Habenaria* (Orchidaceae) in the Itacolomi State Park, Minas Gerais, Brazil. **Sitientibus série Ciências Biológicas,** v. 4, n 1/2, p. 25-36, 2004.

BENITES, V. M.; CAIAFA, A. N.; MENDONÇA, E. S.; SCHAEFER, C. E.; KER, J. C. Solos e Vegetação nos Complexos Rupestres de Altitude da Mantiqueira e do Espinhaço. **Floresta e Ambiente,** n. 10, p. 76-85, 2003.

CAIAFA, N. A.; SILVA, A. F. Composição floristica e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais – Brasil. **Rodriguésia,** v. 56, n. 87, p. 163-173, 2005.

COLWELL, R. K.; CODDINGTON, J.A. Estimating terrestrial biodiversity through extrapolation. **Philosophical Transactions of the Royal Society B,** v. 345, n. 1311, p. 101–118, 1994.

CONCEIÇÃO, A. A.; GIULIETTI, A. M. Composição florística e aspectos estruturais de campo rupestre em dois platôs do Morro do Pai Inácio, Chapada Diamantina, Bahia, Brasil. **Hoehnea,** v. 29, p. 37-48, 2002.

CONCEIÇÃO, A. A.; GIULIETTI, A. M.; MEIRELLES, S. T. Ilhas de vegetação em afloramentos de quartzito-arenito no Morro do Pai Inácio, Chapada Diamantina, Bahia, Brasil. **Acta Botanica Brasilica,** v. 21, n. 2, p. 335-347, 2007.

CONDIT, R.; HUBBELL, S. P.; LAFRANKIE, J. V.; SUKUMAR. R.; MANOKARAN, N.; FOSTER, R. B.; ASHTON, P.S. Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. **Journal of Ecology,** v. 84, p. 549-562, 1996.

CONNELL, J. H. Diversity in Tropical Rain Forests and Coral Reefs. **Science,** v. 199, n. 4335, p. 1302-1310, 1978.

COPAM 2008. **Lista das espécies ameaçadas de extinção da flora no Estado de Minas Gerais.** Deliberação Conselho Estadual de Política Ambiental N^{o} 367, Anexo I.

DENGLER, J. Pitfalls in Small-Scale Species-Area Sampling and Analysis. **Folia Geobotanica,** v. 43, p. 269-287, 2008.

DOLNIK, C.; BREUER, M. Scale dependency in the Species-Area Relationship of Plant Communities. **Folia Geobotanica,** v. 43, p. 305-318, 2008.

DUTRA, V. F.; GARCIA, F. C. P.; LIMA, H. C. Caesalpinioideae (Leguminosae) nos Campos Rupestres do Parque Estadual do Itacolomi, MG, Brasil. **Acta Botanica Brasilica,** v. 22, n. 2, p. 547-558, 2008.

DUTRA, V. F.; GARCIA, F. C. P.; LIMA, H. C. Papilionoideae (Leguminosae) nos Campos Rupestres do Parque Estadual do Itacolomi, MG, Brasil. **Acta Botanica Brasilica,** v. 23, n. 1, p. 145-159, 2009.

FORZZA, R. C. (Coord.). **Lista de Espécies da Flora do Brasil.** Acesso online http://floradobrasil.jbrj.gov.br/2010/, Março 2012.

FUNDAÇÃO BIODIVERSITAS (Eds.). **Biodiversidade em Minas Gerais: um atlas para sua conservacão.** Belo Horizonte: Fundação Biodiversitas, Belo Horizonte, 2005, 222p.

GIULIETTI, A. M.; MENEZES, N. L.; PIRANI, J. R.; MEGURO, M.; WANDERLEY, M. G. L. Flora da Serra do Cipó, Minas Gerais: Caracterização e lista das espécies. **Boletim de Botãnica da Universidade de São Paulo,** v. 9, n. 1, p. 1-151, 1987.

HARLEY, R.M.; SIMMONS, N.A. **Florula of Mucugê, a descriptive check-list of a campo rupestre area.** Kew, Royal Botanic Gardens, Kew, Wakehurst Place, Ardingly, West Sussex, 1986.

HUGHES, A. R.; BYRNES, J. E.; KIMBRO, D. L.; STACHOWICZ, J. J. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. **Ecology Letters,** v. 10, p. 849-864, 2007.

HUGHES, A. R. Disturbance and Diversity: An Ecological Chicken and Egg Problem. **Nature Education Knowledge,** v. 1, p. 26, 2010.

IBGE (INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA). **Mapa de Vegetação do Brasil**. 3rd edition. Brasilia: Instituto Brasileiro de Geografia e Estatística, 2004.

JACOBI, C. M.; CARMO, F.F.; VINCENT, R. C.; STEHMANN, J. R. Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. **Biodiversity and Conservation,** v. 16, p. 2185-2200, 2007.

JACOBI, C. M.; CARMO, F.F.; VINCENT, R.C. Estudo fitossociológico de uma comunidade vegetal sobre canga como subsídio para a reabilitação de áreas mineradas no Quadrilátero Ferrífero, MG. **Revista Árvore,** v. 32, n. 2, p. 345-353, 2008.

LEITÃO FILHO, H. F.; ARANHA, C.; BACCHI, O. **Plantas Invasoras de culturas, volumes 1.** São Paulo: HUCITEC, 1982. 291p.

LEMES, F. O. A. **Relações florísticas, fitossociológicas e aspectos edáficos de comunidade de campos rupestres da Serra do Itacolomi e Serra do Ouro Branco, Minas Gerais.** Dissertação (Mestrado em Ecologia de Biomas Tropicais) – Universidade Federal de Ouro Preto, Ouro Preto, 2009.

LIEBSCH, D.; MARQUES, M. C. M.; GOLDENBERG, R. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. **Biological Conservation,** v. 141, p. 1717-1725, 2008.

LOSOS, E. C.; LEIGH JR., E. G. (Eds.) **Tropical Forest Diversity and Dynamism. Findings from a Large-Scale Plot Network.** The University of Chicago Press, Chicago, 2004. 645p.

LYONS, K. G.; BRIGHAM, C. A.; TRAUT, B. H.; SCHWARTZ, M. W. Rare Species and Ecosystem Functioning. **Conservation Biology,** v. 19, p. 1019-1024, 2005.

MARIMON JR., B. H.; HARIDASAN, M. Comparação da vegetação arbórea e características edáficas de um cerradão e um cerrado sensu stricto em áreas adjacentes sobre solo distrófico no leste de Mato Grosso, Brasil. **Acta Botanica Brasilica,** v. 19, n. 4, p. 913-926, 2005.

MARTINELLI, G.; BANDEIRA, J.; BRAGANÇA, J. O. 1989. **Campos de Altitude**. Rio de Janeiro: Ed. Index, 1989. 160p.

MENINI NETO, L.; ALVES, R. J. V.; BARROS, F.; FORZZA, R. C. Orchidaceae do Parque Estadual de Ibitipoca, MG, Brasil. **Acta Botanica Brasilica,** v. 21, n. 3, p. 687-696, 2007.

MESSIAS, M. C. T. B.; LEITE, M. G. P.; MEIRA NETO, J. A. A.; KOZOVITS, A.R. Life-form spectra of quartzite and itabirite rocky outcrop sites, Minas Gerais, Brazil. **Biota Neotropica,** v. 11, n. 1, p. 1-20, 2011.

MOLINO, J. F.; SABATIER, D. Tree Diversity in Tropical Rain Forests: A Validation of the Intermediate Disturbance Hypothesis. **Science,** v. 294, n. 5547, p. 1702-1704, 2001.

MOURÃO, A.; STEHMANN, J. R. Levantamento da flora do campo rupestre sobre canga hematítica couraçada remanescente na Mina do Brucutu, Barão de Cocais, Minas gerais, Brasil. **Rodriguésia,** v. 58, n. 4, p. 775-786, 2007.

MUELLER-DOMBOIS, D.; ELLENBERG, H. **Aims and methods of vegetation ecology.** New York: John Wiley & Sons, 1974, 475p.

NAKAJIMA, J. N.; SEMIR, J. Asteraceae do Parque Nacional da Serra da Canastra, Minas Gerais, Brasil. **Revista Brasileira de Botãnica,** v. 24, n. 4, p. 471-478, 2001.

NERI, A. V.; MEIRA NETO, J. A. A.; SILVA, A. F.; MARTINS, S. V.; BATISTA, M. L. Análise da estrutura de uma comunidade lenhosa em área de cerrado *sensu stricto* no município de Senador Modestino Gonçalves, norte de Minas Gerais, Brasil. **Revista Árvore,** v. 31, n. 1, p. 123-134, 2007.

NEWTON, A. C. **Forest ecology and conservation: a handbook of techniques**. Oxford: Oxford University Press, 2007, 454p.

NIMER, E. **Climatologia do Brasil.** Rio de Janeiro: IBGE, 1989, 421p.

PEEL, M. C.; FINLAYSON, B. L.; MCMAHON, T. A. Updated world map of the Köppen-Geiger climate classification. **Hydrology and Earth System Science,** v. 11, n. 6, p. 1633-1644, 2007.

PERON, M. V. Listagem preliminar da flora fanerogâmica dos campos rupestres do Parque Estadual do Itacolomi – Ouro Preto/Mariana, MG. **Rodriguésia,** v. 41, n. 67, p. 63-69, 1989.

PIRANI, J. R.; GIULETTI, A. M.; MELLO-SILVA, R.; MEGURO, M. Checklist and patterns of geographic distribution of the vegetation of Serra do Ambrósio, Minas Gerais, Brazil. **Revista Brasileira de Botãnica,** v. 67, n. 2, p. 133-147, 1994.

PIRANI, J. R.; MELLO-SILVA, R.; GIULETTI, A. M. Flora de Grão-Mogol, Minas Gerais, Brasil. **Boletim de Botãnica da Universidade de São Paulo,** v. 21, n. 1, p. 1-24, 2003.

REICHELT, G.; WILMANNS, O. **Vegetationsgeographie.** Braunschweig: Westermann, Braunschweig, 1973. 210p.

ROMERO, R.; NAKAJIMA, J. N. Espécies endêmicas do Parque Nacional da Serra da Canastra, Minas Gerias. **Revista Brasileira de Botânica,** v. 22, n. 2 (suplemento), p. 259-265, 1999.

ROSENZWEIG, M. L. **Species diversity in Space and Time.** Cambridge: Cambridge University Press, 1995, 421p.

SAFFORD, H. D. Brazilian Páramos IV. Phytogeography of the campos de altitude. **Journal of Biogeography,** v. 34, p. 1701–1722, 2007.

SAX, D. F.; GAINES, S. D.; BROWN, J. H. Species invasions exceed extinctions on islands worldwide: a comparison of plants and birds. **American Naturalist,** v. 160, n. 6, p. 766–783, 2002.

SAX, D.F.; GAINES, S. D. Species diversity: from global decreases to local increases. **Trends in Ecology and Evolution,** v. 18, n. 11, p. 561-566, 2003.

SCOLFORO, J. R.; CARVALHO, L. M. T. **Mapeamento e inventário da flora nativa e dos reflorestamentos de Minas Gerais.** Lavras: UFLA, 2006. 288p.

SILVA, N. R. S.; MARTINS, S.V.; MEIRA NETO, J. A. A.; SOUZA, A. L. Composição florística e estrutura de uma Floresta Estacional Semidecidual Montana em Viçosa, MG. **Revista Árvore,** v. 28, n. 3, p. 397-405, 2004.

STEHMANN, J. R.; FORZZA, R. C.; SALINO, A.; SOBRAL, M.; COSTA, D.P.; KAMINO, L. H. Y. (Eds.) **Plantas da Floresta Atlântica.** Rio de Janeiro: Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, 2009. 505p.

USHER, M. B. An Assessment of Conservation Values within a large site of Special Scientific Interest in North Yorkshire. **Field Studies,** v. 5, p. 323-348, 1980.

WERNECK, M. S.; PEDRALLI, G.; KOENIG, R.; GISEKE, L.F. Florística e estrutura de três trechos de uma floresta semidecídua na Estação Ecológica do Tripuí, Ouro Preto, MG. **Revista Brasileira de Botânica,** v. 23, n. 1, p. 97-106, 2000.

CHAPTER2*

How many species are there in the Itacolomi State Park?

* This chapter has been submitted to**Plant Ecology and Diversity** on 27/01/2012.

RESEARCH ARTICLE

How many species are there in the Itacolomi State park?

Markus Gastauer[1] and João A. A. Meira Neto[1]*

[1] Laboratório de Ecologia Vegetal, Departamento de Biologia Vegetal, Universidade Federal de Viçosa, 36570-000 Viçosa, Minas Gerais, Brazil

* Correspondence: João Augusto Alves Meira Neto, Departamento de Biologia Vegetal, Campus UFV s/n, 36570-000 Viçosa, MG, Brazil. Tel.: +55 31 3899 1955, Fax: +55 31 3899 2580, Email: j.meira@ufv.br

Running title: How many species are there in the Itacolomi State Park

ABSTRACT

Background: As complete censuses of species richness of larger areas are difficult to realize, other approaches are necessary to achieve these interesting figures.

Aim: Estimate the vascular plant species richness of *campo rupestre* vegetation within the Itacolomi State Park and Brazil by different approaches in order to test consistency of methods for further applications.

Methods: Species-area relationships (SAR), the taxon ratio and the Krishnamani model are applied on species lists from two phytosociological surveys.

Results: Concordantly, species richness has been estimated to the magnitude of 1100 species by the taxon ratio model and the power function of the SAR using the generally accepted slope of 0.25. If we accept a scale break between 0.5 and 1 ha, the total number of plant species of the park´s *campos rupestres* is estimated within the same magnitude by the Krishnamani model (1048 to 1226 species). Beyond that, the species richness of all *campo rupestre* in Brazil is estimated to 3467 (Krishnamani model) and to 4866 (power-law SAR´s extrapolation using a slope of 0.25).

Conclusions: Increased confidence is given to the three methods, because they returned results in the same magnitude for the Itacolomi State Park; this inspires further utilization in other ecosystems.

Keywords: biodiversity, local hotspots of biodiversity, species-area relationship, species richness, taxon ratios.

Introduction

Mankind is interested in answering questions as “How many species are there on earth?” and “How many species are we going to lose because of habitat loss or climate changes?” (May 1988; Scotland and Wortley 2003). Variegating latter, we may ask “How many species do we protect?” or even “How many species can we protect?”

There are about 5 to 10 million of non-microbial species in the world (May 1997). But not only the world´s overall species richness summarized in a single, attention claiming number is an interesting figure but also an understanding of the extent of species distribution to predict extinction rates caused by human impacts or climate change (Lewis 2006), evolve conservation policies (Brooks et al. 2006; Killeen and Solórzano 2008; Pardini et al.2009; Ribeiro et al. 2009), declare biological hotspots (Myers et al. 2000; Orme et al. 2005) and learn more about ecosystem function (May and Beverton 1990).

The global species richness for single taxons, communities or ecosystems is rather estimated by extrapolation than being the result of an unaffordable, complete census (Raven 1985, Grassle and Maciolek 1992, Briggs and Snelgrove 1999, Bebber et al. 2007, Joppa et al. 2010). Such estimated numbers of species (e.g. vascular plant) within a regional entity, from a habitat type or a complete ecosystem, are important figures illustrating the state of current research as well as describing the lack of knowledge (Mora et al. 2011).

Campos rupestres (literally: rock-fields) are montane ecosystems displacing Atlantic Rainforests usually above 900 m above sea level in Southeastern Brazil (Magalhães 1966) and frequently forming the transition to another hotspot of biodiversity, the Brazilian *Cerrado* (Myers et al. 2000). Also showing similarity to other azonal outcrop vegetations from the Neotropics, these species-rich and diverse ecosystems with many endemic species (Pirani et al. 1994; Romero and Nakajima 1999;Conceição et al. 2007; Menini Neto et al. 2007) are composed by specific plant communities (Alves et al. 2007, Conceição and Pirani 2005). *Campos rupestres* occur in the

Brazilian States of Minas Gerais and Bahia, as well as on some sites in Goias State (Alves and Kolbek 2010).

Like other tropical ecosystems, *campo rupestre´s* richness and diversity is threatened by habitat loss and climate changes (Pirani et al. 2003). Increased extinction rates exceeded taxonomical efforts, so that the actual loss of biodiversity cannot be recorded; many species vanish before having been described (Dubois 2003) underlining the importance of accurate estimations to gain an idea about what we are going to lose.

The aim of this paper is to estimate the total number of vascular plants of all *campos rupestres* from the Itacolomi State Park, Minas Gerais, Brazil. Starting from two sets of samples carried out within the park, different approaches are applied and compared. These findings are extrapolated to the whole ecosystem to discuss the actual conservation scenario and outline necessary consequences for the protection of this species-rich ecosystem.

Methods

Starting from two phytosociological surveys of 0.15 ha in Calais and Lagoa Seca, Itacolomi State Park (unpublished data), each one divided in 15 plots of 10 x 10 m, species-area relationships (SAR) were extrapolated using the power model proposed by Arrhenius (1921) as well as the logarithmic function (Gleason 1922). Distance between both surveys is 2.7 km.

As there are some well-studied taxons within the Itacolomi State Park, the taxon ratio model proposed by Colwell and Coddington (1994) is applied.

Finally, we present an approach of decreasing z, i.e. the inclination of the SAR fitted by the porwer model and linearized in the log-log space, of the SARs to compute the number of total species (Krishnamani et al. 2004). For that, equation (5) from cited study is transformed to

$$S_{tot} = \overline{S}\left(\frac{A_2}{A_1}\right)^{z_1} \times \left(\frac{A_0}{A_2}\right)^{z_2} \qquad (1).$$

S is the average number registered in both surveys, A_1 is the size of each sample, A_2 is the rectangular area given by the distance of scale break,

where z_1 changes to z_2, and A_0 is the whole area of the park. z_1 is the average inclination given by the rarefaction of the species-sampling curve with the power model, z_2 is calculated by the following equation:

$$z_2 = -\frac{\left(\frac{\ln \chi}{\ln d}\right)}{2}, \qquad (2)$$

wherein χ is the Sørensen index of similarity and d is the medium distance between both study sites.

The Itacolomi State Park holds 7543 ha; from that, 44% are mapped as *campo rupestre* corresponding an area of 3319 ha (Fujaco et al. 2010).

Results

A total of 161 species had been detected in both study sites, 23 of them occur in both surveys corresponding a Sørensen index of similarity of 0.240. In Lagoa Seca, 76 species had been sampled, the SAR is fitted to $S = 3.308 * A^{0.434}$ by the power model ($R^2 = 0.9915$, $F_{1;3} = 350.9$, $p < 0.001$) and $S = 19.41 * \ln(A) - 67.99$ by the logarithmic model ($R^2 = 0.991$). In Calais, 107 species had been found resulting in an SAR´s fitting of $S = 4.156 * A^{0.4519}$ (power model, $R^2 = 0.9908$, $F_{1;3} = 302.8$, $p < 0.001$) respectively $S = 28.15 * \ln(A) - 100.7$ (logarithmic model, $R^2 = 0.992$).

Extrapolating the logarithmic model to the whole park´s *campo rupestre* area results in an overall plant species richness of 268 (from Lagoa Seca survey) and 387 species (Calais). Using the power model, the number of vascular plant species within the park is estimated to 6077 (Lagoa Seca) or 10409 (Calais).

Accepting an inclination of the SAR´s slope of 0.25, the number of observed species

$$S(A_0) = \left(\frac{A_0}{A_1}\right)^z * S(A_1) \qquad (3)$$

is estimated at average to 1116 species (927 from the Lagoa Seca sample, 1305 from the Calais survey).

Using the taxon ratio model, the total number of species within the park´s *campos rupestres* is estimated to 1148 species (Table 1) considering 8 recently, well-studied taxons.

Table 1

Taxon ratios and estimation of the park´s plant species richness as proposed by Colwell and Coddington (1994).

Source	**Taxon**	**Total number in park´s *campos rupestres***	**Number of species in our survey**	**Factor**	**Estimated number of species**
Dutra et al. 2008	Caesalpinoideae	13	2	6.5	1047
Dutra et al. 2009	Papilionidae	28	8	3.5	564
Coser 2008	Bromeliaceae	21	1	21	3381
Rolim 2007	Pteridophytes	38	4	9.5	1530
Almeida 2008	Asteraceae	219	27	8.11	1306
Alves 1990	Orchidaceae	36	6	6	966
Batista et al. 2004	*Habernaria*	15	2	7.5	1207.5
Thiago Rolim, personal communication	Melastomataceae	71	12	5.92	953
*** * * Total**		**442**	**62**	**7.129**	**1148**

Applying the Krishnamani *et al.* (2004) model, the total number of species to be expected within park´s *campos rupestres* is calculated to 798, when the scale break A_2 is set to the same size as the study area (0.15 ha):

$$S(A_0) = S\left(\frac{A_2}{A_1}\right)^{z_1} x\left(\frac{A_0}{A_2}\right)^{z_2} = 91.5\left(\frac{0.15}{0.15}\right)^{0.443} x\left(\frac{3319}{0.15}\right)^{0.2165} \approx 798 \qquad (4).$$

Discussion

Considering the studies cited in Table 1 plus the 161 species found within our two surveys, 541 species have been detected already within the park´s *campos rupestres*. Further surveys (i.e. Peron 1989; Casarino et al. 2009) might enrich the list. Therefore, approaches estimating the *campo rupestre* species richness of the complete park below this value are discarded.

This includes the extrapolations of the species-area curves fitted by the logarithmic function once proposed by Gleason (1922), nevertheless this model has been used to predict complete species richness successfully in surveys from other ecosystems (Condit et al. 2004).

It is not likely that about half or more of the Atlantic Rain Forest flora (Myers et al. 2000; Stehmann et al. 2009) might be found within the limits of the Itacolomi State Park´s *campos rupestres*. Therefore, the extrapolations of the power model have to be discussed with caution, although this model is well studied and generally well accepted (Brown et al.2002; Martin and Goldenfield 2006), and good fittings (Gastauer, unpublished data) lead into temptation to extrapolate these findings.

In fact, slopes of the linearized species-area relationships are not a sample-size independent figure constant over different magnitudes (Condit et al. 1996; Conner and McCoy 2001), but decrease with increasing sample size (Dolnik and Breuer 2008). This is, because the SAR plotted in the log-log space is triphasic and of sigmoid form (Rosenzweig 1995). Its inclination is scale-dependent: On local spatial scales, the species-area relationship is curvilinear on a log-log plot and follows logarithmic patterns – for that Fisher´s equation does well for extrapolations on local scale as shown by Condit et al.(2004). On regional scales, theory predicts linear species-area curves plotted in the logarithmic space. Rosenzweig (1995) and others propose slopes of about 0.15 for plants from islands and 0.25 for terrestrial plants (Pimm and Raven 2000). Finally, on very large scales exceeding biogeographic units, slopes of SARs steepen toward unity, because processes become uncoupled (Hubbell 2001).

This explains why only the SAR extrapolations from survey data do not work: As our survey is realized on local scale, but our extrapolation spans to the

regional scale, our SARs change from the logarithmic to the power model. Consequently, both power as well as logarithmic fittings deduced from surveys are fractals only.

All we need for our extrapolation is a model describing the left half of the sigmoid form of the SAR plotted in log-log space. Such an approximation on decreasing slopes of linearized species-area relationship was proposed by Krishnamani et al. (2004). Compared to the findings by the taxon ratio model, this model computes lower values for park´s species richness. This is due to the underlying conservative calculation, where the scale break is defined as sample size. Increasing the scale break of both surveys increases species richness (Table 2). Additionally, intermediate surveys might be helpful to introduce a second scale break substantiating the results.

Table 2
Influence of increasing scale break on Itacolomi´s *campos rupestres* species richness.

Scale break [ha]	**Species richness**
0.15	798
0.5	1048
0.7	**1131**
1	1226
2	1435
5	1766

On the other hand, we simply might reduce the slope of the power-low SAR to 0.25, as generally accepted for terrestrial plant communities. As shown, with this assumption we compute the overall species richness of the park´s *campos rupestres* to 1116 species. This is the same magnitude as the taxon ratio (1148) and the Krishnamani model assuming a scale break between 0.5 and 1 ha (1048 to 1226 species).

Confidence is given to our estimations, because three different models independently produce similar results. Furthermore, the magnitude of 1100 species for all *campos rupestres* within the Itacolomi State Park seems to be realistic, as censuses of many species-rich and abundant families like Poaceae, Cyperaceae, Velloziaceae and Rubiaceae are still lacking. Surely, there are many first records for the Itacolomi State Park and undescribed species waiting for research activities. In her taxonomical work, Almeida (2008), for example, succeeded innumerable first records for the Itacolomi State Park and furthermore discovered three new, not yet described species from one family only!

The three approaches have worked as tools to evaluate plant species richness in *campos rupestres*. Realistic results in the same magnitude proof the consistency of the three approaches and inspire further extrapolations as well as applications in other nature reserves or even ecosystems. Its application in further research activities from different vegetation forms is potentially wide, because required information, if not available from literature, is easily gathered.

In Minas Gerais 617,324 ha of *campo rupestre* are registered (Scolforo and Carvalho, 2006), but as mappings are lacking for other Brazilian States like Bahia, Goias and Federal District, we estimate the total amount of *campo rupestre* to the double of that from Minas Gerais. By inserting this value in our SAR, we expect around 4866 species in 1,200,000 ha (Figure 1). By the Krishnamani et al. (2004) model, the *campos rupestres´* total species richness is estimated to 3752 or 4390 assuming a scale break of 0.5 and 1 ha, respectively.

Inverting the taxon ratio model, this would mean that for each species in the park, there should be about three to four in all *campos rupestres*. Complete censuses are rare in literature, but more than the double of all Gesneriaceae detected in the Itacolomi State Park have been found in the Espinhaço Mountain Range from herbarium records only (Araujo et al. 2005). 338 species of Leguminosae, that is 94 species of Caesalpinioideae and 157 Papilionioideae, occur in all *campos rupestres* (Dutra et al. 2008, 2009) – that

is 7.2 times (Caesalpinioideae), 5.6 times (Papillionioideae) more species than have been found in the Itacolomi State Park!

The three models concordantly estimate the richness of all *campo rupestre* to something between 4000 and 5000 species. But is this realistic? Giulietti et al. (1997) guess that there might be found about 4000 plant species within the Espinhaço Mountain Range, an area of about 70,000 km^2 housing most of Brazilian *campo rupestre*. Because one third of that species has already been found in the Serra do Cipó, a conservation unit covering only 300 km^2, their estimation is considered moderate (Rapini et al. 2008).

On the other hand, Stehmann et al. (2009) compile a – still incomplete – list of 14,000 plant species that occur in the Atlantic Rainforest biome. From that, 3,740 species occur in rocky formations. Considering that some area of *campo rupestre* is inserted in the Cerrado biome and that there are waiting still many species from this vegetation type to be described, this data supports our findings.

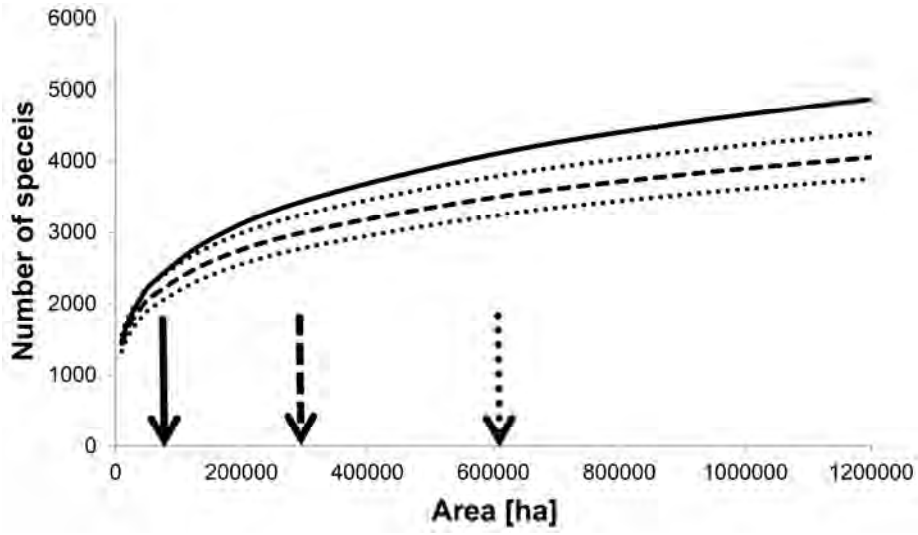


Figure 1

Species-area relationship for all *campo rupestre* vegetation from Brazil, extrapolated with the power (continuous curve, slope z is fixed to 0.25) and the Krishnamani model (dashed and dotted curves). Dashed curve is based on a scale break of 0.7ha, upper dotted curve assumes a scale break of 1 ha, and lower dotted line is calculated with a scale break of 0.5ha. Arrows

indicate already protected area (continuous), area to be protected to conserve 70 to 74 % (dashed) and 90 % (dotted) of species richness from *campo rupestre* vegetation.

This has consequences for conservation activities: Within the 3319 ha from the Itacolomi State nearly one third of all vascular plants from *campo rupestre* are protected from anthropogenic impacts. This exceptional high species richness underlines the importance of the park, justifies conservation activities and it´s declaration as (local) hotspot of biodiversity.

But as the fulfillment and maintenance of ecosystem services depends each species (Isbell et al. 2011), we should protect as much species as possible. Protecting 25% or 300,000 ha of all *campo rupestre*, would conserve about 70 (SAR) to 74 % (Krishnamani model) of all *campo rupestre* species richness (Figure 1). If more than 90 % of all plants from *campo rupestre* should be conserved, more than a half of all *campo rupestre* should be protected.

But this is far from reality: In 2005, between 4 to 5% of the whole Brazilian territory has been protected in integral conservation units (Rylands and Brandon 2005). From the Espinhaço Mountain Range, about 3500 km^2 from a total of 70,000 km^2 are protected in federal or state conservation units - that is only five percent. With other words, only the half of all species potentially occurring in *campo rupestre* vegetation is protected.

Therefore, we should enlarge immediately the area of protected *campo rupestre* to some 10 to 15 %. This would guarantee that relicts of this highly diverse, species-rich and endemic flora are conserved for further generations.

Conclusions

The species richness of the Itacolomi State Park´s *campos rupestres* cannot be extrapolated by fittings of species-area curves from field data from local surveys. This is because the underlying species-area relationship (SAR) is

triphasic and of sigmoid form changing from a logarithmic function on local scales to a power function on regional scales.

Nevertheless, the richness of vascular plants from all *campos rupestres* within the Itacolomi State Park is concordantly estimated to around 1100 species using the taxon ratio, the power function of the species-area relationship with the generally accepted slope of 0.25 as well as by the Krishnamani model considering a scale break between 0.5 and 1 ha.

This richness represents about one fourth of all vascular plants occurring in all *campo rupestre* vegetation. This exceptional high species richness underlines the importance of the Itacolomi State Park. Nevertheless, further conservation areas are required to conserve the majority of this unique vegetation.

Due to the consistency of returned results, the presented approaches show high level of confidence and should be applied in further ecosystems to outline conservation activities and evaluate conservation alternatives.

Notes on Contributors

Markus Gastauer is Ph.D. student of Botany at the Universidade Federal de Viçosa. His research interests are biodiversity patterns, plant-soil interactions as well as succession and dynamics in the Atlantic Rainforest and associated vegetation formations.

Since 1992, João Augusto Alves Meira Neto is professor of botany at the Universidade Federal de Viçosa. His scope is ecology of ecosystems in studies of structure, diversity and succession of vegetation. He investigates relations between vegetation and biotic and abiotic factors in the Atlantic Rainforest, Brazilian Cerrado, Mussunungas and Mediterranean Vegetation.

References

Almeida GSS 2008. Asteraceae Dumort. nos campos rupestres do Parque Estadual do Itacolomi, Minas Gerais, Brasil. Ph.D. thesis, Universidade Federal de Viçosa, Viçosa.

Alves RJV 1990. The Orchidaceae of the Itacolomi State Park in Minas Gerais, Brazil. Acta Botanica Brasilica 4:65-72.

Alves RJV, Cardin L, Kropf MS 2007. Angiosperm disjunction ‘‘Campos Rupestres-Restingas’’ - a re-evaluation. Acta Botanica Brasilica 21:675–685.

Alves RJV, Kolbek J 2010. Can campo rupestre vegetation be floristically delimited based on vascular plant genera? Plant Ecology 207:67–79.

Araujo AO, Souza VC, Chautems A 2005. Gesneriaceae da Cadeia do Espinhaço de Minas Gerais, Brasil. Revista Brasileira de Botânica 28:109-135.

Arrhenius O 1921. Species and area. Journal of Ecology 9:95-99.

Batista JAN, Bianchetti LB, Nogueira RE, Pellizzaro KF, Ferreira FE 2004. The genus Habenaria (Orchidaceae) in the Itacolomi State Park, Minas Gerais, Brazil. Sitientibus Ciências Biológicas 4:25-36.

Bebber DP, Marriott FHC, Gaston KJ, Harris AS, Scotland RW 2007: Predicting unknown species numbers using discovery curves. Proceedings of the Royal Society B 274:1651-1658.

Briggs JC, Snelgrove P 1999. Marine species diversity. Bioscience 49:351-352.

Brooks TM, Mittermeier RA, Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL 2006. Global Biodiversity Conservation Priorities. Science 313:58-61.

Brown JH, Gupta VK, Li BL, Milne BT, Restrepo C, West GB 2002. The fractal nature of nature: power laws, ecological complexity and biodiversity. Philosophical Transactions of the Royal Society B 357:619-626.

Casarino JE, Mynssen CM, Messias MCTB 2009. Schizaeales no Parque Estadual do Itacolomi, Minas Gerais, Brasil. Revista Brasileira de Botânica 32:737-748.

Colwell RK, Coddington JA 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transaction of the Royal Society London, Serie B 345:101-108.

Conceição AA, Pirani JR 2005. Delimitação de habitats em campos rupestres na Chapada Diamantina: substratos, composição florística e aspectos estruturais. Boletim de Botânica da Universidade de São Paulo 23:85-111.

Conceição AA, Giulietti AM, Meirelles ST 2007. Ilhas de vegetação em afloramentos de quartzito-arenito no Morro do Pai Inácio, Chapada Diamantina, Bahia, Brasil. Acta Botanica Brasilica 21:335-347.

Condit R, Hubbell SP, Lafrankie JV, Sukumar R, Manokaran N, Foster RB, Ashton PS 1996. Species-Area and Species-Individual Relationships for Tropical Trees: A Comparison of Three 50-ha Plots. Journal of Ecology 84:549-562.

Condit R, Leigh Jr EG, Lao SL, CTFS Working Group 2004. Species-Area Relationships and Diversity Measures in the Forest Dynamics Plots. In: Losos EC, Leigh Jr EG, editors. Tropical Forest Diversity and Dynamism –

Findings from a Large-Scale Plot Network. Chicago: The University of Chicago Press. P. 79-89.

Conner EF, MacCoy ED 2001. Species-Area Relationships. Encyclopedia of Biodiversity 5:397-411.

Coser TS 2008: Bignoniaceae Juss. dos campos rupestres do Parque Estadual do Itacolomi, Minas Gerias, Brasil: Florística e aspectos fenológicos. Master thesis, Universidade Federal de Viçosa, Viçosa.

Dolnik C, Breuer M 2008. Scale Dependency in the Species-area Relationship of Plant Communities. Folia Geobotanica 43:305-318.

Dubois A 2003. The relationships between taxonomy and conservation biology in the century of extinctions. Comptes rendus Biologies 326:S9-S21.

Dutra VF, Garcia FCP, Lima HC 2008. Caesalpinioideae (Leguminosae) nos Campos Rupestres do Parque Estadual do Itacolomi, MG, Brasil. Acta Botanica Brasilica 22:547-558.

Dutra VF, Garcia FCP, Lima HC 2009. Papilionoideae (Leguminosae) nos Campos Rupestres do Parque Estadual do Itacolomi, MG, Brasil. Acta Botanica Brasilica 23:145-159.

Fujaco MAG, Leite MGP, Messias MCTB 2010. Análise multitemporal das mudanças no uso e ocupação do Parque Estadual do Itacolomi (MG) através de técnicas de geoprocessamento. Revista Escola de Minas 63:695-701.

Giulietti AM, Pirani JR, Harley RM 1997. Espinhaço range region, Eastern Brazil. In: Davis SD, Heywood VH, Herrera-MacBryde O, Villa-Lobos J, Hamilton AC, editors. Centres of plant diversity. A guide and strategies for the conservation, Vol. 3. The Americas. Cambridge: WWF/IUCN. p. 397-404.

Gleasson HA 1922. On the relation between species and area. Ecology 3:159-162.

Grassle JF, Maciolek NL 1992. Deep-sea species richness: regional and local
diversity estimates from quantitative bottom samples. American Naturalist 139:313-341.

Hubbel SP 2001. The Unified Theory of Biodiversity and Biogeography. Princeton (UK): Princeton University Press.

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M 2011. High plant diversity is needed to maintain ecosystem services. Nature 477:199-203.

Joppa L, Roberts DL, Pimm SL 2010. How many species of flowering plants are there? Proceedings of the Royal Society B, doi: 10.1098/rspb.2010.1004.

Killeen TJ, Solórzan LA 2008. Conservation strategies to mitigate impacts from climate change in Amazonia. Philosophical Transactions of the Royal Society London B 363:1881-1888.

Krishnamani R, Kumar A, Harte J 2004. Estimating species richness at large spatial scales using data from small discrete plots. Ecography 27:637-642.

Lewis OT 2006. Climate change, species-area curves and the extinction crisis. Philosophical Transactions of the Royal Society B 361:163-171.

Magalhães GM 1966. Sobre os cerrados de Minas Gerais. Anais da Academia Brasileira de Ciências 38:59-70.

Martin HG, Goldenfield N 2006. On the origin and robustness of power-law species-area relationships in ecology. Proceedings of the National Academy of Sciences 103:10310-10315.

May RM 1988. How Many Species are there on Earth? Science 241:1441-1449.

May RM 1997. The Dimensions of Life on Earth. Nature and Human Society: The Quest for a Sustainable World (ed. by P.H. Raven), pp. 30-45. Washington DC: National Academy of Siences.

May RM, Beverton RJH 1990. How Many Species? Philosophical Transaction of the Royal Society London B 330:293-304.

Menini Neto LM, Alves RJV, Barros F, Forzza RC 2007. Orchidaceae do Parque Estadual de Ibitipoca, MG, Brasil. Acta Botanica Brasilica 21:687-696.

Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B 2011. How Many Species Are There on Earth and in the Ocean? PLoS Biol 9, e1001127. doi:10.1371/journal.pbio.1001127

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J 2000. Biodiversity hotspots for conservation priorities. Nature 403:453-458.

Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Ding T, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Blackburn TM, Gaston KJ,Owens IPF 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature 436:1016-1019.

Pardini R, Faria D, Accacio GM, Laps RR, Mariano-Neto E, Paciencia MLB, Dixo M, Baumgarten J 2009. The challenge of maintaining Atlantic forest biodiversity: A multi-taxa conservation assessment of specialist and

generalist species in an agro-forestry mosaic in southern Bahia. Biological Conservation 142:1178-1190.

Peron MV 1989. Listagem preliminar da flora fanerogâmica dos campos rupestres do Parque Estadual do Itacolomi – Ouro Preto/Mariana, MG. Rodriguésia 67:63-69.

Pimm SL, Raven P 2000. Extinction by numbers. Nature 403:483-483.

Pirani JR, Giuletti AM, Mello-Silva R, Meguro M 1994. Checklist and patterns of geographic distribution of the vegetation of Serra do Ambrósio, Minas Gerais, Brazil. Revista Brasileira de Botânica 67:133-147.

Pirani JR, Mello-Silva R, Giuletti AM 2003. Flora de Grão-Mogol, Minas Gerais, Brasil. Boletim de Botânica da Universidade de São Paulo 21:1-24.

Rapini A, Ribeiro PL, Lambert S, Pirani JR 2008. A flora dos campos rupestres da Cadeia do Espinhaço. Megadiversidade 4:16-24.
Raven PH 1985. Disappearing species: a global tragedy. Futurist 19:8-14.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141-1153.

Rolim LB 2007. Pteridófitas do Parque Estadual do Itacolomi, Minas Gerias, Brasil. Master thesis, Universidade de Brasilia.

Romero R, Nakajima JN 1999. Espécies endêmicas do Parque Nacional da Serra da Canastra, Minas Gerias. Revista Brasileira de Botânica 22:259-265.

Rosenzweig ML 1995. Species diversity in space and time. Cambridge: Cambridge University Press.

Rylands AB, Brandon K 2005. Unidades de conservação brasileiras. Megadiversidade 1:27-35.

Scolforo JR, Carvalho LMT 2006. Mapeamento e inventário da flora nativa e dos reflorestamentos de Minas Gerais. Lavras: UFLA.

Scotland RW, Wortley AH 2003. How many species of seed plants are there? Taxon 52:101-104.

Stehmann JR, Forzza RC, Salino A, Sobral M, Costa DP, Kamino LHY (Org.) 2009. Plantas da Floresta Atlântica. Rio de Janeiro: Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

CHAPTER 3*

Primary forests diagnosis in Brazilian Atlantic Rainforest

* This chapter will soon be submitted to **Anais da Academia Brasileira de Ciências**.

Article

Primary forests diagnosis in Brazilian Atlantic Rainforest

Markus Gastauer[a], Marcos Eduardo Guerra Sobral[b], João Augusto Alves Meira Neto[a]*

[a.] Laboratório de Ecologia Vegetal, Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Campus s/n, 36570-000 Viçosa, MG, Brazil.
[b] Departamento de Ciências Naturais, Universidade Federal de São João del-Rei - Praça Dom Helvécio, 74 - 36301-160, São João del-Rei, MG, Brazil.

Key words: irreplaceability, primary forest trait, species richness, species composition, rarity.

Running title: Primary forests diagnosis

Section: Biological Sciences

* Corresponding author:
Address: Departamento de Biologia Vegetal, Campus UFV s/n, 36570-000, Viçosa, MG, Brasil. Tel.: +55 31 3899 1955; fax: +55 31 3899 2580.

ABSTRACT

Identification of primary forests is an important step in conserving highly diversified, self-sustaining, and irreplaceable ecosystems, but it is not easy to distinguish traits of tropical primary forests from those of secondary forests. In this article it is tested if the floristic composition of an Atlantic Rainforest patch that has never been logged, the Forest of Seu Nico (FSN), Viçosa, Minas Gerais, Brazil, shows characteristics of primary forests. These are elevated percentage of non-pioneer, understory, animal-dispersed and endemic species. With 218 tree species with diameter at breast height greater or equal to 3.2 cm found in one hectare, the FSN species richness is outstanding for the region. The percentages of understory, non-pioneer, animal-dispersed and endemic species from FSN characterize the fragment as a primary forest. Other differences between the FSN and neighboring secondary fragments have been detected, such as increased per hectare basal area as well as increased percentage of rare species. Increased basal area proves once the important role of primary forest for abiotic resource protection like increased CO_2-sequestration. Therefore, these traits could be used in further studies of this type to identify primary forests in the Brazilian Atlantic Rainforest.

INTRODUCTION

Since tropical primary forests show higher species richness and diversity than secondary forests (e.g. Brearley et al. 2004, Barlow et al. 2007, Bihn et al. 2008, Dent & Wright 2009, Browning et al. 2010, Styring et al. 2011), and therefore better fulfillment of ecosystem services and functions depending this biodiversity (Isbell et al. 2011), their unambiguous identification is an important step in conserving highly diversified, self-sustaining, irreplaceable ecosystems. But assess the distinctive tropical primary forests traits in order to distinguish them from secondary forests is not an easy task (Gibson et al. 2011), though important progress has occurred (Liebsch et al. 2008).

Primary forest in this context is an old-growth forest that has experienced little to no recent human disturbance, therefore not being genuinely pristine (Gibson et al. 2011).

Before the Europeans arrived in South America, the Atlantic Rainforest covered between 1.300.000 and 1.500.000 km^2 distributed along nearly the entire Brazilian coast (Câmara 2005). Today, a wide variety of situations have emerged from different patch histories because the formerly continuous area is highly fragmented with only 11 to 16 % of the original vegetation cover remaining (M.C. Ribeiro et al. 2009). Most of these fragments are secondary forests smaller than 100 ha and each has a particular history.

Primary and secondary forests differ not only in species richness and diversity due to recruitment limitations (Peterson & Carson 2008), but in regeneration, stratification, and dispersion strategies of species forming these forests as well (Nunes et al. 2003). These functions may be used to differentiate between primary, old-growth forests and secondary fragments (Liebsch et al. 2008). Therefore, species with similar properties are pooled in ecological guilds (Simberloff & Dayan 1991).

For Atlantic Rainforest, three regeneration (or successional) guilds may be distinguished: Pioneer species which require direct light for germination and establishment; light-demanding climax species which need abundant light only in some phase of their development (germination or establishment, for example); and shadow-tolerant species which prosper in the completely shady conditions of the understory (Gandolfi et al. 1995). Because

environmental conditions, such as nutrient supply and light availability in the understory, change gradually during succession (Tilman 1980, Laurance et al. 2002), the percentage of pioneer species is higher in initial than in climax stages. The criterion for primary forests is less than 10 % pioneer species (Liebsch et al. 2008).

Classifying species in stratification guilds separates understory species reaching heights up to 15 m only from canopy species regularly exceeding this value (Oliveira-Filho et al. 1997). Due to reduced light availability in primary forests and advanced successional stages (Guariguata & Ostertag 2001), the proportion of understory species should amount 50 % or more within a primary forests (Liebsch et al. 2008).

While wind-dispersed species dominate species assemblage in initial phases of succession (Ingle 2003), they are substituted by animal-dispersed species in advanced stages. In primary forests the ecological guild of animal-dispersed species should, by criterion, dominate species composition with more than 80% (Liebsch et al. 2008).

Due to its high level of endemism, the Atlantic Rainforest is considered a hotspot of biodiversity (Myers et al. 2000). Stehmann et al. (2009) listed 14,552 species of vascular plants for the whole ecosystem. From that list, 6,933 species, or 49 %, are endemic to the Atlantic Rainforest. Liebsch et al. (2008) postulate that about 40% of species from a primary forest are endemic to the Atlantic Rainforest.

The Forest of Seu Nico (FSN) in the Bom Sucesso Farm, Viçosa, Minas Gerais, Brazil, is a fragment that, according to its owners was never logged (Campos et al. 2006). In this article, we tested the hypothesis that the floristic composition of the FSN shows characteristics of primary forests, like an elevated percentage of endemic species as well as fewer pioneer species, more understory species and more animal-dispersed species in comparison to secondary fragments in the neighborhood. Furthermore, the suitability of additional traits as criteria for the unambiguous discrimination of primary and secondary forests is evaluated.

MATERIAL AND METHODS

Located in Viçosa, Minas Gerais State, Brazil, at 20°47'44'' S and 42°50'50'' W, the FSN is a forest fragment covering about 36 ha of a small valley.

According to the Köppen system, the climate of Viçosa is characterized as Cwb (Peel et al. 2007). This is a mesothermic climate with mild, rainy summers and dry winters. The predominant soils are deeply intemperished oxisols, but inceptisols are found on slopes and neosols are found in sedimentation areas. According to Velloso et al. (1991), the vegetation is characterized as Submontane Seasonal Semideciduous Forest.

For the sampling, the plot method was applied (Newton 2007): One hectare was divided into 100 quadratic plots of 10 m x 10 m. All trees with a diameter at breast height (dbh) greater or equal to 3.2 cm was tagged and identified. Collected and identified botanical material was deposited in the collection of the herbarium VIC of the UFV.

Nomenclature of species follows the database of Forzza et al. (2010). Classifying species phylogeny follows APG III (2009).

The species accumulation curve was designed grouping two, five, ten, 25, 50, and finally all 100 plots (Condit et al. 1996). This species accumulation curve was fitted with the power model (Arrhenius 1921).

To compare diversity, species richness and composition of the FSN with nearby secondary fragments, species lists was extracted from literature. Species names have been updated according to the database of Forzza et al. (2010). Species that were joined by taxonomists like *Guatteria nigrescens* and *G. australis* or *Piptadenia gonocantha* and *P. communis* were pooled. These updates explain differences in species richness given by the authors of the original texts.

After this updates, species were classified according to their regeneration, stratification and dispersion guilds by consulting the following literature (sorted in alphabetic order, not by relevance): Appolinário et al. (2005), Aquino & Barbosa (2009), Araújo et al. (2005, 2006), Araujo et al. (2010), Brandão et al. (2009), Cappelatti & Schmitt (2009), Carvalho (2006, 2007), Carvalho & Nascimento (2009), Chagas et al. (2001), Colonetti et al. (2009), Higuchi et al. (2008), Leite & Rodrigues (2008), Lemos (2008), Lima et al.

(2010), Lopes et al. (2002), Marangon et al. (2007), Metzger et al. (1997), Norden et al. (2009), Nunes et al. (2003), Oliveira-Filho et al. (2004, 2007), Paula et al. (2004), Peixoto et al. (2004), Pinto et al. (2005), Rolim et al. (1999), Silva et al. (2004), Stranghetti et al. (2003), and Yamamoto et al. (2007).

The evaluation of the characteristic "rarity" follows the suggestions of Oliveira-Filho (2006), and information about endemism follows Oliveira-Filho (2006), Stehmann et al. (2009) and Forzza et al. (2010). In the event of contradictory informations, the species have been allocated to the guild indicated by the majority of references.

RESULTS

In one hectare from the FSN, 2529 living and 100 dead individuals with dbh ≥ 3.2 cm were sampled. Altogether, 218 species from 141 genera and 53 families were detected within the survey (Table 1, detailed list is available from corresponding author upon request). From this data, 799 living and 29 dead individuals has a diameter at breast height less than 4.8 cm. If these species are excluded from the community, species richness is reduced to 204 (Table 1).

Table 1

FSN Summary Tally. N is the number of individual trees, S is the number of species, G is number of genera, F is number of families, H' is Shannon-Wiener diversity index using $\log_{10}$, and α is Fisher´s α. Basal area includes all multiple stems for each individual.

Size Class [cm dbh]	BA [m^2]	N	S	G	F	H'	α ±DP
≥ 3.2	40.165	2529	218	141	53	4.36	57.19 ±2.16
≥ 4.8	39.233	1739	204	133	51	4.41	59.99 ±2.55
≥ 10	35.663	762	154	107	38	4.39	58.21 ±3.41
≥ 30	20.535	108	51	46	23	3.52	37.75 ±6.06
≥ 60	9.782	11	7	7	6	-	-

Table 2

FSN Rankings by Family. The top ten families for trees ≥ 3.2 cm dbh ranked by basal area, number of individual trees, and number of species.

Rank	Family	BA [m^2]	% BA	% Trees	Family	Trees	% Trees	Family	Species
1	Moraceae	6.396	15.9	10.3	Myrtaceae	368	14.6	Fabaceae	21
2	Fabaceae	5.644	14.1	6.3	Siparunaceae	262	10.4	Myrtaceae	19
3	Malvaceae	3.713	9.2	1.0	Moraceae	260	10.3	Rubiaceae	18
4	Myristicaceae	2.776	6.9	3.8	Lauraceae	221	8.7	Lauraceae	15
5	Annonaceae	2.693	6.7	3.6	Rubiaceae	162	6.4	Euphorbiaceae	10
6	Lauraceae	2.397	6.0	8.7	Fabaceae	159	6.3	Meliaceae	10
7	Burseraceae	1.889	4.7	5.3	Burseraceae	135	5.3	Moraceae	10
8	Myrtaceae	1.560	3.9	14.6	Meliaceae	107	4.2	Salicaceae	9
9	Urticaceae	1.493	3.7	1.7	Myristicaceae	96	3.8	Annonaceae	8
10	Rubiaceae	1.422	3.5	6.4	Arecaceae	95	3.8	Melastomataceae	6

Table 3

FSN Ranking by Species. Top ten tree species for trees ≥ 3.2 cm dbh ranked by number of trees and basal area with percentage of total population.

Rank	Species	Trees	% Trees	Species	BA [m^2]	% BA	% Trees
1	*Siparuna guianensis* (Siparunaceae)	254	10.0	*Ficus gomelleira* (Moraceae)	3.405	8.5	< 0.1
2	*Protium warmingiana* (Burseraceae)	121	4.8	*Pseudopiptadenia contorta* (Fabaceae)	3.082	7.7	1.8
3	*Sorocea bonplandii* (Moraceae)	107	4.2	*Virola gardneri* (Myristicaceae)	2.221	5.5	3.1
4	*Myrciaria floribunda* (Myrtaceae)	101	4.0	*Guatteria nigrescens* (Annonaceae)	1.912	4.8	2.6
5	*Euterpe edulis* (Arecaceae)	90	3.6	*Sterculia curiosa* (Malvaceae)	1.840	4.6	0.5
6	*Virola gardneri* (Myristicaceae)	78	3.1	*Ceiba speciosa* (Malvaceae)	1.371	3.4	< 0.1
7	*Helicostylis tomentosa* (Moraceae)	73	2.9	*Protium warmingiana* (Burseraceae	1.292	3.2	4.8
8	*Guatteria australis* (Annonaceae)	67	2.6	*Sorocea bonplandii* (Moraceae)	1.258	3.1	4.2
9	*Bathysa nicholsonii* (Rubiaceae)	60	2.4	*Astronium graveolens* (Anacardiaceae)	0.974	2.4	0.5
10	*Marlieria excoriata* (Myrtaceae)	59	2.3	*Ocotea silvestris* (Lauraceae)	0.821	2.0	0.9

Species and family ranking by basal area, the number of individuals and number of species (the latter for family ranking only) are plotted in Tables 2 and 3.

The species-accumulation curve fitted by the power model shows strong linear correlation in the logarithmic space (Fig. 1, $R^2 = 0.984$, $F_{1;5} = 314.5$, $p < 0.001$ for all individuals with dbh ≥ 3.2 cm and $R^2 = 0.986$, $F_{1;5} = 364.7$, $p < 0.001$ for all individuals with dbh ≥ 4.8 cm).

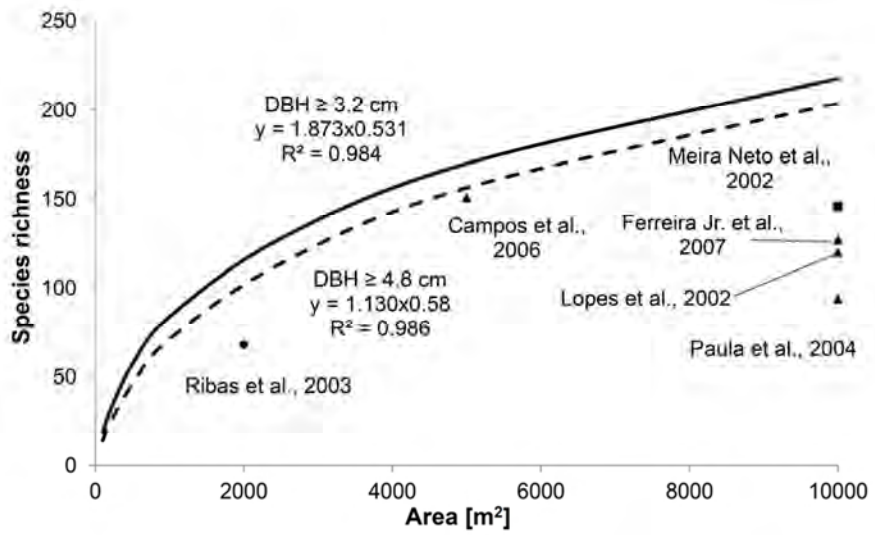


Fig. 1 - Species-accumulation curves and their fittings by the power model for all individuals with dbh ≥ 3.2 cm (continuous line) and all individuals with dbh ≥ 4.8 cm only (dashed line) found within one hectare in the “Forest of Seu Nico”, Viçosa, Minas Gerais, Brazil. Added points indicate species richness from other phytosociological surveys from the region. Solid triangles represent studies considering individuals with a dbh ≥ 4.8 cm, quadrats indicate surveys of all individuals DBH ≥ 3.2 cm, circles indicate studies including all individuals with dbh ≥ 1.6 cm. For further explanations see text.

From species found in our survey, 42 were not listed by Oliveira-Filho (2006). Of the remaining 177 species, 54 are considered rare, very rare or even extremely rare within the Atlantic Rainforest biome (Fig. 2). Based on abundance data, these are 846 or 36.5 % of all individuals from species

listed by given source (data not shown). Rare species with more than 50 individuals are *Protium warmingiana*, *Virola gardneri*, *Helicostylis tomentosa*, *Marlieria excoriata* and *Phyllostemonodaphne geminiflora*. Of them, *H. tomentosa*, *M. excoriata* and *P. geminiflora* are classified as very rare species even. Extremely rare species with more than five individuals are *Guarea pendula* and *Sorocea hillarii*. Also, 5 species, namely *Dalbergia nigra*, *Ocotea odorifera*, *Melanoxylum brauna*, *Euterpe edulis*, and *Coussapoa floccosa* are endangered according to the COPAM (2008) Red List of Minas Gerais State.

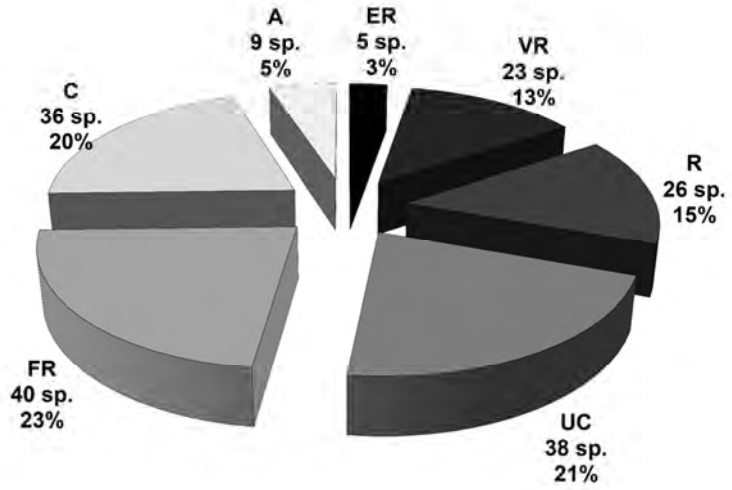


Fig. 2 - Rarity of 177 tree species with dbh ≥ 3.2 cm found within one hectare in the FSN, Viçosa, MG, Brazil, according to Oliveira-Filho (2006). A is abundant, C is common, FR is frequent, UC is uncommon, R is rare, VR is very rare and ER is extremely rare.

Endemic status of 27 species could not be identified. From the remaining 192 species, 74 or nearly 40% are endemic to the Atlantic Rainforest, while 117, or just over 60 %, occur in other vegetation zones such as the Brazilian Cerrado or the Amazon Rainforest.

Only 14 of all 218 species found in the FSN were classified as pioneer species. Excluding those species that we could not classify, this corresponded to 7.9 % of all species and only 3.2 % of all individuals (Fig. 3). 85 % or 179 of all 210 classified species are dispersed by animals. This corresponds to 90 % of all individuals. Of 198 classified species, 113, or 56 %, live in the understory.

Compared to secondary forest fragments of the region, both species richness and the percentage of rare, endemic and zoochorus species of the FSN are amazingly higher (Table 4), some differences are significant (Table 5). The percentage of pioneer species in the FSN is lower than in the other, secondary fragments, but the difference is not significant. The number of individuals and the basal area are significantly higher in the FSN than in surrounding fragments.

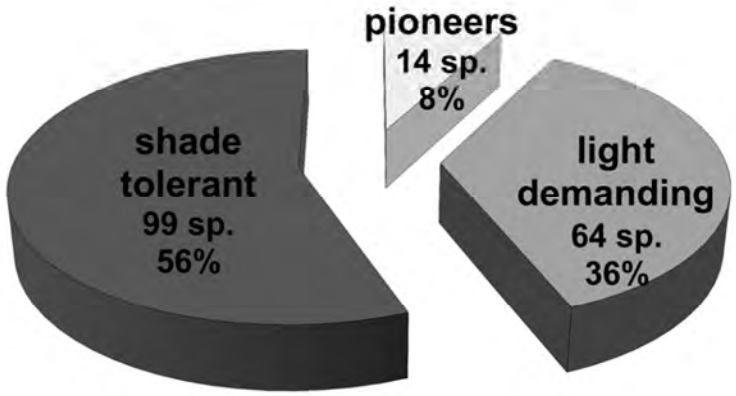


Fig. 3 - Affiliation to successional group of 177 tree species with DBH > 3.2 cm found within one hectare in the FSN, Viçosa, Brazil.

Table 4

Comparison of FSN with surrounding fragments. Surveys from secondary forests are separated by double rule from FSN surveys (Campos *et al.* 2006, our study).

Source	dbh	Sample area [ha]	S	N	BA [m^2]	R	E	P	AD	U
Ribas et al. 2004	1.6	0.2	67	-	-	12.1	21.0	26.9	75.8	47.5
		0.2	68	-	-	16.7	22.6	14.5	78.8	54.1
Meira Neto & Martins 2002	3.2	1	146	-	-	20.2	25.2	15.5	76.2	54.5
Lopes et al. 2002	4.8	1	120	-	-	15.3	24.1	12.1	76.5	50.1
Paula et al. 2004	4.8	1	94	1484	31.98	20.2	23.2	8.5	75.0	45.6
Ferreira Jr. et al. 2007	4.8	1	127	1460	29.68	17.8	22.9	15.7	78.0	52.4
Campos et al. 2006	4.8	0.5	155	1704	38.45	25.6	32.1	13.6	82.0	48.6
Our study	**3.2**	**1**	**218**	**2536**	**42.52**	**30.5**	**38.5**	**7.9**	**85.2**	**56.1**
	4.8	**1**	**204**	**1739**	**41.81**	**29.7**	**39.2**	**8.0**	**85.4**	**55.2**

Notes: dbh is diameter at breast height, S is the survey´s species richness, N is the number of trees, extrapolated to one hectare, BA is basal area per hectare, R is the cumulative percentage of rare, very rare and extremely rare species (for definitions see Oliveira-Filho, 2006), E is percentage of species endemic to the Atlantic Rainforest biome, P is percentage of pioneer species, AD is percentage of animal dispersed species and U is percentage of understory species. Data does not include species that were not classified.

Table 5

Statistical comparison of FSN and surrounding secondary fragments using t-test of independent samples. For abbreviations see notes of Table 4.

	S	N	BA [m^2]	R	E	P	AD	U
FSN	179.5 ±34.65	1721.5 ±24.75[a]	40.13 ±2.38[a]	27.65 ±2.90[a]	35.65 ±5.02[a]	10.8 ±3.96	83.70 ±2.40[a]	51.9 ±4.67
Secondary Fragments	121.75 ±21.51	1472 ±16.97[b]	30.83 ±1.63[b]	18.38 ±2.34[b]	23.85 ±1.03[b]	12.95 ±3.4	76.425 ±1.23[b]	50.65 ±3.82
p (t-test)	0.058	< 0.01	< 0.05	< 0.01	< 0.01	0.522	< 0.01	0.739

Notes: S is the survey´s species richness, N is the number of trees, extrapolated to one hectare, BA is basal area per hectare, R is the cumulative percentage of rare, very rare and extremely rare species (for definitions see Oliveira-Filho, 2006), E is percentage of species endemic to the Atlantic Rainforest biome, P is percentage of pioneer species, AD is percentage of animal dispersed species and U is percentage of understory species. Data does not include species that were not classified.

DISCUSSION

The “Forest of Seu Nico” supports higher tree species richness per hectare than lowland tropical forests, like those on Barro Colorado Island in Panama (Leigh et al. 2004) or the Luquillo Forest of Puerto Rico, United States (Thompson et al. 2004).

Slopes of the fittings of the species-accumulation curves, a measure for spatial turnover or variation between plots, are higher for our study than for wet lowland tropical forests in Barro Colorado Island, Panama (Condit et al. 1996) or West Indian Ghats (Krishnamani et al. 2004). On the other hand, lowland Evergreen Atlantic Rainforests in southern of the Bahia State Bahia,

Brazil, show higher species richness as well as higher spatial turnover (Soares 2010).

The species list from the FSN fulfills all criteria proposed by Liebsch et al. (2008) for old-growth, primary forests since there are less than 10 % of non-pioneer, more than 80 % of zoochorus, more than 50 % understory species and about 40% of species endemic to the Atlantic Rainforest biome. Even if the percentage of endemic species in a study realized by Campos et al. (2006) within the FSN had not completely fulfilled the criterion endemism, in general the percentages in the cited study are still higher than those in the secondary fragments. Except for the fraction of understory species, no criterion is fulfilled by nearby secondary fragments. Therefore, the FSN must be considered an old-growth, primary forest.

For what we know, the FSN is the only forest fragment in Viçosa municipality that fulfills the presented criteria to be identified as a primary forest. Unique species richness and diversity of the old-growth FSN in the region (S.C. Ribeiro et al. 2009) emphasize its special role as a species pool for surrounding forest fragments in a highly degraded and fragmented landscape of Seasonal Semideciduous Forests (Myers and Harms 2009; M.C. Ribeiro et al. 2009) and illustrate its non-substitutability for biological conservation (Bihn et al. 2008; Gibson et al. 2011).

Further differences between the FSN and surrounding secondary fragments from the Viçosa municipality have been detected. The number of rare species and structural parameters like the number of trees per hectare and basal area are higher in the primary FSN.

Rarity itself is a conservation value (Usher et al. 1980), but natural rarity (i.e. Benedetti-Cecchi et al. 2008) must not be confounded with rarity and endangerment due to human impacts: Many species like *Melanoxylum brauna*, *Dalbergia nigra* or *Ocotea odorifera* are compiled in Red Lists (COPAM 2008), but found in many surveys, even in secondary fragments (e.g. Araújo et al. 2005; Marangon et al., 2007; Nunes et al., 2003; Oliveira-Filho et al., 2001; Pinto et al. 2007; Souza 2008). The populations of these species, known for their high timber quality, are endangered by selective logging. Nevertheless, these species are classified as common (*O. odorifera*)

or uncommon (*D. nigra*, *M. brauna*) occurring in many surveys due to effective protection measures.

Naturally rare species have larger fruits or seeds (Vieira et al. 1996) and depend on larger vertebrates for distribution. As these larger animals suffer population reduction or extinction due to habitat destruction and fragmentation (Cullen Jr. et al. 2000), rare plant species dispersion is also reduced. This might influence species composition of secondary forests for a very long time (Silva & Tabarelli 2000) because it takes smaller dispersers longer to complete the job.

Therefore, the percentage of naturally rare species may be used as a criterion to distinguish primary forests from secondary fragments; the borderline should be a minimum of 25% of rare species in primary forests.

Liebsch et al. (2008) use cited criteria like percentage of endemic, understory, non-pioneer and animal-dispersed species to estimate the time necessary for complete recovery of the Atlantic Rainforest after a disturbance. Following their approach and assuming a minimum of 25% rare species in a primary or completely recovered forest, we extrapolate time of recovery as 710 years from our database (without considering Meira Neto & Martins 2002, because exact fragment age is unknown). Because correlation is not significant, this calculation will not be improved further.

Although not available for all studies cited in Table 4, the number of individuals as well as basal area per hectare are lower in secondary forests than in both surveys from the FSN, indicating an increase in the number of individuals and basal area during a forest's successional advance. Studies of community dynamics report that basal area increases with time, but the number of individuals generally decreases (i.e. Ernest et al. 2009; Oliveira-Filho et al. 2007). Such self-thinning, proposed by Yoda *et al.* (1963) for single species stands and by Luyssaert et al. (2008) for species-rich tree communities, cannot be detected by comparing the FSN as a primary, mature forest with secondary fragments.

Higher basal area acquired during successional advance and especially higher average basal area per individual means more above ground biomass and therefore higher CO_2-sequestration (Chave et al. 2001). These findings

agree with Luyssaert et al. (2008) that primary forests are larger global carbon sinks than secondary ones (Gibbs et al. 2007) and support the hypothesis that maintenance of ecosystem services increases with species richness (Duffy 2009; Isbell et al. 2011).

Basal area seems to be a further criterion to distinguish between primary and secondary forests, but the number of individuals must be taken with caution because of contradictory evidences from literature (i.e. Appolinário et al. 2005; Oliveira-Filho et al. 2007).

It is not possible to estimate the time necessary to recover the Atlantic Rainforest as proposed by Liebsch et al. (2008) by basal area because further data are lacking. Nevertheless, this criterion should be used in combination with all other characteristics discussed (percentage of non-pioneer, animal dispersed, understory, rare and endemic species as well as basal area) to identify further primary forests unambiguously in other regions from the Brazilian Atlantic Rainforest.

Elevated species richness and the percentage of endemic, understory, non-pioneer or animal-dispersed species characterize the FSN as a primary forest. Furthermore, the primary FSN shows higher percentage of rare species, higher number of per hectare individuals, and higher per hectare basal area than surrounding secondary forests. Beside the number of individuals, these characteristics may be utilized as additional criteria to identify such primary forests in other regions of the Atlantic Rainforest.

ACKNOWLEDGEMENTS

We are grateful to Gilmar E. Valente, Pedro Paulo de Souza, José Martins Fernandes, Victor Peçanha de Miranda Coelho, Priscila Bezerra de Souza, Michellia Pereira Soares, Walnir Gomes Ferreira Jr., Márcio Luiz Batista and Amilcar Walter Saporetti Jr. for support in the identification process.

RESUMO

Diagnóstico de florestas primárias na Mata Atlântica brasileira. - Identificação de florestas primárias é um passo importante para a conservação de ecossistemas altamente diversificados, auto-sustentáveis e insubstituíveis, mas não é fácil distinguir características de florestas primárias dos de florestas secundárias. Neste artigo, é testada se a composição florística de um fragmento de Mata Atlântica que nunca foi cortada, a Floresta de Seu Nico (FSN), Viçosa, Minas Gerais, Brasil, apresenta características de florestas primárias, tais como percentagens elevadas de: espécies não-pioneiras, espécies dispersas por animais, espécies de sub-bosque e espécies endêmicas. Com 218 espécies de árvores com diâmetro à altura do peito maior ou igual a 3,2 cm encontrados em um hectare, a riqueza de espécies na FSN é considerável para a região. Os percentuais de espécies de não pioneiras, espécies dispersas por animais e espécies de sub-bosque bem como as espécies endêmicas da FSN caracterizam o fragmento como uma floresta primária. Outras diferenças entre a FSN e fragmentos secundários ao redor foram detectados, tais como aumento da área basal por hectare e maior porcentagem de espécies raras. O aumento da área basal prova o importante papel das florestas primárias para a proteção dos recursos abióticos como aumento do seqüestro de CO_2. Além disso, essas novas características podem ser utilizadas em estudos deste tipo para identificar as florestas primárias na Mata Atlântica brasileira.

Palavras-chave: insubstitutabilidade, características de florestas primárias, riqueza de espécies, composição de espécies, raridade.

REFERENCES

APG (Angiosperm Phylogeny Group) III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot J Linn Soc 161: 105–121.

APPOLINÁRIO V, OLIVEIRA FILHO AT AND GUILHERME FAG. 2005. Tree population and community dynamics in a Brazilian tropical semideciduous forest. Rev Bras Bot 28: 347-360.

AQUINO C AND BARBOSA LM. 2009. Classes sucessionais e síndromes de dispersão de espécies arbóreas e arbustivas existentes em vegetação ciliar remanescente (Conchal, SP), como subsídio para avaliar o potencial do fragmento como fonte de propágulos para enriquecimento de áreas revegetadas no Rio Mogi-Guaçu, SP. R Árvore 33: 349-358.

ARAÚJO FS, MARTINS SV, MEIRA NETO JAA, LANI JL AND PIRES IE. 2005. Florística da vegetação arbustivo-arbórea colonizadora de uma área degradada por mineração de caulim, em Brás Pires, MG. R Árvore 29: 983-992.

ARAÚJO FS, MARTINS SV, MEIRA NETO JAA, LANI JL AND PIRES IE. 2006. Estrutura da vegetação arbustivo-arbórea colonizadora de uma área degradada por mineração de caulim, em Brás Pires, MG. R Árvore 30: 107-116.

ARAUJO MM, CHAMI L, LONGHI SJ, AVILA AL AND BRENA DA. 2010. Análise de agrupamento em remanescente de Floresta Ombrófila Mista. Ciência Florestal 20: 1-18.

ARRHENIUS O. 1921. Species and area. J Ecol 9: 95-99.

BARLOW J, GARDNER TA, ARAUJO LS, ÁVILA-PIRES TC, BONALDO AB ET AL. 2007. Quantifying the biodiversity value of tropical primary,

secondary, and plantation forests. Proc Nat Acad Soc. doi: 10.1073/pnas.0703333104

BENEDETTI-CECCHI L, BERTOCCI I, VASELLI S, MAGGI E AND BULLERI F. 2008. Neutrality and the Response of Rare Species to Environmental Variance. PLoS ONE. doi:10.1371/journal.pone.0002777

BIHN JH, VERHAAGH M, BRÄNDLE M AND BRANDL R. 2008. Do secondary forests act as refuges for old growth animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biol Conserv 141: 733-743.

BRANDÃO CFLS, MARANGON LC, FERREIRA RLC, LINS E AND SILVA ACB. 2009. Estrutura fitossociológica e classificação sucessional do componente arbóreo em um fragmento de floresta atlântica em Igarassu – Pernambuco. Rev Bras Cienc Agrár 4: 55-61.

BREARLEY FQ, PRAJADINATA S, KIDD OS AND PROCTOR J. 2004.Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest.For Ecol Manag 195: 385–397.

BROWNING BJ, JORDAN GJ, DALTON PJ, GROVE SJ, WARDLAW TJ AND TURNER PAM. 2010.Succession of mosses, liverworts and ferns on coarse woody debris, in relation to forest age and log decay in Tasmanian wet eucalypt forest. For Ecol Manag 260: 1896-1905.

CÂMARA IG. 2005. Breve história da conservação da Mata Atlântica. In: GALINDO-LEAL C, CÂMARA IG. (Eds.), Mata Atlântica: biodiversidade, ameaças e perspectivas, Fundação SOS Mata Atlântica/Conservação Internacional, São Paulo/Belo Horizonte, Brazil, p. 31-42.

CAMPOS EP, SILVA AF, MEIRA NETO JAA AND MARTINS SV. 2006. Floristica e estrutura horizontal da vegetação arbórea de uma ravina em um fragmento florestal no município de Viçosa, MG. R Árvore 30: 1045-1054.

CAPPELATTI L AND SCHMITT JL. 2009. Caracterização da flora arbórea de um fragmento urbano de Floresta Estacional Semidecidual no Rio Grande do Sul, Brasil. Pesquisas, Botânica 60: 341-354.

CARVALHO FA, NASCIMENTO MT AND BRAGA JMA 2006. Composição e riqueza florística da Floresta Atlântica submontana na região de Imbaú, Município de Silva Jardim, RJ. Acta Bot Bras 20: 727-740.

CARVALHO FA, NASCIMENTO MT AND BRAGA JMA. 2007. Estrutura e composição florística do estrato arbóreo de um remanescente de Mata Atlântica submontana no município de Rio Bonito, RJ, Brasil (Mata Rio Vermelho). R Árvore 31: 717-730.

CARVALHO FA AND NASCIMENTO MT. 2009. Estrutura diamétrica da comunidade e das principais populações arbóreas de um remanescente de Floresta Atlântica Submontana (Silva Jardim-RJ, Brasil). R Árvore 33: 327-337.

CHAGAS RK, OLIVEIRA-FILHO AT, VAN DEN BERG E AND SCOLFORO JRS. 2001. Dinâmica de populações arbóreas em um fragmento de Floresta Estacional Semidecidual Montana em Lavras, Minas Gerais. R Árvore 25: 39-57.

CHAVE J, RIERA B AND DUBOIS MA. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. J Trop Ecol 17: 79–96.

COLONETTI S, CITADINI-ZANETTE V, MARTINS R, SANTOS R, ROCHA E AND JARENKOW JA. 2009. Florística e estrutura fitossociológica em floresta

ombrófila densa submontana na barragem do rio São Bento, Siderópolis, Estado de Santa Catarina. Maringá 31: 387-405.

CONDIT R, HUBBELL SP, LAFRANKIE JV, SUKUMAR R, MANOKARAN N, FOSTER RB AND ASHTON PS. 1996. Species-Area and Species-Individual Relationships for Tropical Trees: A Comparison of Three 50-ha Plots. J Ecol 84: 549-562.

COPAM 2008. Lista das espécies ameaçadas de extinção da flora no Estado de Minas Gerais. Deliberação Conselho Estadual de Política Ambiental No 367, Anexo I.

CULLEN JR. L, BODMER RE AND PADUA CV. 2000. Effects of hunting in habitat fragments of the Atlantic forests, Brazil. Biol Conserv 95: 149-156.

DENT DH AND WRIGHT SJ. 2009. The future of tropical species in secondary forests: A quantitative review. Biol Conserv 142: 2833-2843.

DUFFY JE. 2009.Why biodiversity is important to the functioning of real-world ecosystems. Front Ecol Env. doi:10.1890/070195

ERNEST KM, WHITE EP AND BROWN JH. 2009. Changes in a tropical forest support metabolic zero-sum dynamics. Ecol Lett 12: 507–515.

FERREIRA JR. WG, SILVA AF, MEIRA NETO JAA, SCHAEFER CEGR, DIAS AS, IGNÁCIO M AND MEDEIROS MCMP. 2007. Composição florística da vegetação arbórea de um trecho de Floresta Estacional Semidecídua em Viçosa, Minas Gerais, e espécies de maior ocorrência na região. R Árvore 31: 1121-1130.

FORZZA RC. (coord.) 2010. Lista de Espécies da Flora do Brasil. http://floradobrasil.jbrj.gov.br/2010/. Accessed 26 October 2010.

GANDOLFI S, LEITÃO FILHO HF AND BEZERRA CLF. 1995. Levantamento florístico e caráter sucessional das espécies arbustivo-arbóreas de uma floresta mesófila semidecídua no município de Guarulhos, SP. Rev Bras Biol 55: 753-767.

GIARIGUATA MR AND OSTERTAG R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manag 148: 185-206.

GIBBS HK, BROWN S, NILES JO ANDFOLEY JA. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality.Env Res Lett 2: 1-13.

GIBSON L, LEE TM, KOH LP, BROOK BW, GARDNER TA, BARLOW J, PERES CA, BRADSHAW CJA, LAURANCE WF, LOVEJOY TE AND SODHI NS. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378-381. doi: 10.1038/nature10425

HIGUCHI P, OLIVEIRO-FILHO AT, BEBBER DP, BROWN ND, SILVA AC AND MACHADO ELM. 2008. Spatio-temporal patterns of tree community dynamics in a tropical forest fragment in South-east Brazil. Plant Ecol 199: 125-135.

INGLE NR. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and sucessional vegetation. Oecologia 134: 251-261.

ISBELL F, CALCAGNO V, HECTOR A, CONNOLLY J, HARPOLE WS, REICH PB, SCHERER-LORENZEN M, SCHMID B, TILMAN D, RUIJVEN J, WEIGELT A, WILSEY BJ, ZAVALETA ES AND LOREAU M. 2011. High plant diversity is needed to maintain ecosystem services. Nature 477, 199-203.

KRISHNAMANI R, KUMAR A AND HARTE J. 2004. Estimating species richness at large spatial scales using data from small discrete plots. Ecography 27: 637-642.

LAURANCE WF, LOVEJOY TE, VACONCELOS HL, BRUNA EM, DIRHAM RK, STOUFFER PC, GASCON C, BIERREGAARD RO, LAURANCE SG AND SAMPAIO E. 2002. Ecosystem decay of Amazonia forest fragments: a 22-year investigation. Conserv Biol 16: 605-618.

LEIGH JR. EG, LAO SL, CONDIT R, HUBBELL SP, FOSTER RB AND PÉREZ R. 2004. Barro Colorado Island Forest Dynamics Plot, Panama. In: LOSOS EC AND LEIGH JR. EG. (Eds.), Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network, London: The University of Chicago Press, London, UK, p. 451-463.

LEITE EC AND RODRIGUES RR. 2008. Fitossociologia e caracterização sucessional de um fragmento de Floresta Estacional no suedeste do Brasil. R Árvore 32: 583-595.

LEMOS PHD. 2008. Efeito de borda no componente arbórea de um fragmento de floresta semidecídua, Viçosa, MG. Dissertation, Universidade Federal de Viçosa, 44p.

LIEBSCH D, MARQUES MCM AND GOLDENBERG R. 2008. How long does Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. Biol Conserv 141: 1717-1725.

LIMA ALS, ZANELLA F AND CASTRO LDM. 2010. Crescimento de *Hymenaea courbaril* L. var. *stilbocarpa* (Hayne) Lee et Lang. e *Enterolobium contortisiliquum* (Vell.) Morong (Leguminosae) sob diferentes níveis de sombreamento. Acta Amaz 40: 43-48.

LOPES WP, PAULA A, SEVILHA AC AND SILVA AF. 2002. Composição da flora arbórea de um trecho de Floresta Estacional no Jardim Botânica da Universidade Federal de Viçosa (Face Sudoeste), Viçosa, Minas Gerais. R Árvore 26: 339-347.

LUYSSAERT S, SCHULZE ED, BÖRNER A, KNOHL A, HESSENMÖLLER D, LAW BE, CIAIS P AND GRACE J. 2008. Old-growth forests as global carbon sinks. Nature 455: 213-215.

MARANGON LC, SOARES JJ, FELICIANO ALP, LINS CF AND BRANDÃO S. 2007. Estrutura fitossociológica e classificação sucessional do componente arbóreo de um fragmento de Floresta Estacional Semidecidual, no município de Viçosa, Minas Gerais. Cerne 13: 208-221.

MEIRA NETO JAA AND MARTINS FR. 2002. Composição florística de uma Floresta Estacional Semidecidual Montana no município de Viçosa-MG. R Árvore 26: 437-446.

METZGER JP, BERNACCI LC AND GOLDENBERG R. 1997. Pattern of tree species diversity in riparian forest fragments of different widths (SE Brazil). Plant Ecol 133: 135-152.

MYERS JA AND HARMS KE. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. Ecol Lett 12: 1250-1260.

MYERS N, MITTERMEIER RA, MITTERMEIER CG, FONSECA GAB AND KENT J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

NEWTON AC. 2007. Forest ecology and conservation: a handbook of techniques. Oxford: Oxford University Press, 454 p.

NORDEN N, CHAVE J, BELBENOIT P, CAUBÈRE A, CHÂTELET P, FORGET PM, PIÉRA B, VIERS J AND THÉBAUD C. 2009. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. J Ecol 97: 186-197.

NUNES YRF, MENDONÇA AVR, BOTEZELLI L, MACHADO ELM AND OLIVEIRA-FILHO AT. 2003. Variações da fisionomia, diversidade e composição de guildas da comunidade arbórea em um fragmento de floresta semidecidual em Lavras, MG. Acta Bot Bras 17: 213-229.

OLIVEIRA-FILHO AT, MELLO JM AND SCOLFORO JRS. 1997. Effects of past disturbances and edges on tree community strucutre and dynamics within a fragment of tropical semideciduous forest in south eastern Brazil over a five-year period (1987-1992) Plant Ecol 131: 45-66.

OLIVEIRA-FILHO AT, CURI N, VILELA EA AND CARVALHO DA. 2001. Variation in tree community composition and structure with changes in soil properties within a fragment of semideciduos forest in south-eastern Brazil. Edinb J Bot 58: 139-158.

OLIVEIRA-FILHO AT. 2006. Catálogo das árvores nativas de Minas Gerais: mapeamento e inventário da flora native e dos reflorestamentos de Minas Gerais. Editora UFLA, Lavras, 423 p.

OLIVEIRA-FILHO AT, CARVALHO DA, VILELA EA, CURI N AND FONTES MAL. 2004. Diversity and structure of the tree community of a fragment of tropical secondary forest of the Brazilian Atlantic Forest domain 15 and 40 years after logging. Rev Bras Bot 4: 685-701.

OLIVEIRA-FILHO AT, CARVALHO WAC, MACHADO ELM, HIGUCHI P, APPOLINÁRIO V, CASTRO GC, SILVA AC, SANTOS RM, BORGES LF, CORRÊA BS AND ALVES JM. 2007. Dinâmica da comunidade e populações arbóreas da borda e interior de um remanescente florestal na Serra da

Mantiqueira, Minas Gerais, em um intervalo de cinco anos (1999-2004). Rev Bras Bot 30: 149-161.

PAULA A, SILVA AF, MARCO JR. P, SANTOS FAM AND SOUZA AL. 2004. Sucessão ecológica da vegetação arbóres em uma Floresta Estacional Semidecidual, Viçosa, MG, Brasil. Acta Bot Bras 18: 407-423.

PEEL MC, FINLAYSON BL AND MCMAHON TA. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Sys Sci 11: 1633-1644.

PEIXOTO GL, MARTINS SV, SILVA AF AND SILVA S. 2004. Composição florística do componente arbórea de um tracho de Floresta Atlântica na Área de Proteção Ambiental da Serra da Capoeira Grande, Rio de Janeiro, RJ, Brasil. Acta Bot Bras 18: 151-160.

PETERSON CJ AND CARSON WP. 2008. Process contraining woody species succession on abandoned pastures in the tropics: on the relevance of temperate models of succession. In: CARSON PC AND SCHNITZER AS. (Eds.), Tropical Forest Community Ecology, Singapore:Ho Printing Pte Ltd, Singapore, Singapore, p 367-383.

PINTO LVA, BOTELHO SA, OLIVEIRA-FILHO AT AND DAVIDE AC. 2005. Estudo da vegetação como subsídio para propostas de recuperação das nascentes da Bacia hidrográfica do Riberão Santa Cruz, Lavras, MG. R Árvore 29: 775-793.

PINTO SIC, MARTINS SV, SILVA AG, BARROS NF, DIAS HCT AND SCOSS LM. 2007. Estrutura do componente arbustivo-arbóreo de dois estádios sucessionais de Floresta Estacional Semidecidual na Reserva Florestal Mata do Paraiso, Viçosa, MG, Brasil. R Árvore 31: 823-833.

RIBAS RF, MEIRA NETO JAA, SILVA AF AND SOUZA AL. 2004. Composição florística da dois trechos em diferentes etapas serais de uma Floresta Estacional Semidecidual em Viçosa, Minas Gerais. R Árvore 27: 821-830.

RIBEIRO MC, METZGER JP, MARTENSEN AC, PONZONI FJ AND HIROTA MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142: 1141–1153.

RIBEIRO SC, JACOVINE LAG, SOARES CPB, MARTINS SV, SOUZA AL AND NARDELLI AMB. 2009. Quantificação de biomassa e estimativa de estoque de carbono em uma floresta madura no município de Viçosa, Minas Gerais. R Árvore 33: 917-926.

ROLIM SG, COUTO HTZ AND JESUS RM. 1999. Mortalidade e recrutamento de árvores na Floresta Atlântica em Linhares (ES). Scientia forestalis 55: 49-69.

SILVA JMC AND TABARELLI M. 2000. Tree species impoverishment and the future flora of the Atlantic forest in northeast Brazil. Nature 404: 72-74.

SILVA CT, REIS GC, REIS MGF, SILVA E AND CHAVES RA. 2004. Avaliação temporal da florística arbórea de uma Floresta Secundária no município de Viçosa, Minas Gerais. R Árvore 28: 429-441.

SIMBERLOFF D AND DAYAN T. 1991. The guild concept and the structure of ecological communities. Ann Rev Ecol Evol Syst 22: 115-143.

SOARES MP. 2010. Estudos de diversidade de comunidade e populações vegetais em Floresta Atlântica de Tabuleiros no norte do Espírito Santo e sul da Bahia. Dissertation, Universidade Federal de Viçosa, 83 p.

SOUZA PB. 2008. Diversidade florística e atributos pedológicos ao longo de uma encosta com Floresta Estacional Semidecidual Submontana, zona de amortecimento do Parque Estadual do Rio Doce, MG. Dissertation, Universidade Federal de Viçosa, 138 p.

STEHMANN JR, FORZZA RC, SALINO A, SOBRAL M, COSTA DP AND KAMINO LHY. (Org.) 2009. Plantas da Floresta Atlântica. Rio de Janeiro: Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, 505 p.

STRANGHETTI V, ITURALDE RB, GIMENEZ LR AND ALMELLA D. 2003.Florística de um fragmento florestal do sítio São Pedro, município de Potirendaba, Estado de São Paulo. Maringá 25: 167-172.

STYRING AR, RAGAI R, UNGGANG J, STUEBING R, HOSNER PA AND SHELDON FH. 2011. Bird community assembly in Bornean industrial tree plantations: Effects of forest age and structure. For Ecol Manag 261: 531-544.

TILMAN D. 1980. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton: Princeton University Press, 376 p.

THOMPSON J, BROKAW N, ZIMMERMANN JK, WAIDE RB, EVERHAM III EM AND SCHAEFER DA.2004. Luquillo Forest Dynamics Plot, Puerto Rico, United States. In: LOSOS EC AND LEIGH JR. EG. (Eds.), Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network. London: The University of Chicago Press, London, UK, p. 540-550.

USHER MB. 1980. An Assessment of Conservation Values within a large site of Special Scientific Interest in North Yorkshire. Field Studies 5: 323-348.

VELOSO HP, RANGEL FILHO ALR AND LIMA JCA. 1991. Classificação da Vegetação Brasileira, adaptada a um Sistema Universal. Departamento de

Recursos Naturais e Estudos Ambientais do Intituto Brasileiro de Geografia e Estatística – Rio de Janeiro: IBGE, 124 p.

VIEIRA ICG, SALOMÃO RP, ROSA NA, NEPSTAD DC AND ROMA JC. 1996. O renascimento da floresta no rastro da agricultura. Ciência Hoje 20: 38-44.

YAMAMOTO LF, KINOSHITA LS AND MARTINS FR. 2007. Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. Acta Bot Bras 21: 553-573.

YODA K, KIRA T, OGAWA H AND HOZUMI K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J Biol Osaka City Univ 14, 107-132.

Supplement Material

GASTAUER M, SOBRAL MEG AND MEIRANETO JAA. 201x. Primary Forests Diagnosis in Brazilian Atlantic Rainforest. Anais da Academia Brasileira de Ciências xx: xxx-xxxx.

TABLE S1

Abundance (N), rarity and endemic status and affiliation to ecological guilds of tree species with dbh ≥ 3.2 cm found within one hectare from the FSN.

Family / *Species name*	N	Rarity and endemism	Affiliation to ecological guilds
Achariaceae			
Carpotrochebrasiliensis (Raddi) Endl.	6	uc-yes	sha-zoo-us
Anacardiaceae			
Astronium fraxinifolium Schott	4	c-no	sha-ane-us
Astronium graveolens Jacq.	13	fr-no	sha-ane-cp
Tapirira guianensis Aubl.	9	a-no	lig-zoo-us
Tapirira obtusa (Benth.) J.D. Mitch.	7	c-no	sha-zoo-cp
Annonaceae			
Annona cacans Warm.	4	c-yes	lig-zoo-cp
Guatteria australis A. St.-Hil.	67	fr-yes	sha-zoo-us
Guatteria villosissima Saint-Hilaire	1	uc-no	lig-zoo-us
Guatteria sp.1	5	-	--zoo--
Guatteria sp. 2 *	1	-	--zoo--
Rollinia laurifolia Schltdl	6	fr-yes	lig-zoo-cp
Xylopia brasiliensis Spreng.	3	fr-yes	lig-zoo-cp
Xylopia sericea A. St.-Hil.	3	fr-no	pio-zoo-us
Apocynaceae			
Aspidosperma olivaceum Müll. Arg.	3	fr-yes	sha-ane-us
Aspidosperma polyneuron Müll. Arg.	5	uc-yes	sha-ane-us
Aspidosperma subincanum Mart.	3	fr-no	sha-ane-us
Tabernaemontana hystrix Steud.	2	uc-yes	pio-zoo-us
Aquifoliaceae			
Ilex cerasifolia Reissek	2	uc-no	sha-zoo-us
Araliaceae			
Dendropanax cuneatus (DC.) Decne. & Planch.	1	c-no	lig-zoo-sb
Schefflera morototoni (Aubl.) Maguire *et al.*	6	c-no	pio-zoo-cp
Arecaceae			
Astrocaryum aculeatissimum (Schott) Burret	5	r-yes	sha-zoo-us
Euterpe edulis Mart.	90	uc-no	sha-zoo-us
Asteraceae			
Vernonanthera diffusa (Less.) H.Rob.	1	c-no	pio-ane-cp

Continued …

Table S1: Continued.

Family / *Species name*	N	Rarity and endemism	Affiliation to ecological guilds
Bignoniaceae			
Handroanthus chrysotrichus (Mart. ex A. DC.) Mattos *	1	--no	lig-ane-us
Jacaranda macrantha Cham.	10	fr-no	lig-ane-cp
Sparattosperma leucanthum (Vell.) K. Schum.	2	uc-no	lig-ane-us
Burseraceae			
Protium heptaphyllum (Aubl.) Marchand	8	c-no	lig-zoo-cp
Protium warmingianum Marchand	121	r-no	sha-zoo-cp
Trattinnickia ferruginea Kuhlm.	6	vr-yes	--zoo-cp
Cannabaceae			
Celtis iguanaea (Jacq.) Sarg.	1	c-no	pio-zoo-us
Cardiopteridaceae			
Citronella paniculata (Mart.) R.A. Howard	4	uc-yes	sha-zoo-us
Caricaceae			
Jacaratia cf. *heptaphylla* (Vell.) A. DC.	1	er-yes	sha-zoo-us
Celastraceae			
Maytenus floribunda Reissek	1	r-no	sha-zoo-us
Maytenus robusta Reissek	25	fr-no	sha-zoo-us
Maytenus salicifolia Reissek	3	fr-no	sha-zoo-us
Salacia elliptica (Mart. ex Schult.) G. Don	3	fr-no	sha-zoo-us
Chrysobalanaceae			
Hirtella hebeclada Moric. *ex* DC.	13	uc-yes	sha-zoo-cp
Licania belemii Prance	2	er-yes	--zoo-cp
Clusiaceae			
Kielmeyera albopunctata Saddi	3	--yes	----cp
Garcinia brasiliensis Mart.	8	fr-no	lig-zoo-us
Tovomita glazioviana Engl.	7	--yes	lig-zoo-cp
Tovomitopsis saldanhae Engl.	10	--yes	sha-zoo-cp
Combretaceae			
Terminalia glabrascens Mart.	1	c-no	sha-ane-us
Cordiaceae			
Cordia sellowiana Cham.	4	c-no	lig-zoo-cp
Elaeocarpaceae			
Sloanea hirsuta (Schott) Planch ex Benth.	1	fr-yes	sha-zoo-us
Erythroxylaceae			
Erythroxylum daphnites Mart.	1	uc-no	--zoo-us
Erythroxylum pelleterianum A. St.-Hil.	1	fr-no	lig-zoo-us
Euphorbiaceae			
Alchornea glandulosa Poepp. & Endl.	3	fr-no	pio-zoo-cp
Alchornea triplinervia (Spreng.) Müll. Arg.	2	c-no	lig-zoo-cp
Aparisthmium cordatum (A.Juss.) Baill.	4	uc-no	lig-aut-us
Croton floribundus Spreng.	4	c-no	pio-aut-cp
Mabea fistulifera Mart.	3	fr-no	pio-aut-cp
Maprounea guianensis Aubl.	2	fr-no	sha-aut-cp
Sapium glandulosum (L.) Morong	4	c-no	pio-zoo-cp
Euphorbiaceae sp.1	1	---	-----

Continued …

Table S1: Continued.

Family / ***Species name***	N	Rarity and endemism	Affiliation to ecological guilds
Euphorbiaceae sp.2 *	2	---	-----
Euphorbiaceae sp.3 *	1	---	-----
Fabaceae			
Andira fraxinifolia Benth.	2	c-no	sha-zoo-us
Apuleia leiocarpa (Vogel) J.F. Macbr.	18	fr-no	lig-ane-cp
Caesalpinaceae sp.1	1	---	-----
Copaifera langsdorffii Desf.	15	a-no	lig-zoo-cp
Dalbergia nigra (Vell.) Allemao ex Benth.	3	uc-yes	lig-ane-cp
Hymenaea sp.1	2	---	-----
Inga capitata Desv.	24	uc-no	lig-zoo-cp
Inga cylindrica (Vell.) Mart.	7	uc-no	sha-zoo-cp
Inga vera Willd.	2	fr-no	lig-zoo-cp
Inga sp.1	1	---	--zoo-cp
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima	1	fr-no	sha-ane-cp
Machaerium caratinganum Kuhlm. & Hoehne	1	--yes	lig-ane--
Machaerium nyctitans (Vell.) Benth.	8	c-yes	lig-ane-cp
Machaerium sp.1 *	1	---	--ane--
Melanoxylon brauna Schott	2	uc-yes	sha-ane-cp
Ormosia arborea (Vell.) Harms	2	uc-yes	lig-zoo-cp
Peltophorum dubium (Spreng.) Taub.	2	uc-no	lig-zoo-cp
Piptadenia gonoacantha (Mart.) J.F. Macbr.	6	c-no	pio-ane-cp
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima	45	uc-no	lig-ane-cp
Swartzia acutifolia Vogel	1	r-yes	sha-zoo-cp
Swartzia myrtifolia Sm.	15	r-no	lig-zoo-us
Humiriaceae			
Vantanea obovata (Nees & Mart.) Benth. *	1	vr-no	--zoo-us
Lacistemaceae			
Lacistema pubescens Mart.	7	uc-no	lig-zoo-us
Lauraceae			
Aniba firmula (Nees & C. Mart.) Mez	22	fr-no	sha-zoo-cp
Cinnamomum glaziovii (Mez) Kosterm.	1	--yes	sha-zoo-cp
Cryptocarya moschata Nees & C. Mart. ex Nees	1	vr-yes	sha-zoo-cp
Nectandra lanceolata Nees & Mart.	7	fr-no	sha-zoo-cp
Nectandra oppositifolia Nees	3	c-no	sha-zoo-cp
Ocotea corymbosa (Meisn.) Mez	8	c-no	lig-zoo-cp
Ocotea dispersa (Nees) Mez	24	uc-yes	lig-zoo-us
Ocotea odorifera (Vell.) Rohwer	27	c-yes	sha-zoo-cp
Ocotea pulchella (Nees & Mart.) Mez	1	uc-no	lig-zoo-us
Ocotea silvestris Vattimo-Gil	24	vr-yes	sha-zoo-us
Ocotea sp.1	19	---	--zoo--
Phyllostemonodaphne geminiflora (Mez) Kosterm.	59	vr-yes	lig-zoo-us
Urbanodendron verrucosum (Nees) Mez	23	r-yes	sha-zoo-us

Continued …

Table S1: Continued.

Family / *Species name*	N	Rarity and endemism	Affiliation to ecological guilds
Lauraceae sp.1	1	---	--zoo-us
Lauraceae sp.2	1	---	--zoo-us
Lecydithaceae			
Cariniana estrellensis (Raddi) Kuntze	3	c-no	sha-ane-cp
Cariniana legalis (Mart.) Kuntze	1	uc-yes	sha-ane-cp
Lythraceae			
Lafoensia glyptocarpa Koehne	8	--no	sha---cp
Malvaceae			
Ceiba speciosa (A. St.-Hil.) Ravenna	1	uc-no	lig-ane-cp
Eriotheca candolleana (K. Schum.) A. Robyns	13	fr-no	lig-ane-us
Luehea grandiflora Mart. & Zucc.	2	c-no	lig-ane-us
Sterculia curiosa (Vell.) Taroda	12	vr-yes	lig-zoo-cp
Melastomataceae			
Miconia brunnea DC.	1	r-yes	--zoo-us
Miconia budlejoides Triana	3	r-yes	sha-zoo-us
Miconia cinnamomifolia (DC.) Naudin	1	c-yes	pio-zoo-us
Miconia minutiflora (Bonpl.) DC.	1	uc-no	--zoo-cp
Miconia tristis Spring	1	r-yes	lig-zoo-us
Mouriri glazioviana Cogn.	14	uc-no	sha-zoo-us
Meliaceae			
Cabralea canjerana (Vell.) Mart.	1	a-no	lig-zoo-cp
Cedrela fissilis Vell.	2	a-no	lig-zoo-cp
Guarea fistulosa W. Palacios	1	---	--zoo-cp
Guarea guidonia (L.) Sleumer	1	fr-no	sha-zoo-cp
Guarea macrophylla Vahl	15	c-no	sha-zoo-cp
Guarea pendula R.da Silva Ramalho, A.L. Pinheiro & T.D. Penn.	11	er-yes	sha-zoo-us
Trichilia catigua A. Juss.	34	fr-no	sha-zoo-us
Trichilia emarginata (Turcz.) C. DC.	35	uc-yes	sha-zoo-us
Trichilia lepidota Mart.	5	uc-no	sha-zoo-cp
Trichilia pallida Sw.	2	c-no	sha-zoo-cp
Monimiaceae			
Mollinedia schottiana (Spreng.) Perkins	5	r-no	lig-zoo-us
Moraceae			
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	4	r-no	lig-zoo-us
Brosimum guianense (Aubl.) Huber	49	uc-no	lig-zoo-cp
Ficus gomelleira Kunth & C.D. Bouché	1	fr-no	sha-zoo-cp
Ficus luschnathiana (Miq.) Miq.	1	r-no	lig-zoo-cp
Ficus enormis Mart. *ex* Miq.	1	fr-no	sha-zoo-cp
Helicostylis tomentosa (Poepp. & Endl.) Rusby	73	vr-no	lig-zoo-cp
Maclura tinctoria (L.) D. Don ex Steud.	4	c-no	lig-zoo-cp
Naucleopsis oblongifolia (Kuhlm.) Carauta	1	r-yes	sha-zoo-cp
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Wess. Boer	107	fr-no	sha-zoo-us
Sorocea hilariana Gaudich.	19	er-yes	Sha-zoo-us

Continued …

Table S1: Continued.

Family / *Species name*	N	Rarity and endemism	Affiliation to ecological guilds
Myristicaceae			
Virola gardneri (A. DC.) Warb.	78	r-yes	sha-zoo-cp
Virola bicuhyba (Schott *ex.* Spreng.) Warb.	18	uc-yes	sha-zoo-cp
Myrsinaceae			
Ardisia cf. *catharinensis* Mez	1	vr-yes	--zoo-us
Cybianthus fuscus Mart. *	1	--no	--zoo--
Myrsine umbellata Mart.	5	c-yes	sha-zoo-us
Myrtaceae			
Calyptranthes brasiliensis Spreng.	20	vr-yes	sha-zoo-us
Campomanesia xanthocarpa (Mart.) O. Berg	1	fr-yes	lig-zoo-us
Eugenialambertiana DC.	47	--no	sha-zoo-us
Eugenia dodonaeifolia Cambess.	3	uc-yes	sha-zoo-us
Eugenia florida DC.	10	a-no	sha-zoo-us
Eugenia leptoclada O.Berg	4	vr-yes	sha-zoo-us
Marlierea excoriata Mart.	59	r-yes	sha-zoo-us
Marlierea suaveolens Cambess.	1	--yes	sha-zoo-us
Marlierea cf. *teuscheriana* (O.Berg) D.Legrand	21	r-yes	sha-zoo-us
Myrcia anceps (Spreng.) O. Berg	2	vr-yes	sha-zoo-us
Myrciaria floribunda (H.West ex Willd.) O.Berg	101	c-no	sha-zoo-us
Myrcia pallida (Cambess.) O. Berg	13	---	sha-zoo--
Myrcia pubipetala Miq.	11	uc-yes	sha-zoo-us
Myrcia splendens (Sw.) DC.	21	a-no	lig-zoo-us
Myrcia sp.1	24	---	--zoo--
Neomitranthes sp.1	26	---	--zoo-us
Plinia cf. *grandifolia* (Mattos) Sobral	1	vr-yes	sha-zoo-us
Psidium cf. *oblongatum* O. Berg	1	--yes	--zoo--
Myrtaceae sp.1	2	---	--zoo--
Nyctaginaceae			
Guapira hirsuta (Choisy) Lundell	4	uc-yes	sha-zoo-us
Guapira opposita (Vell.) Reitz	11	c-no	sha-zoo-us
Pisonia ambigua Griseb.	10	r-no	lig-zoo-cp
Nyctaginaceae sp.1	3	---	--zoo--
Ochnaceae			
Ouratea polygyna Engl.	8	vr-yes	sha-zoo-us
Olacaceae			
Heisteria silvianii Schwacke	7	uc-yes	sha-zoo-us
Tetrastylidium grandiflorum (Baill.) Sleumer	20	vr-yes	sha-zoo-us
Oleaceae sp.1 *	1	---	--zoo--
Peraceae			
Pera glabrata (Schott) Poepp. ex Baill.	2	a-no	lig-zoo-cp
Phyllanthaceae			
Hieronyma alchorneoides Allemão	2	fr-no	lig-zoo-cp
Margaritaria nobilis L. f.	2	r-no	sha-zoo-cp
Piperaceae			
Piper arboreum Aubl.	9	fr-no	sha-zoo-us
Piper gigantifolium C. DC. *	2	--no	--zoo-us

Continued …

Table S1: Continued.

Family / *Species name*	N	Rarity and endemism	Affiliation to ecological guilds
Rhamnaceae			
Colubrina glandulosa Perkins	1	uc-no	lig-zoo-cp
Rosaceae			
Prunus myrtifolia (L.) Urb.	1	c-no	lig-zoo-cp
Rubiaceae			
Alseis floribunda Schott	31	r-no	lig-zoo-us
Amaioua guianensis Aubl.	18	c-no	sha-zoo-us
Bathysa cuspidata (St. Hil.) Hook.f. *ex* K.Schum.	7	vr-yes	sha-aut-us
Bathysa nicholsonii K. Schum.	60	vr-yes	sha-aut-us
Genipa americana L.	1	fr-no	lig-zoo-cp
Guettarda viburnoides Cham. & Schltdl.	3	c-no	lig-zoo-us
Ixora gardneriana Benth.	12	r-yes	sha-zoo-us
Psychotria carthagenensis Jacq.	10	fr-no	sha-zoo-us
Psychotria conjungens Müll. Arg. *	1	er-yes	sha-zoo-us
Psychoria myriantha Müll. Arg.	1	--yes	sha-zoo-us
Psychotria nuda (Cham. & Schltdl.) Wawra	5	r-yes	sha-zoo-us
Psychotria vellosiana Benth. *	1	c-no	lig-zoo-us
Psychotria sp.1 *	2	---	--zoo--
Randia ferox (Cham. & Schltdl.) DC. *	2	fr-yes	lig-zoo-us
*Rudgea jasminoide*s (Cham.) Müll.Arg.	6	fr-no	sha-zoo-us
Rubiaceae sp.1 *	2	---	--zoo--
Rutaceae			
Hortia brasiliana Vand. ex DC.	1	uc-yes	--zoo-cp
Zanthoxylum rhoifolium Lam.	2	a-no	lig-zoo-us
Sabiaceae			
Meliosma itatiaiae Urb.	8	vr-yes	--zoo-us
Salicaceae			
Casearia arborea (Rich.) Urb.	9	fr-no	lig-zoo-cp
Casearia decandra Jacq.	1	c-no	sha-zoo-cp
Casearia gossypiosperma Briq.	6	fr-no	lig-ane-us
Casearia sylvestris Sw.	2	a-no	pio-zoo-us
Casearia ulmifolia Vahl ex Vent.	30	uc-no	lig-zoo-us
Macrothumia kuhlmannii (Sleumer) M.H.Alford	2	vr-yes	--zoo-cp
Prockia crucis P. Browne ex L.	1	r-no	lig-zoo-us
Xylosma prockia (Turcz.) Turcz.	2	uc-no	lig-zoo-us
Salicaceae sp.1	5	---	--zoo--
Sapindaceae			
Allophylus edulis (A. St.-Hil. *et al.*) Hieron. ex Niederl.	1	fr-no	sha-zoo-us
Cupania vernalis Cambess.	3	c-no	lig-zoo-cp
Matayba elaeagnoides Radlk.	12	--no	sha-zoo-cp
Sapotaceae			
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	24	c-no	sha-zoo-cp
Chrysophyllum lucentifolium Cronquist	28	vr-no	sha-zoo-us

Continued …

Table S1: Continued.

Family / *Species name*	N	Rarity and endemism	Affiliation to ecological guilds
Chrysophyllum cf. *marginatum* (Hook. & Arn.) Radlk.	2	fr-no	sha-zoo-cp
Chrysophyllum sp.1	2	---	--zoo--
Pouteria caimito (Ruiz & Pav.) Radlk.	24	r-no	sha-zoo-cp
Pradosia lactescens (Vell.) Radlk.	2	vr-no	sha-zoo-cp
Siparunaceae			
Siparuna guianensis Aubl.	254	c-no	sha-zoo-us
Siparuna reginae (Tul.) A. DC.	8	r-no	sha-zoo-us
Solanaceae			
Brunfelsia uniflora (Pohl) D. Don	1	uc-no	lig-zoo-us
Cestrum mariqitense Kunth	2	vr-no	--zoo-us
Cestrum sp. 1	2	---	--zoo--
Solanaceae sp. 1	1	---	--zoo--
Urticaceae			
Cecropia hololeuca Miq.	9	fr-yes	pio-zoo-cp
Coussapoa floccosa Akkermans & C.C. Berg	1	vr-yes	--zoo-us
Coussapoa microcarpa (Schott) Rizzini	3	r-yes	sha-zoo-cp
Pourouma guianensis Aubl.	31	r-no	pio-zoo-cp
Vochysiaceae			
Qualea multiflora Mart.	1	vr-yes	sha-zoo-cp
Unknown family			
Unidentified sp.1	1	---	-----
Unidentified sp.2	1	---	-----
218 species	**2529**		

Notes: a is abundant, c is common, fr is frequent, uc is uncommon, r is rare, vr is very rare, er is extremely rare, yes is species endemic to the Atlantic Rainforest biome, no is species not endemic to the Atlantic Rainforest biome, pio is pioneer species, lig is light depending climax species, sha is shade tolerant climax species, ane is anemochorus, aut is autochorus, zoo is zoochorus, us is species of understory, cp is canopy species. Species marked with * do not occur with dbh ≥ 4.8 cm.

CHAPTER 4*

Community Dynamics in a Species-Rich Old-growth Forest Patch from Viçosa, Minas Gerais, Southeastern Brazil

* This chapter was submitted to the journal **Acta Botanica Brasilica** on 20/04/2012.

Community Dynamics in a Species-Rich Old-growth Forest Patch from Viçosa, Minas Gerais, Southeastern Brazil

Markus Gastauer[1,2]
João Augusto Alves Meira Neto[1,3]

[1] Laboratório de Ecologia, Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Campos Universitário s/n, 36570-000 Viçosa, Minas Gerais, Brasil
[2] Centro de Ciências Ambientais Floresta-Escola Environmental Research Center, Frutal, Brasil
[3] Corresponding author: j.meira@ufv.br

RESUMO – (Dinâmica da comunidade de um fragmento florestal primário rico em espécies de Viçosa, Minas Gerais, Sudeste do Brasil). A teoria ecológica prevê estabilidade na forma de um equilíbrio mais ou menos estável para a riqueza de espécies, o número e a biomassa de indivíduos em ecossistemas maduros. O objetivo deste estudo foi testar se essa estabilidade existe em uma das últimas florestas primárias, a Floresta do Seu Nico (FSN), do município de Viçosa, durante um período de nove anos. Em uma parcela de um hectare, censos de todas as árvores com diâmetro à altura do peito (DAP) maior ou igual de 3,2 cm foram realizados em 2001 e 2010. A riqueza de espécies e diversidade foram comparados. Além das taxas de crescimento anual, de mortalidade e de recruitamento, o ganho e a perda da área basal foram calculados. Durante o período de observação, a riqueza de espécies diminuiu de 224 para 218, o número de indivíduos aumentou de 2485 para 2529. A área basal por hectare, em geral uma medida de biomassa, aumentou de 37,86 m^2 ha^{-1} em 2001 para 40,16 m^2 ha^{-1} em 2010. Espécies pouco frequentes (menos de 10 indivíduos no primeiro censo) apresentam maior mortalidade do que recrutamento. As nove espécies mais abundantes no censo de 2001 mostraram aumento em abundância. Essas alterações talvez refletem impactos graves na comunidade devido à perda de habitat e a fragmentação avançada na paisagem adjacente, bem como maior disponibilidade de recursos devido à mudança climática.

Palavras-chave: comunidade dinâmica, desmatamento, fragmentação da paisagem, riqueza de espécies, taxa de imigração

ABSTRACT – (Community Dynamics in a Species-Rich Old-Growth Forest Patch from Viçosa, Minas Gerais, Southeastern Brazil). Ecological theory predicts stability in the form of more or less stable equilibrium for species richness, number and biomass of individuals in mature ecosystems. The aim of this study was to test whether this stability was given during a nine year examination period in one of the last old-growth forests, the Forest of Seu Nico (FSN) in the Viçosa municipality. In a one-hectare plot of the FSN, censuses of all trees with diameter at breast height (dbh) greater or equal to 3.2 cm were carried out in 2001 and 2010. Species richness and diversity were compared. Beside growth, recruitment and mortality rate, the gains and losses of basal area were computed. During the observation period, species richness decreased from 224 to 218 and the number of individuals increased from 2485 to 2529. The per hectare basal area, a measure for overall biomass, increased from 37.86 m^2 ha^{-1} in 2001 to 40.16 m^2 ha^{-1} in 2010. Uncommon species (less than 10 individuals in the first census) showed higher mortality than recruitment. The nine most abundant species from 2001 increased in abundance. These alterations congruently reflect severe impacts on the community perhaps due to advanced habitat loss and fragmentation of the surrounding landscape as well as higher resource availability due to climate change.

Key words: community dynamics, habitat loss, immigration rate, landscape fragmentation, species richness

Introduction

Climate change (IPCC 2007; Matesanz *et al.* 2010), habitat destruction and fragmentation (Wright 2010) threaten global species richness and diversity. As tropical forests account for major part of terrestrial biodiversity (Millennium Ecosystem Assessment 2005), these forests should be affected in serious ways. To outline and understand the influences of changes on forest communities, their species richness and diversity, it is necessary to conduct long term monitoring studies, so-called community dynamics (Losos & Leigh 2004).

Species composition within a defined community undoubtedly varies over time (Rosenzweig 1995; Hubbell 2001; Magurran 2011). These variations depend on disturbance regime (Connell 1978; Molino & Sabatier 2001), ecological drift and stochasticity (Hubbell 2001). On the other hand, the modification of formerly continuous forests into fragments of variable size and shape alters the ecological processes of the forest`s natural dynamics as well (Tabarelli *et al.* 2004). Furthermore, elevated temperatures, higher atmospheric CO_2 concentrations and other factors that accompany climate change might influence resource availability and therefore growth, mortality and recruitment of trees within forest communities (Ernest *et al.* 2009).

Among tropical forests, the South American Atlantic Rainforest is one of the most diverse ecosystems (Stehmann *et al.* 2010). Due to its high degree of endemism and endangered status it is considered a biodiversity *hotspot* (Myers *et al.* 2000). Once covering up to 1,500,000 km^2 (Câmara 2005), only 11 % of the original Atlantic Rainforest remains, most of it as small secondary forest patches (Ribeiro *et al.* 2009). Species rich old-growth forests like the Forest of Seu Nico (FSN) in Viçosa municipality, Minas Gerais, Brazil (Campos *et al.* 2006, unpublished data) are extremely rare.

The aim of this study is to test whether the tree community from an FSN one hectare plot shows stability in the form of dynamic equilibrium during a nine year period regarding species richness (MacArthur & Wilson 1967), the number of individuals or zero-sum dynamics (Hubbell 2001), individual`s basal area and metabolic rate (Ernest *et al.* 2009). Furthermore, changes in species richness, diversity, the number of individuals, basal area, mortality

and recruitment from the FSN one hectare plot are discussed against the background of intense landscape fragmentation and climate change.

Materials and Methods

The FSN, located at 20°47'44'' S and 42°50'50'' W on the Bom Sucesso Farm, Viçosa, Minas Gerais, Brazil, is a 35 ha forest patch that, according to its owners, never has been logged (Campos *et al.* 2006). According to Köppen, the climate of the region is characterized as Cwb (Peel *et al.* 2007). This is a mesothermic climate with mild, rainy summers and dry winters. The predominant soils are deeply intemperished oxisols, which are found within a small-scaled mosaic of inceptisols on slopes and neosols in sedimentation areas of valley bottoms. The predominant vegetation is characterized as Submontane Seasonal Semideciduous Forest (Veloso *et al.* 1991).

Within the FSN, an area of 100 x 100 m was marked and divided into 100 plots of 10 x 10 m. During the first census in 2001 (Irsigler 2001), all trees with diameter at breast height (dbh) greater than or equal to 3.2 cm within this one hectare plot were tagged and identified. During a second census in 2010, the dbh of all surviving individuals within the 100 plots was measured and recruits, i.e. untagged individuals with dbh greater or equal to 3.2 cm, were tagged and identified as well.

To compare species richness from different censuses, the species-area relationship (SAR) was calculated using the power model $S=cA^z$ proposed by Arrhenius (1921) to fit the species-accumulation curve. S is the number of species, A is the area and c and z are constants corresponding the intercept with the y-axis (c) and the inclination (z) of the linearized SAR after log transformation of data. For the fitting, we assessed the average number of species of groups of two, five, ten, 25, 50, and finally all 100 plots from the FSN one hectare plot. Only neighboring plots were grouped.

Linearized in the logarithmic space, the slope of the SAR describes the difference between plots and it is therefore interpreted as spatial turnover, or β-diversity (Condit *et al.* 1996). For statistical comparison of the values, the LINEST function in Microsoft Excel™ was used. Biodiversity indices of

Simpson, Shannon-Wiener and Fisher`s α were computed with the software EstimateS for all censuses (Colwell & Coddington 1994).

The community dynamics were calculated as proposed by Losos & Lao (2004). To calculate the average growth rate between censuses, the diameter increment for each tree between censuses was divided by the interval (in years) between both censuses. The average growth rate is the average of the growth rates of all trees fulfilling inclusion criteria.

Mortality rate MR of trees between both censuses is the natural logarithm of the proportion of trees at the first census that survived to the second divided by time between both censuses:

$$MR = \frac{\ln(N_S)}{T} \qquad (1).$$

Here, T is the average census interval in years between censuses. The number of survived trees N_S is the number of (living) individuals in the first census minus not-detected individuals or individuals that died during the interval between censuses.

Recruitment rate (RR) of trees is

$$RR = \frac{\ln(\frac{N_S + N_R}{N_S})}{T} \qquad (2),$$

where N_R is the number of new trees appearing between censuses, i.e. recruits.

Basal area loss (BA_{loss}) includes basal area lost from mortality and from stem breakages below 3.2 cm dbh. The loss of basal area between censuses is the total basal area of trees at the first census that died, or declined to < 3.2 cm dbh by the second (AB_M) divided by time between censuses:

$$BA_{loss} = \frac{AB_M}{T} \qquad (3).$$

Basal area gain (BA_{gain}) is computed from the total gain in basal area of trees in the first census:

$$BA_{gain} = \frac{BA_{S2} - BA_{S1}}{T} \qquad (4),$$

with BA_{S1} being the basal area during the first census of trees surviving from one census to the other. BA_{S2} is the basal area of these individuals from the

second census. For calculation of demographic dynamics, all stems of multiple-stemmed individuals were included.

In addition to calculating dynamic figures for the whole community, they were also calculated for different size classes. Size class I includes individuals with dbh between 3.2 and 9.9 cm, size class II from 10 to 29.9 cm and size class III includes all individuals with dbh greater than or equal to 30 cm. Species were classified according to their regeneration, stratification and dispersal strategies: Community dynamics were calculated separately for all pioneer and all non-pioneer species (Swaine & Whitmore 1988), for all understory species reaching heights up to 15 m at maximum, for all canopy species usually reaching heights above 15 m (Oliveira-Filho *et al.* 1997), and animal-dispersed and non-animal-dispersed species. Furthermore, dynamics were calculated separately for all species endemic to the Atlantic Rainforest biome as well as all non-endemic species. Information about successional, dispersal and stratification strategy was withdrawn from literature; species not classified were not considered in the calculation.

Results

Plot Census History

The number of individuals in the FSN one hectare plot increased, but the number of species declined from 224 in 2001 to 214 in 2010 (Table 1). While ten species from the examined community went extinct, only four immigrated to the FSN one hectare plot (Table 2). The net loss of six species reduces slope z of the SAR (Figure 1). These differences are not significant, with z = 0.545 ±0.032 in 2001 and z = 0.531 ±0.030 in 2010. The diversity of the FSN one hectare plot decreased between 2001 and 2010 (Table 3).

The basal area increased from 37.86 $m^2 * ha^{-1}$ in 2001 to 40.16 $m^2 * ha^{-1}$ in 2010.

Table 1. FSN Plot Census History.

Census	Dates	Number of Trees (≥ 3.2 cm dbh)	Number of Species (≥ 3.2 cm dbh)	Basal area [m^2 ha^{-1}]
First	October 2000 – May 2001	2485	224	37.86
Second	Dezember 2009 – February 2010	2529	218	40.16

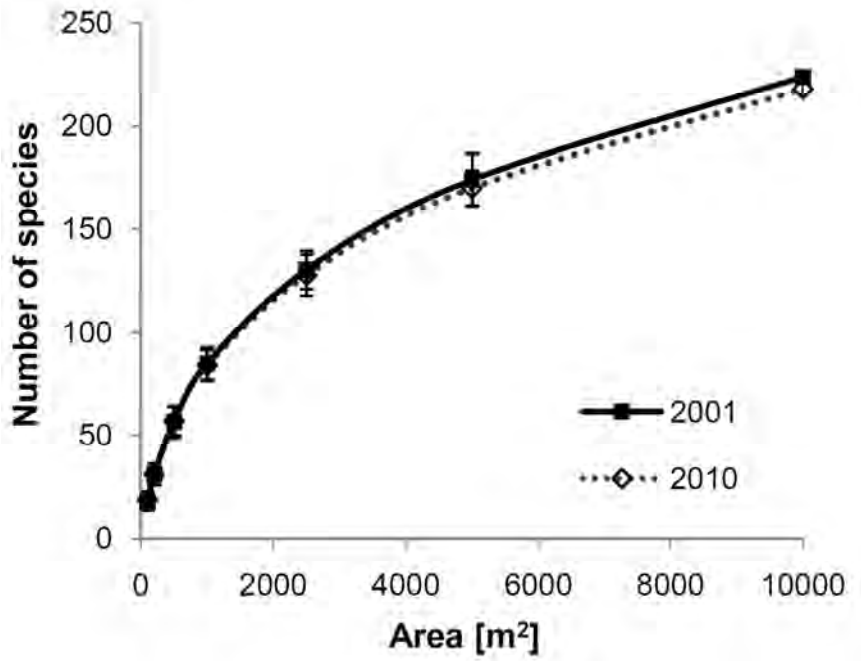


Figure 1. Rarefaction of the species accumulation curve for both censuses from the FSN one hectare plot. Species-area relationship, fitted by the power model does not differ significantly (2001: log number of species = 0.545 (±0.032) log area + 0.233 (±0.099), 2010: 0.531 (± 0.030) log area + 0.273 (±0.093)).

Table 2. Abundance of species with dbh > 3.2, their endemic status and affiliation to ecological guilds from two census of a tree community analyzed in the FSN one hectare plot. Notes: yes is species endemic to the Atlantic Rain Forest biome, no is species not endemic to the Atlantic Rain Forest biome, pio is pioneer species, npio is non-pioneer species, zoo is animal dispersed species, nzoo is not animal dispersed species, us is species of understory, cp is canopy species.

Family / *Species name*	**2001**	**2010**	**Endemism**	**Affiliation to ecological guilds**
ACHARIACEAE				
Carpotroche brasiliensis (Raddi) Endl.	x	x	yes	npio/zoo/us
ANACARDIACEAE				
Astronium fraxinifolium Schott	x	x	no	npio/nzoo/us
Astronium graveolens Jacq.	x	x	no	npio/nzoo/cp
Tapirira guianensis Aubl.	x	x	no	npio/zoo/us
Tapirira obtusa (Benth.) J.D. Mitch.	x	x	no	npio/zoo/cp
ANNONACEAE				
Annona cacans Warm.	x	x	yes	npio/zoo/cp
Guatteria australis A. St.-Hil.	x	x	yes	npio/zoo/us
Guatteria villosissima Saint-Hilaire	x	x	no	npio/zoo/us
Guatteria sp.1	x	x	-	-/zoo/-
Guatteria sp. 2 *	x	x	-	-/zoo/-
Rollinia laurifolia Schltdl	x	x	yes	npio/zoo/cp
Xylopia brasiliensis Spreng.	x	x	yes	npio/zoo/cp
Xylopia sericea A. St.-Hil.	x	x	no	pio/zoo/us
APOCYNACEAE				
Aspidosperma olivaceum Müll. Arg.	x	x	yes	npio/nzoo/us
Aspidosperma polyneuron Müll. Arg.	x	x	yes	npio/nzoo/us
Aspidosperma subincanum Mart.	x	x	no	npio/nzoo/us
Himatanthus phagedaenicus (Mart.) Woodson	x		yes	npio/nzoo/-
Tabernaemontana hystrix Steud.	x	x	yes	pio/zoo/us
AQUIFOLIACEAE				
Ilex cerasifolia Reissek	x	x	no	npio/zoo/us
ARALIACEAE				
Dendropanax cuneatus (DC.) Decne. & Planch.	x	x	no	npio/zoo/sb
Schefflera morototoni (Aubl.) Maguire *et al.*	x	x	no	pio/zoo/cp
ARECACEAE				
Astrocaryum aculeatissimum (Schott) Burret	x	x	yes	npio/zoo/us
Euterpe edulis Mart.	x	x	no	npio/zoo/us
Syagrus romanzoffiana (Cham.) Glassman	x		no	npio/zoo/cp
ASTERACEAE				
Vernonanthera diffusa (Less.) H.Rob.	x	x	no	pio/nzoo/cp

Continued …

Table 2. Continued.

Family / *Species name*	2001	2010	Endemism	Affiliation to ecological guilds
BIGNONIACEAE				
Handroanthus chrysotrichus (Mart. ex A. DC.) Mattos *	x	x	no	npio/nzoo/us
Jacaranda macrantha Cham.	x	x	no	npio/nzoo/cp
Sparattosperma leucanthum (Vell.) K. Schum.	x	x	no	npio/nzoo/us
BURSERACEAE				
Protium heptaphyllum (Aubl.) Marchand	x	x	no	npio/zoo/cp
Protium warmingianum Marchand	x	x	no	npio/zoo/cp
Trattinnickia ferruginea Kuhlm.	x	x	yes	-/zoo/cp
CANNABACEAE				
Celtis iguanaea (Jacq.) Sarg.		x	no	pio/zoo/us
CARDIOPTERIDACEAE				
Citronella paniculata (Mart.) R.A. Howard	x	x	yes	npio/zoo/us
CARICACEAE				
Jacaratia cf. *heptaphylla* (Vell.) A. DC.	x	x	yes	npio/zoo/us
Jacaratia spinosa (Aubl.) A. DC.	x		no	npio/zoo/cp
CELASTRACEAE				
Maytenus floribunda Reissek	x	x	no	npio/zoo/us
Maytenus robusta Reissek	x	x	no	npio/zoo/us
Maytenus salicifolia Reissek	x	x	no	npio/zoo/us
Salacia elliptica (Mart. ex Schult.) G. Don	x	x	no	npio/zoo/us
CHRYSOBALANACEAE				
Hirtella hebeclada Moric. *ex* DC.	x	x	yes	npio/zoo/cp
Licania belemii Prance	x	x	yes	-/zoo/cp
CLUSIACEAE				
Kielmeyera albopunctata Saddi	x	x	yes	-/-/cp
Garcinia brasiliensis Mart.	x	x	no	npio/zoo/us
Tovomita glazioviana Engl.	x	x	yes	npio/zoo/cp
Tovomitopsis saldanhae Engl.	x	x	yes	npio/zoo/cp
COMBRETACEAE				
Terminalia glabrascens Mart.	x	x	no	npio/nzoo/us
CORDIACEAE				
Cordia sellowiana Cham.	x	x	no	npio/zoo/cp
ELAEOCARPACEAE				
Sloanea hirsuta (Schott) Planch ex Benth.	x	x	yes	npio/zoo/us
ERYTHROXYLACEAE				
Erythroxylum daphnites Mart.	x	x	no	-/zoo/us
Erythroxylum pelleterianum A. St.-Hil.	x	x	no	npio/zoo/us
EUPHORBIACEAE				
Alchornea glandulosa Poepp. & Endl.	x	x	no	pio/zoo/cp
Alchornea triplinervia (Spreng.) Müll. Arg.	x	x	no	npio/zoo/cp
Aparisthmium cordatum (A.Juss.) Baill.	x	x	no	npio/nzoo/us
Croton floribundus Spreng.	x	x	no	pio/nzoo/cp
Croton hemiargyreus Müll. Arg.	x		-	/////
Mabea fistulifera Mart.	x	x	no	pio/nzoo/cp

Continued …

Table 2. Continued.

Family / *Species name*	2001	2010	Endemism	Affiliation to ecological guilds
Maprounea guianensis Aubl.	x	x	no	npio/nzoo/cp
Sapium glandulosum (L.) Morong	x	x	no	pio/zoo/cp
Euphorbiaceae sp.1	x	x	-	-/-/-
Euphorbiaceae sp.2 *	x	x	-	-/-/-
Euphorbiaceae sp.3 *	x	x	-	-/-/-
FABACEAE				
Andira fraxinifolia Benth.	x	x	no	npio/zoo/us
Apuleia leiocarpa (Vogel) J.F. Macbr.	x	x	no	npio/nzoo/cp
Caesalpinaceae sp.1	x	x	-	-/-/-
Copaifera langsdorffii Desf.	x	x	no	npio/zoo/cp
Dalbergia nigra (Vell.) Allemao ex Benth.	x	x	yes	npio/nzoo/cp
Hymenaea sp.1	x	x	-	-/-/-
Inga capitata Desv.	x	x	no	npio/zoo/cp
Inga cylindrica (Vell.) Mart.	x	x	no	npio/zoo/cp
Inga vera Willd.	x	x	no	npio/zoo/cp
Inga sp.1	x	x	-	-/zoo/cp
Inga sp. 2	x		-	-/-/-
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima	x	x	no	npio/nzoo/cp
Machaerium caratinganum Kuhlm. & Hoehne	x	x	yes	npio/nzoo//
Machaerium nyctitans (Vell.) Benth.	x	x	yes	npio/nzoo/cp
Machaerium sp.1 *	x	x	-	-/nzoo/-
Melanoxylon brauna Schott	x	x	yes	npio/nzoo/cp
Moldenhawera sp.	x		-	-/-/-
Ormosia arborea (Vell.) Harms	x	x	yes	npio/zoo/cp
Peltophorum dubium (Spreng.) Taub.	x	x	no	npio/zoo/cp
Piptadenia gonoacantha (Mart.) J.F. Macbr.	x	x	no	pio/nzoo/cp
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima	x	x	no	npio/nzoo/cp
Swartzia acutifolia Vogel	x	x	yes	npio/zoo/cp
Swartzia myrtifolia Sm.	x	x	no	npio/zoo/us
HUMIRIACEAE				
Vantanea obovata (Nees & Mart.) Benth. *		x	no	-/zoo/us
LACISTEMACEAE				
Lacistema pubescens Mart.	x	x	no	npio/zoo/us
LAURACEAE				
Aniba firmula (Nees & C. Mart.) Mez	x	x	no	npio/zoo/cp
Cinnamomum glaziovii (Mez) Kosterm.	x	x	yes	npio/zoo/cp
Cryptocarya moschata Nees & C. Mart. ex Nees	x	x	yes	npio/zoo/cp
Nectandra lanceolata Nees & Mart.	x	x	no	npio/zoo/cp
Nectandra oppositifolia Nees	x	x	no	npio/zoo/cp
Ocotea corymbosa (Meisn.) Mez	x	x	no	npio/zoo/cp
Ocotea dispersa (Nees) Mez	x	x	yes	npio/zoo/us
Ocotea odorifera (Vell.) Rohwer	x	x	yes	npio/zoo/cp
Ocotea pulchella (Nees & Mart.) Mez	x	x	no	npio/zoo/us

Continued ...

Table 2: Continued

Family / *Species name*	2001	2010	Endemism	Affiliation to ecological guilds
Ocotea silvestris Vattimo-Gil	x	x	yes	npio/zoo/us
Ocotea sp.1	x	x	-	-/zoo/-
Persea wildenowii Kosterm.	x		yes	npio/zoo/cp
Phyllostemonodaphne geminiflora (Mez) Kosterm.	x	x	yes	npio/zoo/us
Urbanodendron verrucosum (Nees) Mez	x	x	yes	npio/zoo/us
Lauraceae sp.1	x	x	-	-/-/-
Lauraceae sp.2	x	x	-	-/-/-
Lauraceae sp.3	x		-	-/-/-
LECYDITHACEAE				
Cariniana estrellensis (Raddi) Kuntze	x	x	no	npio/nzoo/cp
Cariniana legalis (Mart.) Kuntze	x	x	yes	npio/nzoo/cp
LYTHRACEAE				
Lafoensia glyptocarpa Koehne	x	x	no	npio/-/cp
MALVACEAE				
Ceiba speciosa (A. St.-Hil.) Ravenna	x	x	no	npio/nzoo/cp
Eriotheca candolleana (K. Schum.) A. Robyns	x	x	no	npio/nzoo/us
Luehea grandiflora Mart. & Zucc.	x	x	no	npio/nzoo/us
Sterculia curiosa (Vell.) Taroda	x	x	yes	npio/zoo/cp
MELASTOMATACEAE				
Miconia brunnea DC.	x	x	yes	-/zoo/us
Miconia budlejoides Triana	x	x	yes	npio/zoo/us
Miconia cinnamomifolia (DC.) Naudin	x	x	yes	pio/zoo/us
Miconia minutiflora (Bonpl.) DC.	x	x	no	-/zoo/cp
Miconia tristis Spring	x	x	yes	npio/zoo/us
Mouriri glazioviana Cogn.	x	x	no	npio/zoo/us
MELIACEAE				
Cabralea canjerana (Vell.) Mart.	x	x	no	npio/zoo/cp
Cedrela fissilis Vell.	x	x	no	npio/zoo/cp
Guarea fistulosa W. Palacios	x	x	-	-/zoo/cp
Guarea guidonia (L.) Sleumer	x	x	no	npio/zoo/cp
Guarea macrophylla Vahl	x	x	no	npio/zoo/cp
Guarea pendula R.da Silva Ramalho, A.L. Pinheiro & T.D. Penn.	x	x	yes	npio/zoo/us
Trichilia catigua A. Juss.	x	x	no	npio/zoo/us
Trichilia emarginata (Turcz.) C. DC.	x	x	yes	npio/zoo/us
Trichilia lepidota Mart.	x	x	no	npio/zoo/cp
Trichilia pallida Sw.	x	x	no	npio/zoo/cp
MONIMIACEAE				
Mollinedia schottiana (Spreng.) Perkins	x	x	no	npio/zoo/us
Monimiaceae sp.	x		-	-/-/-
MORACEAE				
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	x	x	no	npio/zoo/us
Brosimum guianense (Aubl.) Huber	x	x	no	npio/zoo/cp
Ficus gomelleira Kunth & C.D. Bouché	x	x	no	npio/zoo/cp

Continued ...

Table 2: Continued

Family / *Species name*	2001	2010	Endemism	Affiliation to ecological guilds
Ficus luschnathiana (Miq.) Miq.	x	x	no	npio/zoo/cp
Ficus enormis Mart. *ex* Miq.	x	x	no	npio/zoo/cp
Helicostylis tomentosa (Poepp. & Endl.) Rusby	x	x	no	npio/zoo/cp
Maclura tinctoria (L.) D. Don ex Steud.	x	x	no	npio/zoo/cp
Naucleopsis oblongifolia (Kuhlm.) Carauta	x	x	yes	npio/zoo/cp
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Wess. Boer	x	x	no	npio/zoo/us
Sorocea hilariana Gaudich.	x	x	yes	Npio/zoo/us
MYRISTICACEAE				
Virola gardneri (A. DC.) Warb.	x	x	yes	npio/zoo/cp
Virola bicuhyba (Schott *ex.* Spreng.) Warb.	x	x	yes	npio/zoo/cp
MYRSINACEAE				
Ardisia cf. *catharinensis* Mez	x	x	yes	-/zoo/us
Cybianthus fuscus Mart. *		x	no	-/zoo/-
Myrsine umbellata Mart.	x	x	yes	npio/zoo/us
MYRTACEAE				
Calyptranthes brasiliensis Spreng.	x	x	yes	npio/zoo/us
Campomanesia xanthocarpa (Mart.) O. Berg	x	x	yes	npio/zoo/us
Eugenialambertiana DC.	x	x	no	npio/zoo/us
Eugenia dodonaeifolia Cambess.	x	x	yes	npio/zoo/us
Eugenia florida DC.	x	x	no	npio/zoo/us
Eugenia leptoclada O.Berg	x	x	yes	npio/zoo/us
Marlierea excoriata Mart.	x	x	yes	npio/zoo/us
Marlierea suaveolens Cambess.	x	x	yes	npio/zoo/us
Marlierea cf. *teuscheriana* (O.Berg) D.Legrand	x	x	yes	npio/zoo/us
Myrcia anceps (Spreng.) O. Berg	x	x	yes	npio/zoo/us
Myrciaria floribunda (H.West ex Willd.) O.Berg	x	x	no	npio/zoo/us
Myrcia pallida (Cambess.) O. Berg	x	x	-	Npio/zoo/-
Myrcia pubipetala Miq.	x	x	yes	npio/zoo/us
Myrcia splendens (Sw.) DC.	x	x	no	npio/zoo/us
Myrcia sp.1	x	x	-	-/zoo/-
Neomitranthes sp.1	x	x	-	-/zoo/us
Plinia cf. *grandifolia* (Mattos) Sobral	x	x	yes	npio/zoo/us
Psidium cf. *oblongatum* O. Berg	x	x	yes	-/zoo/-
Myrtaceae sp.1	x	x	-	-/zoo/-
NYCTAGINACEAE				
Guapira hirsuta (Choisy) Lundell	x	x	yes	npio/zoo/us
Guapira opposita (Vell.) Reitz	x	x	no	npio/zoo/us
Pisonia ambigua Griseb.	x	x	no	npio/zoo/cp
Nyctaginaceae sp.1	x	x	-	-/zoo/-
OCHNACEAE				
Ouratea polygyna Engl.	x	x	yes	npio/zoo/us

Continued ...

Table 2: Continued

Family / *Species name*	2001	2010	Endemism	Affiliation to ecological guilds
OLACACEAE				
Heisteria silvianii Schwacke	x	x	yes	npio/zoo/us
Tetrastylidium grandiflorum (Baill.) Sleumer	x	x	yes	npio/zoo/us
Oleaceae sp.1 *	x	x	-	-/zoo/-
PERACEAE				
Pera glabrata (Schott) Poepp. ex Baill.	x	x	no	npio/zoo/cp
PHYLLANTHACEAE				
Hieronyma alchorneoides Allemão	x	x	no	npio/zoo/cp
Margaritaria nobilis L. f.	x	x	no	npio/zoo/cp
PIPERACEAE				
Piper arboreum Aubl.	x	x	no	npio/zoo/us
Piper gigantifolium C. DC. *	x	x	no	-/zoo/us
RHAMNACEAE				
Colubrina glandulosa Perkins	x	x	no	npio/zoo/cp
ROSACEAE				
Prunus myrtifolia (L.) Urb.	x	x	no	npio/zoo/cp
RUBIACEAE				
Alseis floribunda Schott	x	x	no	npio/zoo/us
Amaioua guianensis Aubl.	x	x	no	npio/zoo/us
Bathysa cuspidata (St. Hil.) Hook.f. *ex* K.Schum.	x	x	yes	npio/aut/us
Bathysa nicholsonii K. Schum.	x	x	yes	npio/aut/us
Genipa americana L.	x	x	no	npio/zoo/cp
Guettarda viburnoides Cham. & Schltdl.	x	x	no	npio/zoo/us
Ixora gardneriana Benth.	x	x	yes	npio/zoo/us
Psychotria carthagenensis Jacq.	x	x	no	npio/zoo/us
Psychotria conjungens Müll. Arg. *	x	x	yes	npio/zoo/us
Psychoria myriantha Müll. Arg.	x	x	yes	npio/zoo/us
Psychotria nuda (Cham. & Schltdl.) Wawra	x	x	yes	npio/zoo/us
Psychotria vellosiana Benth. *	x	x	no	npio/zoo/us
Psychotria sp.1 *	x	x	-	-/zoo/-
Randia ferox (Cham. & Schltdl.) DC. *	x	x	yes	npio/zoo/us
*Rudgea jasminoide*s (Cham.) Müll.Arg.	x	x	no	npio/zoo/us
Rubiaceae sp.1 *		x	-	-/zoo/-
RUTACEAE				
Hortia brasiliana Vand. ex DC.	x	x	yes	-/zoo/cp
Zanthoxylum rhoifolium Lam.	x	x	no	npio/zoo/us
SABIACEAE				
Meliosma itatiaiae Urb.	x	x	yes	-/zoo/us
SALICACEAE				
Casearia arborea (Rich.) Urb.	x	x	no	npio/zoo/cp
Casearia decandra Jacq.	x	x	no	npio/zoo/cp
Casearia gossypiosperma Briq.	x	x	no	npio/nzoo/us
Casearia sylvestris Sw.	x	x	no	pio/zoo/us
Casearia ulmifolia Vahl ex Vent.	x	x	no	npio/zoo/us

Continued ...

Table 2: Continued

Family / *Species name*	2001	2010	Endemism	Affiliation to ecological guilds
Macrothumia kuhlmannii (Sleumer) M.H.Alford	x	x	yes	-/zoo/cp
Prockia crucis P. Browne ex L.	x	x	no	npio/zoo/us
Xylosma prockia (Turcz.) Turcz.	x	x	no	npio/zoo/us
Salicaceae sp.1	x	x	-	-/zoo/-
SAPINDACEAE				
Allophylus edulis (A. St.-Hil. *et al.*) Hieron. ex Niederl.	x	x	no	npio/zoo/us
Cupania vernalis Cambess.	x	x	no	npio/zoo/cp
Matayba elaeagnoides Radlk.	x	x	no	npio/zoo/cp
SAPOTACEAE				
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	x	x	no	npio/zoo/cp
Chrysophyllum lucentifolium Cronquist	x	x	no	npio/zoo/us
Chrysophyllum cf. *marginatum* (Hook. & Arn.) Radlk.	x	x	no	npio/zoo/cp
Chrysophyllum sp.1	x	x	-	-/zoo/-
Pouteria caimito (Ruiz & Pav.) Radlk.	x	x	no	npio/zoo/cp
Pradosia lactescens (Vell.) Radlk.	x	x	no	npio/zoo/cp
SIPARUNACEAE				
Siparuna guianensis Aubl.	x	x	no	npio/zoo/us
Siparuna reginae (Tul.) A. DC.	x	x	no	npio/zoo/us
SOLANACEAE				
Brunfelsia uniflora (Pohl) D. Don	x	x	no	npio/zoo/us
Cestrum mariqitense Kunth	x	x	no	-/zoo/us
Cestrum sp. 1	x	x	-	-/zoo/-
Solanaceae sp. 1	x	x	-	-/zoo/-
URTICACEAE				
Cecropia hololeuca Miq.	x	x	yes	pio/zoo/cp
Coussapoa floccosa Akkermans & C.C. Berg	x	x	yes	-/zoo/us
Coussapoa microcarpa (Schott) Rizzini	x	x	yes	npio/zoo/cp
Pourouma guianensis Aubl.	x	x	no	pio/zoo/cp
VOCHYSIACEAE				
Qualea multiflora Mart.	x	x	yes	npio/zoo/cp
UNKNOWN FAMILY				
Unidentified sp.1	x	x	-	-/-/-
Unidentified sp.2	x	x	-	-/-/-
Unidentified sp.3	x		-	-/-/-
218 species				

Table 3. Changes in tree species diversity during a nine-year period with the FSN one hectare plot.

	2001	2010
Fisher´s α	59.69	57.2
	±2.25	±2.17
Shannon-Wiener	4.42	4.37
Simpson	43.08	39.87

Community Dynamics

As the number of individuals increased during examination period, the recruitment rate exceeded mortality (Table 4). The increase in basal area during the observation period was manifested in higher basal area gains than basal area losses.

While common species with 10 or more individuals in the first census showed nearly identical mortality and recruitment rates, the mortality rate of uncommon species (less than 10 individuals) was higher than the recruitment rate.

In comparison to the whole community, pioneer and non-animal dispersed species showed disproportionately high mortality. Recruitment of understory species exceeds mortality, while endemic species showed lesser recruitment than mortality (Table 4).

Table 4. Tree Demographic Dynamics in a nine-year period (2001-2010) from the FSN one hectare plot. Abundance class is referred to abundance of first census.

Category	Growth Rate [mm*yr^{-1}]	Mortality Rate [%*yr^{-1}]	Recruitment Rate [%*yr^{-1}]	BA_{Loss} [m^2*ha^{-1}*yr^{-1}]	BA_{Gain} [m^2*ha^{-1}*yr^{-1}]
All	1.123	1.645	1.836	0.473	0.729
Size Class [cm dbh]					
3.2-9.9	0.810	1.883	2.691	0.791	0.149
10-29.9	1.796	0.977	2.074	0.153	0.324
≥30	2.100	1.749	2.479	0.241	0.256
Abundance class					
Uncommon (≤ 9)	1.312	2.086	1.775	0.185	0.224
Common (≥ 10)	1.080	1.540	1.557	0.289	0.505
Successional group					
Pioneer species	1.556	3.366	1.737	0.090	0.035
Non-pioneer species	1.110	1.587	1.838	0.385	0.693
Disperal group					
Zoochorus species	0.621	1.480	1.728	0.336	0.598
Others	1.238	2.860	0.611	0.125	0.122
Vertical position					
Understory species	0.485	1.726	3.529	0.143	0.326
Dossel species	0.905	1.440	0.987	0.319	0.390
Endemism					
Endemics	1.068	1.607	1.231	0.144	0.254
Others	1.234	1.630	1.711	0.314	0.450

Population Dynamics

Eight of the nine most abundant species from 2001 increased in abundance, with only *Bathysia nicholsonii* less present in 2010 than in 2001 (Table 5). Of the 20 species with the highest basal areas, 10 increased their basal area by more than 10 %. Five species showed moderate to high increase and only five species showed a decrease in basal area.

Species-ranks from both censuses showed s-shaped form (Figure 2). Due to lower species richness and higher abundance of common species in 2010, the curve was bent down. Differences are not significant.

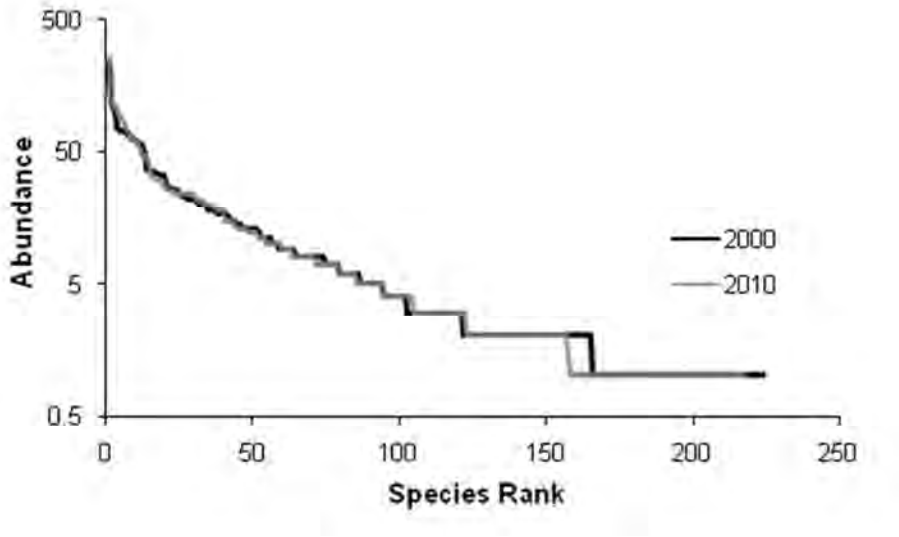


Figure 2. Species rank from two censuses from the FSN one hectare plot (2001 and 2010), Viçosa, Minas Gerais, Brazil.

Table 5. Species ranking in both census from the FSN one hectare plot based on species abundance (left half) and based on basal area (right half). + is moderate increase (less than 5%), ++ is high increase (between 5 and 10%), +++ is very high increase (more than 10%), - is moderate loss (less than 5%), – is high loss (between 5 and 10 %) and --- is very high loss (more than 10%).

Rank		Number of Trees			% of Trees		Basal Area			% of Trees
(2010)	Species	2010	2001	Diff	(2010)	Species	2010	2001	Diff	(2010)
1	*Siparuna guianensis* Aubl. (Siparunaceae)	254	240	+	10.04	*Ficus gomelleira* Kunth & C.D. Bouché (Moraceae)	3.41	3.09	++	0.04
2	*Protium warmingiana* March, L. (Burseraceae)	121	115	+	4.784	*Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima (Fabaceae)	3.08	2.99	+	1.78
3	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. &Wess. Boer (Moraceae)	107	101	+	4.231	*Virola gardneri* (A. DC.) Warb. (Myristicaceae)	2.22	1.88	+++	3.08
4	*Myrciaria floribunda* (H.WestexWilld.) O.Berg (Myrtaceae)	101	77	+++	3.994	*Guatteria nigrescens* Mart. (Annonaceae)	1.91	1.71	+++	2.65
5	*Euterpe edulis* Mart. (Arecaceae)	90	68	+++	3.559	*Sterculia chicha* A. St.-Hil. Ex Turpin (Malvaceae)	1.84	1.95	--	0.47

Continued…

Table 5. Continued.

6	*Virola gardneri* (A. DC.) Warb. (Myristicaceae)	78	59	+++	3.084	*Ceiba speciosa* (A. St.-Hil.) Ravenna (Malvaceae)	1.37	1.30	++	0.04
7	*Helicostylis tomentosa* (Poepp. &Endl.) Rusby (Moraceae)	73	72	+	2.887	*Protium warmingiana* March, L. (Burseraceae)	1.29	1.09	+++	4.78
8	*Guatteria nigrescens* Mart. (Annonaceae)	67	65	+	2.649	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. &Wess. Boer (Moraceae)	1.26	1.13	+++	4.23
9	*Bathysa nicholsonii* K. Schum. (Rubiaceae)	60	71	---	2.372	*Astronium graveolens* Jacq. (Anacardiaceae)	0.97	1.00	-	0.51
10	*Marlieria excoriata* Mart. (Myrtaceae)	59	61	-	2.333	*Ocotea silvestris* Vattimo (Lauraceae)	0.82	0.65	+++	0.95
11	*Phyllostemonodaphne geminiflora* (Mez) Kosterm. (Lauraceae)	59	62	-	2.333	*Casearia ulmifolia* Vahl ex Vent. (Salicaceae)	0.73	0.68	++	1.19
12	*Brosimum guianense* (Aubl.) Huber(Moraceae)	49	48	+	1.938	*Pourouma guianensis* Aubl. (Urticaceae)	0.66	0.82	---	1.23
13	*Eugenia cf. lambertiana* O. Berg (Myrtaceae)	47	37	+++	1.858	*Helicostylis tomentosa* (Poepp. &Endl.) Rusby (Moraceae)	0.64	0.55	+++	2.89
14	*Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima (Fabaceae)	45	56	--	1.779	*Euterpe edulis* Mart. (Arecaceae)	0.64	0.51	+++	3.56
15	*Trichilia emarginata* (Turcz.) C. DC. (Meliaceae)	35	33	+	1.384	*Bathysa nicholsonii* K. Schum. (Rubiaceae)	0.59	0.68	---	2.37
16	*Trichilia catigua* A. Juss. (Meliaceae)	34	36	--	1.344	*Brosimum guianense* (Aubl.) Huber (Moraceae)	0.59	0.52	+++	1.94
17	*Alseis floribunda* (Standl.) Steyerm. (Rubiaceae)	31	26	+++	1.226	*Siparuna guianensis* Aubl. (Siparunaceae)	0.58	0.57	+	10.04
18	*Pourouma guianensis* Aubl. (Urticaceae)	31	35	---	1.226	*Guarea macrophylla* Vahl (Meliaceae)	0.56	0.59	--	0.59
19	*Casearia ulmifolia* Vahl ex Vent. (Salicaceae)	30	36	---	1.186	*Virola oleifera* (Schott) A.C. Sm. (Myristicaceae)	0.55	0.47	+++	0.71
20	*Chrysophyllum lucentifolium* Cronquist (Sapindaceae)	28	27	+	1.107	*Ocotea odorífera* Rohwer (Lauraceae)	0.54	0.45	+++	1.07

Discussion

The key features of the community dynamics of the FSN one hectare plot, such as recruitment or mortality rate, do not show peculiarities compared to similar studies from the Atlantic Rainforest (Rolim *et al.* 1999; Oliveira-Filho *et al.* 2007) or other tropical forests (i.e. Leigh *et al.* 2004; Thompson *et al.* 2004). The high mortality of pioneer species and higher recruitment of animal dispersed and understory species increase the characteristics of the FSN as an old-growth forest (Liebsch *et al.* 2008).

Nevertheless, although recruitment and mortality indicate normality for the community dynamics of the FSN one hectare plot, the comparison of both censuses reveals some alarming tendencies: As species richness and diversity declined, common species became more common, while rare species became rarer. Vulnerable species endemic to the Atlantic Rainforest biome recruit subproportionally. Furthermore, the number of individuals and the basal area increased.

These tendencies might be coincididental and describing the natural oscillations within the dynamic equilibrium in the Seasonal Semidecidual Atlantic Rainforest. Focusing on the observed alterations of species richness, this would mean that a net loss of six species corresponds to natural oscillations. A net gain of 6 species in nine years, perhaps in the next census or in similar studies, should be due to natural oscillation as well. We are not aware of studies that report a net gain in this magnitude, on the contrary, most dynamic studies done so far relate species loss as well (e.g. Oliveira-Filho *et al.* 1997; Bunyavejchewin *et al.* 2004; Lee *et al.* 2004; Leigh *et al.* 2004; Thompson *et al.* 2004; Werneck & Franceschinelli 2004; Higuchi *et al.* 2008). This generalizes our findings.

Because these observations have been made within a recently (about 150 years ago) logged and fragmentized landscape, they should be discussed in a metacommunity approach. According to the species-area relationships, one of most studied patterns of ecology (Tjørve 2003; Martin & Goldenfeld 2006), habitat loss causes species loss (Pimm & Raven 2000; Ney-Nifle & Mangel 2000; Fischer 2000). But some decades of research work on species-area relationships also revealed that species richness of islands is lower than on

continuous continents of the same area (Rosenzweig 1995; Lomolino 2001). As landscape fragmentation can be interpreted as a transformation of former continuous habitats in small patches forming terrestrial islands, theory predicts that a secondary species loss after landscape fragmentation should happen after a time delay (Rosenzweig 1995).

Species richness found on a site might be considered as the equilibrium between immigration, speciation (Hubbell 2001) and extinction rate (MacArthur & Wilson 1967). Due to logging of surroundings, this equilibrium might be disturbed, and immigration of propagules of new species to the FSN one hectare plot is reduced, while extinction continues causing the observed species loss. In this case, species loss in the FSN will continue for some time until a new equilibrium based on the reduced immigration rate is reached.

These theoretical explications of observed species loss in the FSN one hectare plot are congruent with simulations about species abundance distributions of local communities carried out by Hubbell (2001). In isolated stands, i.e. communities with reduced immigration rates, common species become more common and rare species rarer, as has been observed in the FSN one hectare plot. This is a vicious cycle: Due to isolation, common species become more common in the local community, but also increase their abundance in the metacommunity. As abundance in the local community, even isolated, still depends on species abundance in the metacommunity, this commonness of former already common species aggravates increasing metacommunity abundance even more. Increased mortality of uncommon species and reduced recruitment of species endemic to the Atlantic Rainforest biome supports the evaluation of reported species loss as time-delayed species loss after landscape fragmentation.

On the other hand, we observed increases in basal area and number of individuals. An increase in the number of individuals contradicts the zero-sum assumptions of Hubbell (2001) and self-thinning, i.e. the reduction of the number of individuals coupled with an increase in basal area frequently observed in maturing forest ecosystems (Oliveira-Filho *et al.* 2007).

More individuals in combination with an increasing basal area means more carbon sequestration in above ground biomass (Chave *et al.* 2001), which on

one hand is positive for the abiotic resource protection. But where does it come from? The average annual temperature changed little from 19.95° C in 2000 to 20.17° C in 2010 (UFV 2010), which does not explain a nearly 5 percent increase in the number of individuals and basal area under the requirement of metabolic zero-sum dynamic (Ernest *et al.* 2009).

Lewis *et al.* (2004) report a 0.1 m^2 ha^{-1} yr^{-1} increase of basal area for forest plots spread throughout South America between 1971 and 2002, while we found more than double. The authors of that study cite increased resource availability, increased incoming solar radiation, increases in atmospheric concentrations of CO_2 or an increase in air temperature as the reasons for the increase in basal area. These alterations might be heterogeneous over large scales, but accelerated climate change during the last decade (IPCC 2007) might have elevated the annual basal area increment rate.

As has been shown, alterations in the FSN one hectare plot tree community are explicable with major alterations that confront our environment. Observed species loss, increase of abundance of common species and low recruitment of endemic species are congruent with theoretical consequences of landscape fragmentation. An increase in basal area and the number of individuals might be due to changes in abiotic environments due to climate change. Further censuses in the FSN one hectare plot showing similar tendencies, perhaps supported by periodic measurement of temperature, CO_2-concentration and other climatic data, might acquire certainty, that alarming community changes in one of the last remnant old-growth forests of the region are due to world-wide man-made effects.

Acknowledgments

We are grateful to David Teixeira Irsigler for carrying out the first census in the FSN one hectare plot. Furthermore, we thank Suzano Pulp and Paper for a Ph.D. scholarship for one of the authors (MG) to carry out presented research.

Bibliografic references

Arrhenius, O. 1921. Species and area. **Journal of Ecology 9:** 95-99.

Bunyavejchewin, S.; Baker, P.J.; LaFrankie, J.V. & Ashton, P.S. 2004. Huai Kha Khaeng Forest Dynamics Plot, Thailand. Pp. 482-491. In: Losos, E.C. & Leigh Jr., E.G. (Eds.). **Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network.** London, The University of Chicago Press.

Câmara, I.G. 2005. Breve história da conservação da Mata Atlântica. Pp. 31-42. In: Galindo-Leal, C. & Câmara, I.G. (eds.). **Mata Atlântica: biodiversidade, ameaças e perspectivas.** São Paulo/Belo Horizonte, Fundação SOS Mata Atlântica/Conservação Internacional.

Campos, E.P.; Silva, A.F.; Meira Neto, J.A.A. & Martins, S.V. 2006. Florística e estrutura horizontal da vegetação arbórea de uma ravina em um fragmento florestal no município de Viçosa, MG. **Revista Árvore 30:** 1045-1054.

Chave, J.; Riera, B. & Dubois, M.A. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. **Journal of Tropical Ecology 17:** 79–96.

Colwell, R.K. & Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. **Philosophical Transactions of the Royal Society London B 345:** 101-108.

Condit, R.; Hubbell, S.P.; LaFrankie, J.V.; Sukumar, R.; Manokaran, N.; Foster, R.B. & Ashton, P.S. 1996. Species-Area and Species-Individual Relationships for Tropical Trees: A Comparison of Three 50-ha Plots. **Journal of Ecology 84:** 549-562.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. **Science 199:** 1302-1310.

Ernest, K.M.; White, E.P. & Brown, J.H. 2009. Changes in a tropical forest support metaboliczero-sum dynamics. **Ecology Letters 12:** 507–515.

Fischer, M. 2000. Species loss after habitat fragmentation. **Tree 15:** 396.

Higuchi, P.; Oliveiro-Filho, A.T.; Bebber, D.P.; Brown, N.D.; Silva, A.C. & Machado, E.L.M. 2008. Spatio-temporal patterns of tree community dynamics in a tropical forest fragment in South-east Brazil. **Plant Ecology 199:** 125-135.

Hubbell, S.P. 2001. **The Unified Neutral Theory of Biodiversity and Biogeography.** Princeton/Oxford, Princeton University Press.

IPCC (Intergovernmental Panel on Climate Change) 2007. **Climate Change 2007 – The Physical Science Basis. Contribution of Working Group I to the Forth Assessent Report of the IPCC.** Cambridge, Cambridge University Press.

Irsigler, D. T. 2001. Composição florística e estrutura de um trecho primitivo de Floresta Estacional Semidecídua em Viçosa, MG. Master thesis, Universidade Federal de Viçosa.

Lee, H.S.; Tan, S.; Davies, S.J.; LaFrankie, J.V.; Ashton, P.S.; Yamakura, T.; Itoh, A.; Ohkubo, T. & Harrison, R. 2004. Lambir Forest Dynamics Plot, Sarawak, Malaysia. Pp. 527-539. In: Losos, E.C. & Leigh Jr., E.G. (eds.). **Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network.** London, University of Chicago Press.

Leigh Jr., E.G.; Lao, S.L.; Condit, R.; Hubbell, S.P.; Foster, R.B. & Pérez, R. 2004. Barro Colorado Island Forest Dynamics Plot, Panama. Pp. 451-463. In: Losos, E.C. & Leigh Jr., E.G. (eds.). **Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network.** London, University of Chicago Press.

Lewis, S.L.; Phillips, O.L.; Baker, T.R. et al. 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. **Philosophical Transactions of the Royal Society London B 359:** 421-436.

Liebsch, D., Marques, M.C.M., Goldenberg, R. 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. **Biological Conservation 141:** 1717-1725

Lomolino, M.V. 2001. The species-area relationship: new challenges for an old pattern. **Progress in Physical Geography 25:** 1-21.

Losos, E.C. & Leigh Jr., E.G. 2004. The Growth of a Tree Plot Network. Pp 3-7. In: Losos, E.C. & Leigh Jr., E.G. (eds.). **Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network.** London, The University of Chicago Press.

Losos, E.C. & Lao, S.L. 2004. Forest Dynamics Plots. Introduction. Pp 433-450. In: Losos, E.C. & Leigh Jr., E.G. (eds.). **Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network.** London, The University of Chicago Press.

MacArthur, R. & Wilson, E.O. 1967. **The Theory of Island Biogeography.** Princeton, Princeton University Press.

Magurran, A.E. 2011. Measuring biological diversity in time (and space). Pp. 85-94. In: Magurran, A.E. & McGill, B.J. **Biological Diversity – frontiers in measurement and assessment.** New York, Oxford University Press.

Martin, H.G. & Goldenfield, N. 2006. On the origin and robustness of power-law species-area relationships in ecology. **Proceedings of the National Academy of Sciences 103:** 10310-10315.

Matesanz, S., Escudero, A. & Valladares, F. 2009. Impact on three global change drivers on a Mediterranean shrub. **Ecology 90:** 2609-2621.

Millennium Ecosystem Assessment. 2005. Biodiversity: What is it, where is it, and whyis it important? Pp 18-29. In: **Ecosystems and Human Well-Being: Biodiversity Synthesis. World.** Washington DC, Resources Institute.

Molino, J.F. & Sabatier, D. 2001. Tree Diversity in Tropical Rain Forests: A Validation of the Intermediate Disturbance Hypothesis. **Science 294:** 1702-1704.

Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. **Nature 403:** 853-858.

Ney-Nifle, M. & Mangel, M. 2000. Habitat loss and changes int the species-area relationship. **Conservation Biology 14:** 893-898.

Oliveira-Filho, A.T.; Mello, J.M. & Scolforo, J.R.S. 1997. Effects of past disturbances and edges on tree community strucutre and dynamics within a fragment of tropical semideciduous forest in south eastern Brazil over a five-year period (1987-1992). **Plant Ecology 131:** 45-66.

Oliveira-Filho, A.T.; Carvalho, W.A.C.; Machado, E.L.M.; Higuchi, P., Appolinário, V.; Castro, G.C.; Silva, A.C.; Santos, R.M.; Borges, L.F., Corrêa, B.S. & Alves, J.M. 2007. Dinâmica da comunidade e populações arbóreas da borda e interior de um remanescente florestal na Serra da Mantiqueira, Minas Gerais, em um intervalo de cinco anos (1999-2004). **Revista Brasileira de Botanica 30:** 149-161.

Peel, M.C.; Finlayson, B.L. & McMahon, T.A. 2007. Updated world map of the Köppen-Geiger climate classification. **Hydrology and Earth System Science 11:** 1633-1644.

Pimm, S.L. & Raven, P. 2000. Extinction by numbers. **Nature 403:** 483-483.

Ribeiro, M.C.; Metzger, J.P.; Martensen, A.C.; Ponzoni, F.J. & Hirota, M.M. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation 142:** 1141–1153.

Rolim, S.G.; Couto, H.T.Z. & Jesus, R.M. 1999. Mortalidade e recrutamento de árvores na Floresta Atlântica em Linhares (ES). **Scientia forestalis 55:** 49-69.

Rosenzweig, M.L. 1995. **Species diversity in space and time.** Cambridge, Cambridge University Press.

Stehmann, J.R.; Forzza, R.C.; Salino, A.; Sobral, M.; Costa, D.P. & Kamino, L.H.Y. (org.) 2009. **Plantas da Floresta Atlântica.** Rio de Janeiro, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Swaine, M.D. & Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. **Vegetatio 75:** 81-86.

Tabarelli, M.; Silva, J.M.C. & Gascon, C. 2004. Forest fragmentation, synergisms and the impoverishment of neotropical forests. **Biodiversity and Conservation 13:** 1419-1425.

Thompson, J.; Brokaw, N.; Zimmermann, J.K.; Waide, R.B.; Everham III, E.M. & Schaefer, D.A. 2004. Luquillo Forest Dynamics Plot, Puerto Rico, United States. Pp 540-550. In: Losos, E.C. & Leigh Jr., E.G. (eds.) **Tropical Forest Diversity and Dynamism – Findings from a Large-Scale Plot Network.** London, University of Chicago Press.

Tjørve, E. 2003. Shapes and functions of species-area curves: a review of possible models. **Journal of Biogeography 30:** 827-835.

UFV (Universidade Federal de Viçosa) 2010. **Dados meteorológicos da Estação de Viçosa.** Viçosa.

Veloso, H.P.; Rangel Filho, A.L.R. & Lima, J.C.A. 1991. **Classificação da Vegetação Brasileira, adaptada a um Sistema Universal.** Rio de Janeiro, Departamento de Recursos Naturais e Estudos Ambientais do Intituto Brasileiro de Geografia e Estatística – IBGE.

Werneck, M.S. & Franceschinelli, E.V. 2004. Dynamics of a dry forest fragment after the exclusion of humandisturbance in southeastern Brazil. **Plant Ecology 174:** 337–346.

Wright, S.J. 2010. The future of tropical forests. **Annals of the New York Academy of Sciences 1195:** 1-27.

CHAPTER 5*

Hubbell´s Theory at Age Ten: (Counter-)Evidence for Neutral Species Distribution in a Primary Forest Patch from Southeastern Brazil?

* This chapter will be submitted to the scientific journal **Biotropica**.

PAPER

Running Heads

LRH: Gastauer and Meira Neto

RRH: (Counter-)Evidence for Neutral Species Distribution

Hubbell´s Theory at Age Ten: (Counter-)Evidence for Neutral Species Distribution in a Primary Forest Patch from Southeastern Brazil?

Markus Gastauer[1], João Augusto Alves Meira Neto[1*]

[1]Laboratório de Ecologia, Departamento de Biologia Vegetal, Universidade Federal de Viçosa, MG, Brazil.

[*] Corresponding author: j.meira@ufv.br

ABSTRACT

Aim of this article is to discuss, how 218 tree species co-exist within a single hectare in the primary Forest of Seu Nico within the Atlantic Rainforest. Is there an extremely heterogeneous environment providing different ecological niches where interspecific competition acts? Does environmental heterogeneity select species with specific traits? Or are all species equivalent or “neutral” from an ecological perspective and their occurrence and spatial distribution depends on chance only? Different community parameters like the species-environmental correlations, species abundance distribution (SAD) and the phylogenetic structure of the community are analyzed to arrive at a coherent answer. Species-environmental correlations are weak compared to other studies. Although FSN one hectare plot shows a short environmental gradient dividing the plot in an upper Hillside and a lower Bottom, soil properties and understory light availability explain only around 8% of spatial species distribution. From all classic and neutral models tested, observed SAD from FSN is best fit with Hubbell´s algorithm supporting neutrality. Phylogenetic structure of the FSN community shows strong and significant phylogenetic overdistribution for plots of 10 x 10 and 20 x 20 m within the FSN one hectare plot. This indicates niche assembly theories in combination with interspecific competition to organize the composition of local communities and the spatial distribution of species within them. As environmental variables like edaphic factors and understory light availability show short gradients only explaining little spatial species distribution, we conclude that negative density-dependent factors like the Connell-Janzen-hypothesis maintain species richness in megadiverse ecosystems like the FSN.

Keywords: species-environmental correlations, species abundance distribution, phylogenetic community structure, niche assembly theory, phylogenetic overdistribution, neutral forces, spatial species distribution, Atlantic Rainforest.

Within a single hectare of a primary Atlantic Rainforest patch, the so-called Forest of Seu Nico (FSN) from Viçosa, Minas Gerais, Southeastern Brazil, we found more than 218 tree species. This count does not include lianas, epiphytic plants, understory herbs or bamboo species which will increase plant species richness even further. This raises the question: How can so many species coexist (Rosindell *et al.* 2011)?

Species might differ from each other in ecological terms, so that they are sorted along environmental gradients (Leibold *et al.* 2004). Such niche assembly theories are stressed when we observe plant species abundance to correlate with some kind of environmental variables (i.e. Magnago 2009, Ferreira Jr. *et al.* 2007, Neri 2007, Tolentino 2011). Tilman (1980), for example, proposes nutrient supply and light availability as determining factors. On a larger scale, this should result in similar plant communities on similar habitats.

But is this true? If yes, what means “sorted” and what maintains plant communities constant? Is it interspecific competition that causes exclusion of some species under a given environment so that always the same species coexist within the same habitat (Tilman 1980, Dierschke 1994)? Do trade-offs between colonization and competition abilities reduce the germination and seedling development of pioneer species beneath the dense canopy of mature forests, while they colonize clearings after windfall or logging rapidly and with success (Muller-Landau 2008)?

On the other hand, what is the role of stochasticity, dispersion, speciation and ecological drift? Can chance explain species abundance and spatial distribution? In his Unified Neutral Theory of Biogeography and Biodiversity (UNTBB), Hubbell (2001) highlights the importance of chance and dispersal limitations for community organization and makes predictions about the species abundance distribution (SAD) within a community under stochastic ecological drift that differ from classic lognormal and logserie models.

Can UNTBB be congruent with some kind of environmental sorting as observed in many studies? For that, we must discuss the possible underlying mechanisms of such sorting: Consider two species, a and b and one habitat A, where only species a occurs. If there are no dispersal limitations for

species b, the absence of b in A might be due to the fact that species a is the superior competitor that uses all resources because of faster development, deeper roots or other adaptations, so that nothing remains for b. As such interspecific competition due to similar resource exploration should be higher among closely related species, community should be phylogenetically overdistribute (Chave 2009). Such overdistribution is incompatible with UNTBB and would reforce niche assembly theories.

On the other hand, the absence of species b in the habitat might be due to inappropriate conditions (frost, water deficit, heat, etc.) of the habitat. Such environmental filtering lets more similar and therefore more closely related species coexist causing phylogenetic clustering within the community (Chave 2009) coinciding with UNTBB (Hubbell 2001).

In a phylogenetic approach proposed by Webb (2000) is tested, if community is formed by more closely or more distant related species. Phylogenetic overdispersion, i.e. more distant related species coexist, is a hint for interspecific competition, while phylogenetic clustering, i.e. community is built up by closely related species, indicates environmental filtering (Kembel & Hubbell 2006).

The objective of this study was to test if niche assembly or neutral forces rule the species-rich tree community of one hectare in the primary FSN. Because of lack of replications (Alonso & McKane 2004), different community parameters are explored to arrive at a more coherent answer as proposed by Harte (2003): Understory light availability and chemical soil properties are correlated with the distribution and the abundance of tree species. In a second part, it is examined which classic or neutral model explains observed SAD from FSN best. Finally, the phylogenetic structure of the community is analyzed to detect phylogenetic overdispersion or clustering.

METHODS

STUDY SITE – The Forest of Seu Nico (FSN) situated at 20°47'44'' S and 42°50'50'' W in the Bom Sucesso Farm, Viçosa, Minas Gerais, Brazil, is a forest patch that, according to its owners, never has been logged (Campos *et al.* 2006). Minor selective wood extraction in the recent past maintained the patch´s characteristics as a primary forest.
According to Köppen, the climate of the region is characterized as Cwb (Peel *et al.* 2007). This is a mesothermic climate with mild, rainy summers and dry winters. Landscape´s predominant soils are deeply intemperished oxisols, which are found within a small-scaled mosaic of inceptisols on slopes and neosols in sedimentation areas. The predominant vegetation is characterized as Submontane Seasonal Semideciduous Forest (Veloso *et al.* 1991).

TREE CENSUS – For this study, the plot method has been applied (Newton, 2007): One hectare was divided into 100 quadratic plots of 10 m x 10 m. All trees with a diameter at breast height (dbh) greater or equal to 3.2 cm have been tagged and identified. Collected and identified material is incorporated in the collection of the herbarium VIC of the UFV. Nomenclature of species follows the database of Forzza *et al.* (2010). Classifying species phylogeny follows state of affairs (APG III 2009).

ENVIRONMENTAL DATA – Three soil samples were collected in each plot and analyzed in the labs of the Soil Department, Federal University of Viçosa, Minas Gerais, Brazil. For each sample, soil was taken from five equally distributed points within the plot: The upper 20 cm of the soil were collected by a hoe after the organic layers have been removed; soil from all five points was mixed. From that mixture, 500 g were weighted, stored in a plastic bag and transported to the lab. Before analysis of soil acidity (pH), concentration of phosphor (P), potassium (K), calcium (Ca), magnesium (Mg), aluminium (Al), nitrogen (N), organic matter (OM), interchangeable bases (SB), cation

exchange capacity (CTC), saturation of bases (V) and of aluminium (M) as well as remnant phosphorus (P-rem), the samples were dried on air for three days.

To define pedo-environments, a principal component analysis (PCA) was run with the software PC-ORD for Windows version 4.14 (McCune & Mefford, 1999). The soil variables pH, P, Ca, Al, N, OM, CTC and M entered in the analysis.

The understory light availability was analyzed by hemispherical photography. A digital camera (Nikon Coolpix 5700) was combined with an adapter and a fish-eye lens (Nikon FC-E9). For photography, the camera was mounted on a tripod. Within each plot, one photo was taken from plot´s center at an altitude of one meter above soil level. As direct light affects data interpretation and analysis, hemispherical photos were taken only when sky was perfectly overcast. Canopy openness, i.e. the percentage of open sky seen from beneath a forest canopy, as well as the amount of direct, diffuse and total solar radiation transmitted by the canopy were calculated by the software Gap Light Analyzer 2.0.

SPECIES DISTRIBUTION AND ENVIRONMENTAL VARIABLES – Correlations between the distribution of species and environmental variables were analyzed by canonical correspondence analysis (CCA, Ter Braak, 1988) using the software PC-ORD.

Three different environmental matrices were used to maximize cumulative percentage of explained data inertia: The first one was based on soil data only (pH, P, Ca, Al, N, CTC, M and OM), the second one on understory light availability only (percentage of canopy openess and total solar radiation transmitted by the canopy). The last one is a combination of above presented soil matrix with percentage of canopy openess.

In the CCA, environmental data were crossed with the vegetation matrices containing all species with more than 20 individuals. This corresponds 35 from 218 species found within the FSN one hectar plot and 1748 from 2529 individuals.

The Monte Carlo Permutation Test was applied to verify the significance of the correlations between the emergent species patterns and soil variables in the final CCA.

To gain an idea about the amount of cumulative percentage of explained variance due to stochasticity, we crossed the soil matrix with simulated vegetation matrices by CCA. By the random generater from Microsoft Excel™, the distribution of all 2529 individuals from the one hectare has been randomized within the 100 plots maintaining their species identity. From these randomized species distribution, species with 20 or more individuals formed the randomized vegetation matrices. 10 different randomized vegetation matrices have been run in CCA to gain an average value plus standard deviation.

SPECIES ABUNDANCE DISTRIBUTION (SAD) – Observed SAD was compared with theoretically expected SAD from different classic and neutral models. For that, observed and theoretical SAD were binned in Preston octaves, using the original binning method proposed by Preston (1948), where octave limits are the following integers: 0-1, 1-2, 2-4, 4-8, 8-16, 16-32 individuals, and so on. The number of species with abundances in the limit between two octaves was divided between the octaves.

The different theoretical SAD were calculated using the following resources: The logserie has been calculated according to Magurran (2004). Note that Magurran (2004) uses another binning method in her working examples.

The expected lognormal SAD has been calculated using the formula

$$S(R) = S_0 \cdot e^{-(a^2 R^2)} \qquad (1),$$

in which S(R) is the number of species in the R^{th} octave to the left and the right of the modal octave, i.e. octave containing most species, S_0 is the number of species within that modal octave and a is the width of the distribution calculated by

$$a = \frac{1}{\sqrt{2\sigma}} \qquad (2),$$

where σ is the standard deviation of observed SAD (Oliveira & Batalha 2005).

To increase fitting, the modal octave has been replaced manually to octaves at the left or the right. Furthermore, the exponent $-(a^2R^2)$ from equation (1) has been altered in steps of 0.05 to increase fitting.

The zero-sum SAD under the assumptions of ecological drift has been simulated using the algorithm given in the Hubbell´s textbook about the UNTBB (p. 291, Hubbell 2001) varying the Unified Biodiversity Number θ in steps of 1 and the Migration Rate m in steps of 0.05 until best fit has been reached. For each simulated pair of θ and m, the algorithm was run 500 times using the MatLab extension hubbell.m written by Brian McGill (McGill 2003).

The SAD of two analytical solutions for the zero-sum assumption (presented in McKane *et al.* 2000 and Volkov *et al.* 2003) were calculated using a MatLab extension package offered by Brian McGill.

Observed SAD has been compared with expected data using a χ^2 test, where

$$\chi^2 = \sum \frac{(O_i - E_i)^2}{E} \qquad (3).$$

In this case, O_i is the observed number of species in the i^{th} octave and E_i – according to selected model – is the expected number of species within i^{th} octave. Fitting probabilities have been calculated.

PHYLOGENETICS – To check the community composition for phylogenetic clustering or overdispersion, the net relatedness index (NRI) as well as the nearest taxon index (NTI) have been calculated for each plot with the software phylocom (Webb 2000, Webb *et al.* 2002). In this case, NRI is based on the difference between observed and randomized mean phylogenetic distance (MPD) between all species from the sample. NTI is computed from the mean nearest phylogenetic taxon distance (MNTD) for each sample.

NRI and NTI have been calculated assuming two different null models. The unconstrained null model maintains the number of species from each plot, but the identities of species occurring in each plot are randomized from

metacommunity. Within the model, all species from species pool or metacommunity have the same chance to be included in the null communities (Webb *et al.* 2011). In the constrained null model, the number of species per survey or plot and frequency of occurrence of each species across samples are held constant when species co-occurrences in samples are randomized (Gotelli & Entsminger 2003). This model does not introduce new species from the metacommunity.

The FSN tree community has been transformed in a phylogenetic tree by the phylomatic function from the phylocom software (Webb & Donoghue 2005). With that function, an user-supplied list of species is attached to a master tree at a terminal position as possible, using the internal node names of the master tree. The tree R200703050.bl has been defined as aged master tree. Final tree of FSN community is given in Figure S1 in the supplementary material.

RESULTS

ENVIRONMENTAL DATA – Analyzed plots are situated on a hillside with northern exposition in a small valley. The main draining stream of the valley runs about 35 m from the northern edge of the permanent plot (Fig. 1). The lower, northern part of the permanent plot is planar. The rest of the censused area is a more or less steep hillside divided by a small tributary valley that begins on the Southern border (around plots #96 and #97) and opens in Northern direction.

By PCA, 39 plots forming the planar Bottom of the FSN one hectare plot are separated graphically from 61 plots forming the Hillside with steeper inclination (Fig. 2). The separation in Bottom and Hillside is supported by chemical soil analyses. Hillside shows lower pH, lower nutrient contents (N, P, K), less Ca and Mg, more Al, lower V and effective CTC (Table 1).

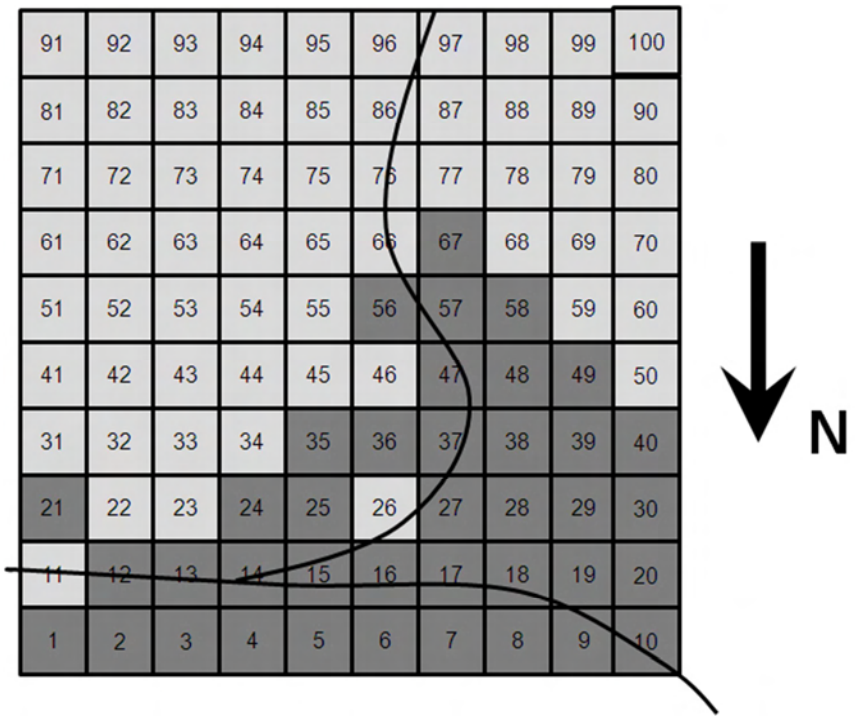


FIGURE 1.Outline of the Forest of Seu Nico (FSN) one hectare plot with pathways (black lines). Numbers in quadrates represent plot number. Dark grey plots are distinguishable from light grey plots by chemical soil properties via principal component analysis (PCA, see Figure 2). In the text, dark grey plots are called Bottom, while light grey plots form the Hillside. Edge length of each quadrat is 10 m.

Canopy openess varied from 1.8 to 8.1 % within parcels (at average 4.56 ±1.34%), this influences understory light availability (Table 2).

pH does not correlate with percentage of canopy openess, but is correlated weakly with the amount of total solar radiation transmitted by the canopy (Fig. 3): The lower pH, more light reaches understory. Al, on the other hand, is significantly correlated with percentage of canopy openess and total solar radiation transmitted by the canopy (Fig. 4).

Percentage of canopy openess and total solar radiation transmitted by canopy is not correlated to number of individuals or species per plot, but pH correlates positively with per plot basal area and negatively with number of species and individuals per plot (Fig. 5).

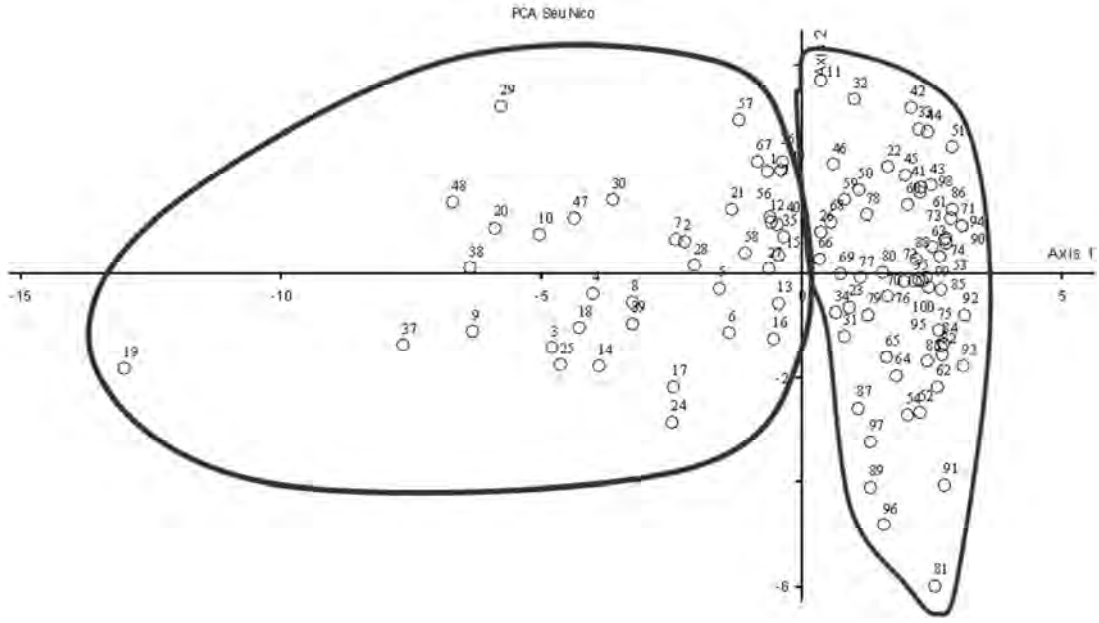


FIGURE 2. Separation of two pedo-environments (left: Bottom, right: Hillside) by principal component analysis (PCA) due to differences in soil properties within the FSN plot, Viçosa, Minas Gerais, Brazil.

TABLE 1. Chemical soil properties of both pedo-environments from the FSN plot, Viçosa, Minas Gerais, Brazil.

	Bottom	**Hillside**	**P (t-test)**
pH (H_2O)	4.70 ±0.31	4.26 ±0,15	$< 10^{-3}$
N (dag/kg)	0.27 ±0.03	0.24 ±0.03	$< 10^{-3}$
P (mg/dm^3)	2.48 ±0.68	2.31 ±0.57	0.21
K (mg/dm^3)	88.78 ±36.85	45.39 ±10.22	$< 10^{-3}$
Ca [cmol$_c$/dm^3]	1.17 ±0.65	0.21 ±0.15	$< 10^{-3}$
Mg [cmol$_c$/dm^3]	0.77 ±0.35	0.18 ±0.10	$< 10^{-3}$
Al [cmol$_c$/dm^3]	0.83 ±0.38	1.96 ±0.41	$< 10^{-3}$
H + Al [cmol$_c$/dm^3]	8.07 ±0.88	10.00 ±1.32	$< 10^{-3}$
Base saturation [cmol$_c$/dm^3]	2.16 ±1.07	0.50 ±0.24	$< 10^{-3}$
Efective Cation Exchange Capacity [cmol$_c$/dm^3]	3.00 ±0.76	2.45 ±0.31	$< 10^{-3}$
Cation Exchange Capacity at pH 7.0 [cmol$_c$/dm^3]	10.23 ±0.84	10.51 ±1.31	0.33
Index of Base Saturation [%]	20.57 ±8.97	4.81 ±2.42	$< 10^{-3}$
Index of Aluminium Saturation [%]	32.20 ±16.65	79.25 ±10.44	$< 10^{-3}$
Organic matter [dag/kg]	5.31 ±0.61	5.22 ±0.79	0.56
Remnant phosphorus [mg/L]	28.78 ±2.80	24.88 ±2.43	$< 10^{-3}$

TABLE 2. Understory light availability in 100 plots of 10 x 10 m within the FSN. Canopy Open is percentage of canopy openess, Trans Direct is the direct solar radiation transmitted by the canopy, Trans Diffuse is the diffuse ratiation transmitted by the canopy and Trans Total is the sum of Trans Direct and Trans Total.

	Average ±DP	**Minimum**	**Maximum**
Canopy Open [%]	4.56 ±1.34	1.81	8.07
Trans Direct [mol/m^2/d]	1.82 ±0.63	0.38	3.81
Trans Diffuse [mol/m^2/d]	1.37 ±0.38	0.62	2.4
Trans Total [mol/m^2/d]	**3.19 ±0.97**	**1.01**	**6.2**

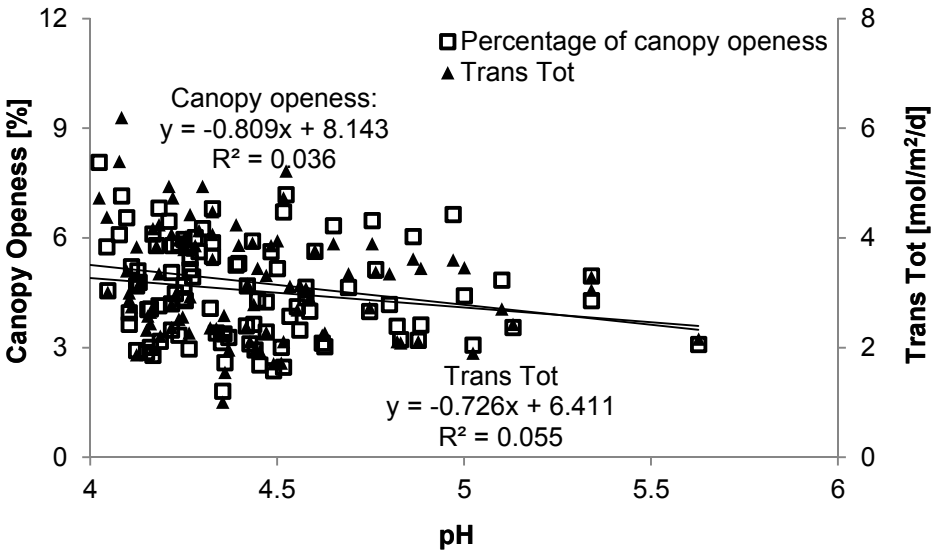


FIGURE 3. Relationships between soil´s pH and percentage of canopy openess and total radiation transmitted by the canopy (Trans Tot). Relationship between pH and total radiation transmitted by the canopy is significative with $F_{1;98}$ = 5.788 ($p < 0.05$), between pH and percentage of canopy openess is not ($F_{1;98}$ = 3.701, $p > 0.05$).

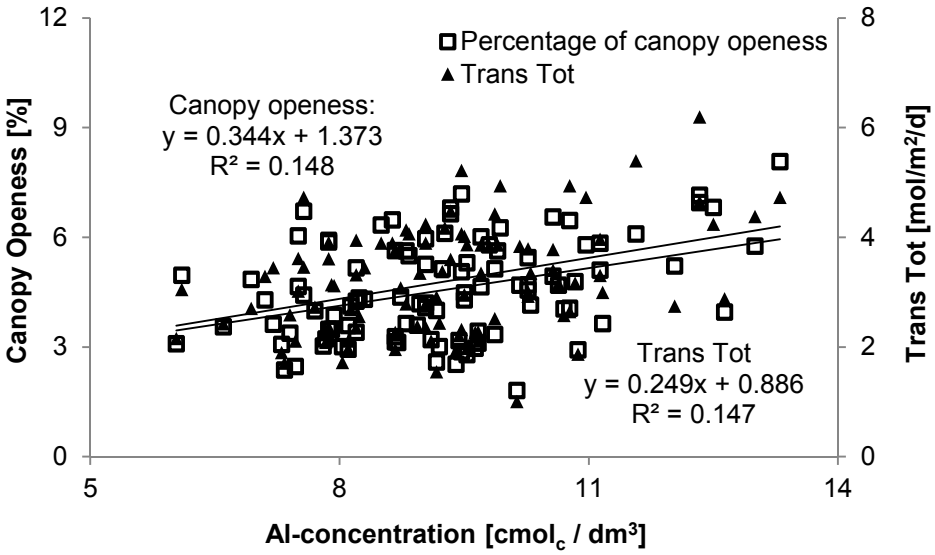


FIGURE 4: Relationships between soil´s Al-concentration and percentage of canopy openess and total radiation transmitted by the canopy (Trans Tot). Both relationship are significant with $F_{1;98} = 17.03$ ($p < 10^{-3}$, canopy openess) and $F_{1;98} = 16.99$ ($P < 10^{-3}$, total radiation transmitted by canopy).

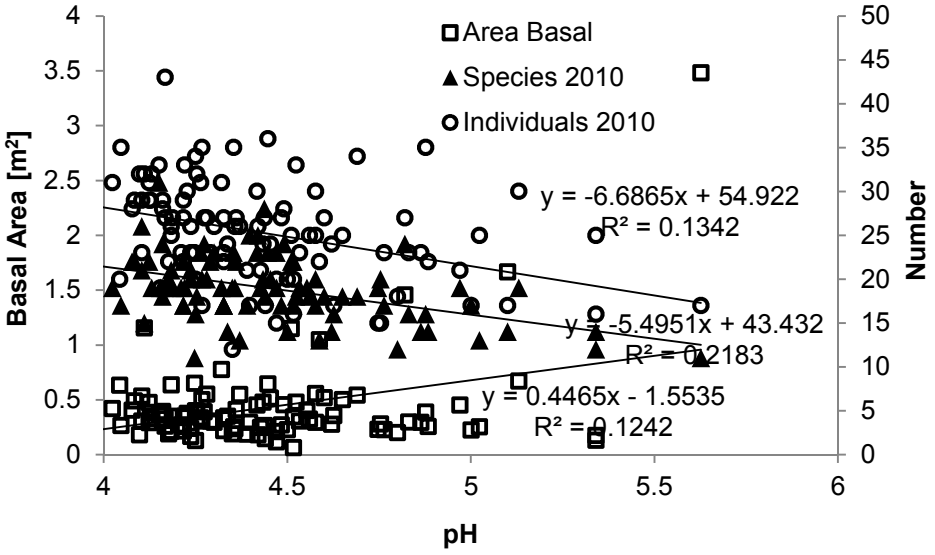


FIGURE 5. Relationships between soil´s pH, per plot basal area and per plot number of species and individuals. All three relationships are significant with $F_{1;98} = 13.892$ ($p < 10^{-3}$, basal area), $F_{1;98} = 18.07$ ($p < 10^{-3}$, number of species) and $F_{1;98} = 15.20$ ($P < 10^{-3}$, number of individuals).

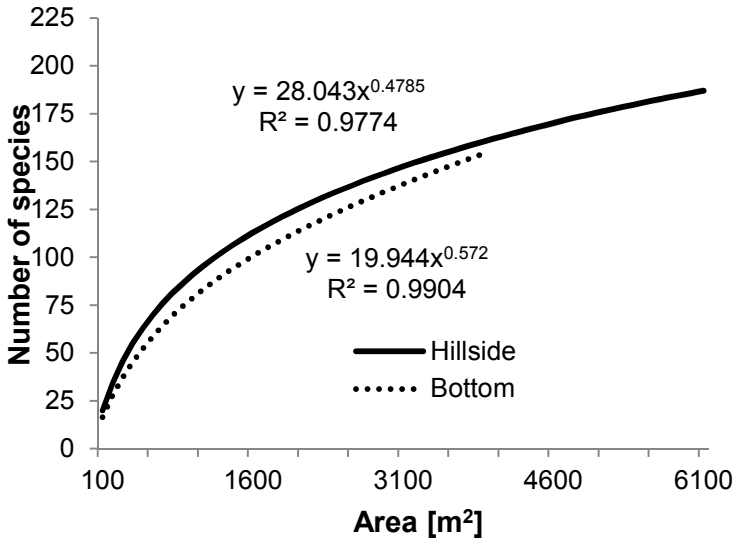


FIGURE 6. Species-sampling curve for both pedo-environments from the FSN plot, Viçosa, Minas Gerais, Brazil. Log transformation of data linearizes curves, intercept of species-sampling curve from hillside is higher than from Bottom, while Bottom shows higher slope than Hillside. Differences are significantly (Hillside: Species richness = 0.479 (±0.009) Area + 0.491 (±0.032), Bottom: Species richness = 0.572 (±0.009) Area + 0.156 (±0.030)).

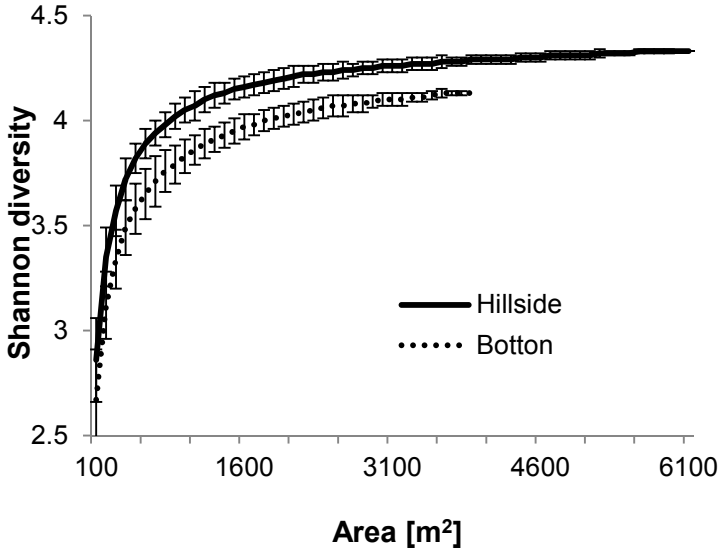


FIGURE 7. Shannon diversity including standard deviation for both pedo-environments from the FSN plot, Viçosa, Minas Gerais, Brazil.

As a consequence of these correlations, species richness (Fig. 6) and Shannon diversity (Fig. 7) within plots from the Bottom is lower than on Hillside. Percentage of canopy openess is higher in plots from Hillside than from Bottom (Hillside: 4.83 ±1.35%, Valley Bottom: 4.13 ±1.21%, difference significant with p (t-test) = 0.01), amount of solar radiation transmitted by canopy as well (Hillside: 3.40 ±1.02 mol/m^2/d, Bottom: 2.86 ±0.78 mol/m^2/d, difference significant with p (t-test) = 0.005).

SPECIES DISTRIBUTION AND ENVIRONMENTAL VARIABLES – Soil data explain 12.9 % of species distribution (Table 3). Eigenvalues and species-environmental correlations are significant with p = 0.01 according to the Monte Carlo Permutation test.

The graphical ordination of the CCA results (Fig. 8) shows that all species except *Chrysophyllum gonocarpum* are arranged in a single, diffuse cloud. Species on the left half occur with disproportionately higher abundances in the Bottom, while species on the right half of that cloud have their core area of distribution in the Hillside. Separation variables are pH, Ca, Al and M.

Understory light availability explains 13.1% of variance in species distribution data, but neither Eigenvalues nor species-environment correlations are significant according to the Monte Carlo permutation test. If instead percentage of canopy openness is added to soil matrix, cumulative percentage of explained data inertia increases from 12.9 to 13.0 %. Eigenvalues and species-environment correlations do not differ from values calculated for soil variables only.

Soil variables pH, P, Ca, Al, N, OM, m and CTC explain altogether 4.68 (±0.33) of data variance of randomized vegetation matrices. Monte Carlos permutation tests of Eigenvalues and species-environment correlations are not significant.

Table 3. Cumulative percentage of explained variance in species data, Eigenvalue and Species-Environment Correlations (Pearson Correlations) by soil variables in the FSN plot, Viçosa, Minas Gerais, Brazil.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalue	0.172	0.065	0.025
Variance in species data			
% of variance explained	7.4	3.3	2.2
Cumulative % explained	7.4	10.7	12.9
Pearson Correlation, Spp-Envt	0.863	0.723	0.677
Kendall (Rank) Corr., Spp-Envt	0.627	0.453	0.428

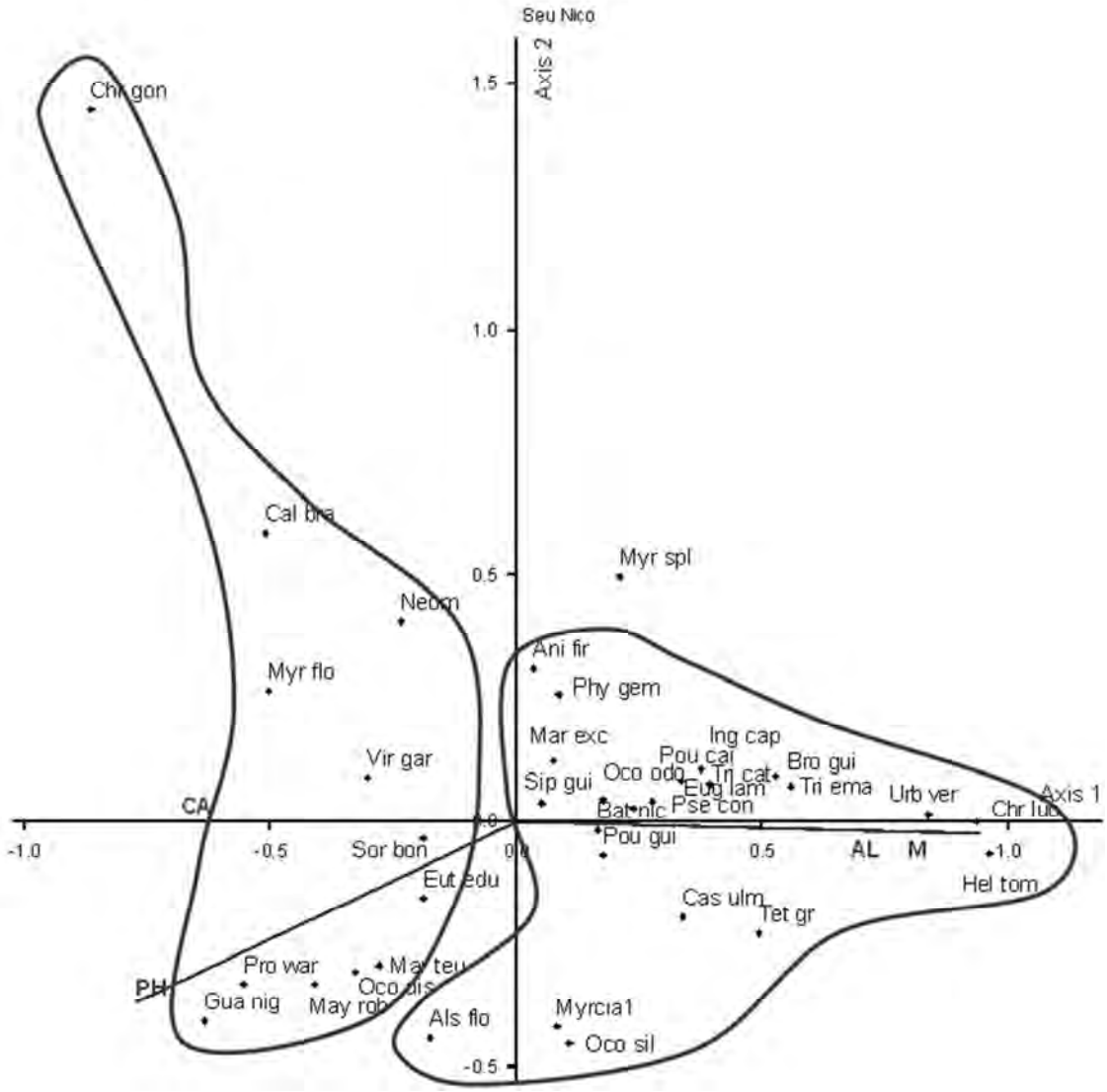


FIGURE 8. Ordination diagram of the species and soil variables in the first two ordination axes derived from CCA of the 35 species with 20 or more

trees sampled. Species in the left bubble occur with disproportional higher abundance in the smaller Bottom, while species in the right bubble are clustered in the Hillside. Als flo is *Alseis floribunda* Schott, Ani fir is *Aniba firmula* (Nees & C. Mart.) Mez, Bat nic is *Bathysa nicholsonii* K. Schum., Bro gui is *Brosimum guianense* (Aubl.) Huber, Cal bra is *Calyptranthes brasiliensis* Spreng., Cas ulm is *Casearia ulmifolia* Vahl ex Vent., Chr gon is *Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl., Chr luc is *Chrysophyllum lucentifolium* Cronquist, Eug lam is *Eugenialambertiana* DC., Eut edu is *Euterpe edulis* Mart., Gua nig is *Guatteria australis* A. St.-Hil., Ing cap is *Inga capitata* Desv., Hel tom is *Helicostylis tomentosa* (Poepp. & Endl.) Rusby, Mar exc is *Marlierea excoriata* Mart., Mar teu is *Marlierea* cf. *teuscheriana* (O.Berg) D.Legrand, May rob is *Maytenus robusta* Reissek, Myr flo is *Myrciaria floribunda* (H.West ex Willd.) O.Berg, Myr spl is *Myrcia splendens* (Sw.) DC., Myrcia1 is *Myrcia* sp.1, Neom is *Neomitranthes* sp.1, Oco dis is *Ocotea dispersa* (Nees) Mez, Oco odo is *Ocotea odorifera* (Vell.) Rohwer, Oco sil is *Ocotea silvestris* Vattimo-Gil, Phy gem is *Phyllostemonodaphne geminiflora* (Mez) Kosterm., Pou cai is *Pouteria caimito* (Ruiz & Pav.) Radlk., Pou gui is *Pourouma guianensis* Aubl., Pro war is *Protium warmingianum* Marchand, Pse con is *Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima, Sip gui is *Siparuna guianensis* Aubl., Sor bon is *Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & Wess. Boer, Tet gr is *Tetrastylidium grandiflorum* (Baill.) Sleumer, Tri cat is *Trichilia catigua* A. Juss., Tri ema is *Trichilia emarginata* (Turcz.) C. DC., Urb ver is *Urbanodendron verrucosum* (Nees) Mez, Vir gar is *Virola gardneri* (A. DC.) Warb..

Table 5. Comparison of the fittings of observed SAD from the FSN by five different theoretical models.

Model	Fitting parameters	X^2	P
Hubbell´s algorithm (Hubbell 2001)	θ = 59, m = 1	5.09	0.75
Logserie (Fisher et al. 1943)	α = 57.2	5.58	0.69
Analytical solution 1 (McKane *et al.* 2000)	θ = 57.3, m = 1	5.72	0.68
Lognormal (Preston 1948)	-	9.40	0.31
Analytical solution 2 (Volkov *et al.* 2003)	θ = 92.3, m = 0.16	85.21	$< 10^{-3}$

SAD – From tested theoretical models, Hubbell´s algorithm fits observed data best (Table 5; Fig. 9), followed by logserie model and the analytical solution offered by McKane *et al.*. Defeated on rank four and five, lognormal model and the analytical solution offered by Volkov *et al.* are placed.

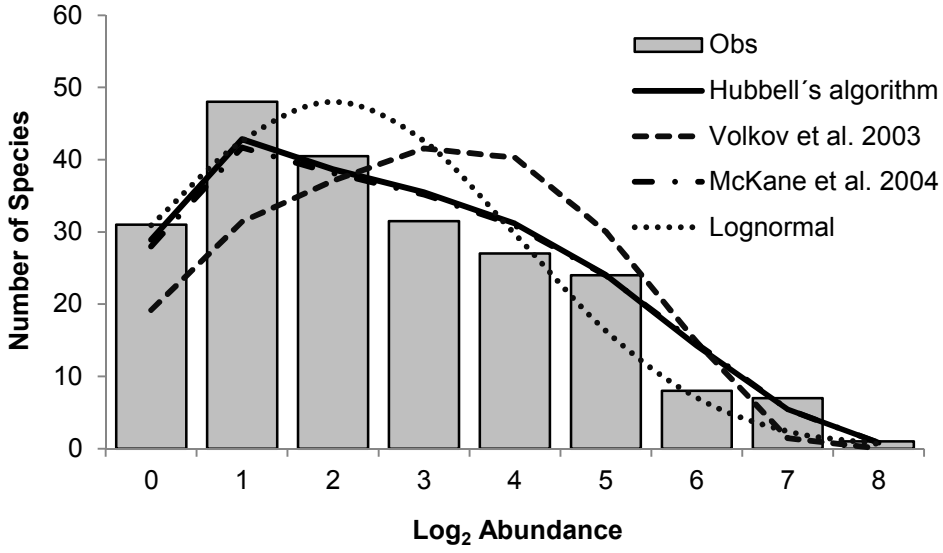


FIGURE 9. Comparison of the observed SAD from the FSN and five different theoretical models. Fittings are given in Table 5.

PHYLOGENETIC STRUCTURE – The phylogenetic structure of tree communities in the FSN is highly variable depending on the choice of null models and indices used for comparison. Using the unconstrained null model, the NRI indicates phylogenetic overdispersion at spatial scales from 10 x 10 m to 20 x 20 m as well as for both pedo-environments (mean NRI < 0, Table 6). The NTI, according to the unconstrained null model, indicates phylogenetic clustering. NRI and NTI from spatial scales of 10 x 10 m and 20 x 20 m are significantly different from zero.

According to the constrained null model, mean community phylogenetic structure (NRI and NTI) across the entire plot did not differ from zero, except at pedo-environmental level, where NTI was much smaller than zero indicating phylogenetic overdistribution.

Table 6. Net relatedness index (NRI) and nearest taxon index (NTI) computed by the constrained und unconstrained null models for different spatial scales for the tree community of the FSN one hectare plot. Significant P values indicate that the phylogenetic structure at a given spatial scale differed from zero according to a one sample t test.

		NRI			NTI		
Spatial Scale	**N**	**Mean**	**SD**	**P**	**Mean**	**SD**	**P**
	Unconstrained null model						
10 x 10 m	100	-0.975	0.858	0.001	0.247	1.034	0.019
20 x 20 m	25	-1.141	0.749	0.001	0.626	0.959	0.003
Pedo-environments	2	-1.036	1.575	0.523	0.870	0.837	0.381
	Constrained null model						
10 x 10 m	100	-0.003	1.061	0.979	0.008	1.013	0.938
20 x 20 m	25	-0.034	1.047	0.873	-0.053	1.110	0.813
Pedo-environments	2	0.025	1.938	0.989	-0.371	0.594	0.539

DISCUSSION

Percentage between soil´s pH and understory light availability has been detect by Meira-Neto *et al.* (2005) in nearby forests as well. As the correlation between pH and biomass shows, productivity of plots depends soil properties. Less acid soils are able to support a higher amount of biomass but species richness and diversity is higher in less productive areas. But as recent findings show, these results should neither be generalized nor over-interpreted (Adler *et al.* 2011).

Nevertheless there is a soil gradient within the FSN one hectar plot influencing other variables like per plot biomass, canopy openess and solar radiation transmitted by canopy, the spatial distribution of plant species does not respond to that gradient in a clear and articulated way. Along the entire gradient species vary only in abundance explaining low Eigenvalues.

Around 12.9 % of observed data variance is explained by soil variables. Compared to other studies of this kind (i.e. Botrel *et al.* 2002, Souza *et al.* 2003, Carvalho *et al.* 2005), this is a very low value. As soil variables from the FSN one hectar plot explain around 5 % of randomized communities, this should be discounted so that soil variables explain effectively only around 8 % of species distribution within the FSN one hectar plot. 92 % remain unexplained. Similar findings from species rich forests have been found by Matos (2012).

Percentage of explained variance does not increase adding understory light availability to the environmental matrix. This seems to be logically, because the understory light availability or canopy openess is a result of the actual vegetation. It might influence further regeneration, but to test that, other methods should be applied (i.e. Higuchi *et al.* 2006, Newton 2007).

Low cumulative percentage of explained variance might be due to overlooked variables. But we expect further soil variables like soil type or drainage to support, reinforce and, at most, refine the already described gradient between Hillside and Bottom.

Therefore, low percentage of explained variance and low Eigenvalues might be either due to high amount of stochastic variance or some unseen, perhaps biotic environmental variables like plant-plant, plant-herbivor or plant-desease interactions. The first explanation citing stochastic variation or random noise would support the hypothesis of neutral forces organizing the distribution of species in the FSN, while especially biotic interactions would reforce niche theories.

Hubbell´s algorithm fits observed SAD from the FSN one hectare plot best supporting the assumptions of stochasticity and ecological drift from the UNTBB. These findings stand in contrast to calculations from McGill (2003) and McGill *et al*. (2006). In contrast to Volkov *et al.* (2003), their analytical approach fits the SAD from the FSN one hectare plot worse than the lognormal model.
Nevertheless, observed SAD is not fit significantly by Hubbell´s algorithm, the probability that SAD derived from UNTBB does not differ from observed data amounts only 0.75. Therefore, the probability that both distributions – observed and predicted – differ, is still 25 %.

Sample size is for sure an important parameter when testing SAD: The larger the sample, the better the relative abundance of rare species is assessed (Dornelas & Connolly 2008), the smaller is the number of rare species with one individual only (Lopez *et al.* 2012) and differences between theoretical models become more visible (McGill 2011). Furthermore, the larger sample size, the better the models fit (McGill 2011).
Even if there are other – more ecological – interpretations (see Box 1), McGill (2011) considers the fitting parameters only as geometric descriptors of the shape of the SAD. In this case, migration rate m, being 1 at the FSN one hectar plot, describes the shape of the right tail of the species rank and the number of rare species, while θ of 59 might be seen as a scaling parameter affecting especially the left half of the species rank (McGill *et al.* 2006).
This makes comparison between different surveys possible. The Barro Colorado Island Forest Dynamics Plot in Panama, for example, θ amounts

50, while m is 0.1 (Hubbell 1997). Therefore, relative abundance of most abundant species from FSN is lower than that of BCI, furthermore, the relative presence of rare species that occur with one individual only, is higher in the FSN. But as the relative abundance of rare species decreases with increasing sample effort, m for sure is not a sample-size independent index calling this interpretation into question.

Because of different indices and null models computed in our phylogenetic approach, the results are ambiguous indicating to phylogenetic overdispersion for some plots and phylogenetic clustering in others. These kinds of problems are familiar to those using different indices (Magurran 2004, 2011, Maurer & McGill 2011), and discussions about pros and contras of different null models are found in Gotelli & Graves (1996) or Wilson (1995). High confidence is given to the slight phylogenetic overdispersion indicated by NRI from the unconstrained null model for plots of 10 x 10 m and of 20 x 20 m, because this index considers all species within the community and not only the pair of nearest neighbor like the NTI. Furthermore, this index shows highest significance and a similar study (Kembel & Hubbell 2006) confirm this outcome.

Before we discuss the consequences of these findings, we should highlight some methodological problems accompanied by this analysis. There is a high degree of uncertainty to classify and date branching events within the megatree R200703050.bl (Wikstrom *et al.* 2001, Davies *et al.* 2004). As age of most internal nodes of the megatree remain unknown, the phylomatic function from the phylocom package distributes them equally between two familiar nodes. Therefore, all genera within a family and all species within a genus receive the same age. It´s unlikely that all branching and speciation events occured simultaneously within a clade!

As we will show in the next chapter, results from phylogenetic approach depend on the furnished species pool. In our analysis, we considered only tree species occurring in the FSN one hectare plot. For sure, a lot of more species occur within the FSN forest patch and within the Viçosa region being potential candidates to occur in the FSN one hectare plot as well (Ribas *et al.*

2004, Paula *et al.* 2004, Campos *et al.* 2006, Ferreira Jr. *et al.* 2007, Pinto *et al.* 2007). Furthermore, liana species, species from the understory herb layer and epiphytes are not considered for analysis. This might influence outcomes of our phylogenetic approach as well.

Although SAD is fitted best by the ecological drift model and final CCA with different soil variables explains little variance, tree community from the FSN one hectare plot shows a slight phylogenetic overdispersion indicating that niche formation and competition between different species play the more important role in the organization of the species composition of a community than environmental filtering.

In the FSN one hectare plot, abiotic environmental variables do not determine the formation of different ecological niches explaining the co-existence of 218 species. This is once due to the fact that soil variables are not capable of explaining more than 8 % of spatial species distribution. Climate explains only around 12 % of spatial species distribution in the whole Atlantic Rainforest (Oliveira-Filho & Fontes 2000), but certainly there is little climatic variance within the FSN one hectare plot.

Remain biotic factors like pathogens or herbivory to form ecological niches. Such variables might show a very high spatial and temporal turnover explaining high species richness and amount of rare species within tropical forests. The Connell-Janzen hypothesis (Janzen 1970, Connell 1971), for example, says that the increase of specialized diseases and herbivores near the mother plant impedes germination and reduces seedling development of conspecific individuals in the neighborhood (Harms *et al.* 2001). Fitness of conspecific individuals increases with distance to mother plant (Zimmermann *et al.* 2008). Such negative density-dependent factors might form ecological niches causing phylogenetic overdistribution.

Nevertheless we detected significant phylogenetic overditribution, niche determination is diffuse, because neutral forces are still working in the community. Dispersal limitations, accidental ecological drift and stochasticity contribute to the organization of community composition as well, so that SAD patterns hit the predictions made by UNTBB.

Trying to explain species richness in a megadiverse tropical forest, this article gives evidence for both niche assembly and neutral theories. Community composition and its parameters, i.e. phylogenetic composition and SAD, are best explicated using both models.

Therefore, UNTBB should not be reduced to a pool of null hypothesis as done by Bell (2001). Instead, further predictions from UNTBB like the role of dispersal limitations on broader spatial scales on local community composition should be examined.

To synthesize both theories and explain species richness and community composition patterns in megadiverse tropical forests, further research activity should therefore focus on three subjects: First, the role of dispersal limitations should be highlighted. Then, it should be examined, why SAD models assuming ecological drift by chance do well to explain species abundance data. At last, the role of biotic factors influencing germination, seedling development and plant fitness should be analyzed.

BOX 1. WHAT DO THE FITTING PARAMETERS OF HUBBELL´S ALGORITHM MEAN?

Hubbell (2001) calls m the migration rate corresponding the percentage of recruits arriving at the local community from the metacommunity. The unified biodiversity number θ describes the link between metacommunity size J_M and species rate v under the zero-sum assumption, i.e. each dying individual is immediately substituted by a recruiting one.

Therefore, migration rate m of 1 as achieved in the FSN indicates the absence of dispersal limitations between the theoretical metacommunity and the FSN. But as the FSN is an isolated forest patch surrounded by logged agricultural areas, this might support its characteristics as a primary forest.

Assuming a θ of 59, speciation rate is easily achieved within Hubbell´s model: The original extension of the Atlantic Rainforest was about 1,500,000 km^2. Assuming 2529 individual trees per hectare with dbh > 3.2 cm, this corresponds $3.8 * 10^{11}$ individuals within the original Atlantic Rainforest and a speciation rate v of $7.8 * 10^{-11}$. With other words: At average a new tree species is formed every $8 * 10^{11}$ birth events.

If we assume an average of 250 years from birth to death of an individual tree, we could conclude to the magnitude of about 1.5 trillion birth (and death) events within the whole Atlantic Rainforest per year (before the Europeans arrived in South America). This figure multiplied with the speciation rate gives the amount of new species per year (0.11). Its reciprocal, around 8.5 in our calculation, is the average time in years between two speciation events.

As speciation as well as extinction events depend a similar stochasticity and number of species at equilibrium should be constant (Hubbell 2001), extinction rate should have the same magnitude as speciation rate in the undisturbed metacommunity (MacArthur & Wilson 1967). Consequently, one tree species going extinct in about 8 to 9 years in the Atlantic Rainforest might be interpreted as the natural extinction rate. More extinction events than that should be interpreted – due to our calculation – as the result of anthropogenic impacts.

Acknowledgements

We are grateful to Suzano Pulp and Paper for a Ph.D. scholarship for one of the authors (MG) to carry out presented research.

References

ADLER, P.B., E. W. SEABLOOM, E. T. BORER, ET AL. 2011. Productivity Is a Poor Predictor of Plant Species Richness. Science 333: 1750-1753.

ALONSO, D. AND A. J. MCKANE. 2004. Sampling Hubbell´s neutral theory of biodiversity. Ecological Letters 7: 901-910. Doi: 10.1111/j.1461-0248.2004.00640.x

APG (ANGIOSPERM PHYLOGENY GROUP) III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot J Linn Soc 161: 105–121.

BOTREL, R. T., A. T. OLIVEIRA-FILHO, L. A. RODRIGUES, AND N. CURI. 2002. Influência do solo e topografia sobre as variações da composição florística e estrutura da comunidade arbóreo-arbustiva de uma Floresta Estacional Semidecidual em Ingaí, MG. Rev Bras Bot 25: 195-213.

BELL, G. 2001. Neutral macroecology. Science 293: 2413-2418.

CAMPOS, E.P., A. F. SILVA, J. A. A. MEIRA NETO, AND S.V. MARTINS. 2006. Floristica e estrutura horizontal da vegetação arbórea de uma ravina em um fragmento florestal no município de Viçosa, MG. R Árvore 30: 1045-1054.

CARVALHO, D. A. C., A. T. OLIVEIRA-FILHO, E. A. VILELA, N. CURI, E. VAN DEN BERG, M. A. L. FONTES, AND L. BOTEZELLI. 2005. Distribuição de espécies arbóreo-arbustivas ao longo de um gradiente de solos e topografia em um

trecho de floresta ripária do Rio São Francisco em Três Marias, MG, Brasil. Rev Bras Bot 28: 329-345.

CHAVE, J. 2009. Competition, Neutrality, and Community Organization. In: LEVIN, S. A. (Ed.). The Princeton Guide to Ecology, pp. 264-273. Princeton University Press, Princeton, UK.

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain Forest trees. In BOER, P. J. AND GRADWELL, G. R. (Eds.). Dynamics of Populations, pp 198-310. Center for Agricultural Publishing and Documentation, Wageningen, BE.

DAVIES, T. J., T. G. BARRALOUGH, M. W. CHASE, P. S. SOLTIS, D. E. SOLTIS, AND V. SAVOLAINEN. 2004. Darwin´s abominable mystery: Insights from a supertree of the angiosperms. PNAS 101: 1904-1909. www.pnas.org/cgi/doi/10.1073/pnas.0308127100

DIERSCHKE, H. 1994. Pflanzensoziologie. Grundlagen und Methoden. Ulmer, Stuttgart, 683p.

DORNELAS, M. AND S. R. CONNOLLY. 2008. Multiple nodes in a coral species abundance distribution. Ecology Letters 11: 1008-1016.

FERREIRA JR. W. G., A. F. SILVA, J. A. A. MEIRA-NETO, C. E. G. R. SCHAEFER, A. S. DIAS, M. IGNÁCIO AND M. C. M. P. MEDEIROS. 2007. Composição florística da vegetação arbórea de um trecho de Floresta Estacional Semidecídua em Viçosa, Minas Gerais, e espécies de maior ocorrência na região. R Árvore 31: 1121-1130.

FISHER, R. A., A. S. CORBET, AND C. B. WILLIAMS. 1943. The relation between the number of species and the number of individuals in a random sample of an animal populations. J Am Ecol 12: 42-58.

FORZZA, R. C. (coord.) 2010. Lista de Espécies da Flora do Brasil. Online access at http://floradobrasil.jbrj.gov.br/2010/, November 2011.

GOTELLI, N. J. AND G. ENTSMINGER. 2003. Swap algorithms in null model analysis. Ecology 84: 532-535.

GOTELLI, N. J. AND G. R. GRAVES. 1996. Null Models in Ecology. Smithsonian Institution Press, Washington, USA, 388 p.

HARMS, K. E., R. CONDIT, S. P. HUBBELL, AND R. B. FOSTER. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. J Ecol 89: 947-959.

HARTE, J. 2003. Tail of death and resurrection. Nature 424, 1006-1007.

HIGUCHI, P., M. G. F. REIS, G. G. REIS, A. L. PINHEIRO, C. T. SILVA, AND C. H. R. OLIVEIRA. 2006. Composição florística da regeneração natural de espécies arbóreas ao longo de oito anos em um fragmento de Floresta Estacional Semidecidual em Viçosa, MG. R. Árvore 30: 893-904.

HUBBELL, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs 16: S9-21.

HUBBELL, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton and Oxford, UK, 448 p.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501-528.

KEMBEL, S. W. AND S. P. HUBBELL. 2006. The phylogenetic structure of a neotropical forest tree community. Ecology 87: S86-S99.

LEIBOLD, M. A., M. HOLYOAK, N. MOUQUET, P. AMARASEKARE, ET AL. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601-613. doi: 10.1111/j.1461-0248.2004.00608.x

LOPEZ, L. C. S., M. P. A. FRACASSO, D. O. MESQUITA, A. R. T. PALMA, AND P. RIUL. 2012. The relationship between percentage of singletons and sampling effort: A new approach to reduce the bias of richness estimates. Ecological Indicators 14: 164-169.

MACARTHUR, R. AND E. O. WILSON. 1967.The Theory of Island Biogeography. Princeton University Press, Princeton, 203 p.

MAGNAGO, L. F. S. 2009. Gradiente vegetacional e pedológico em floresta de restinga no Espírito Santo, Brasil. Master thesis, Universidade Federal de Viçosa, Viçosa, BR.

MAGURRAN, A. E., 2004. Measuring Biological Diversity. Wiley, Oxford, UK, 260 p.

MATOS, F. A. R. 2012. Master thesis, Universidade Federal de Viçosa, Viçosa, BR.

MAURER, B. A. AND B. J. MCGILL. 2011. Measurement of species diversity. *In*MAGURRAN, A. E. AND B. J. MCGILL (eds.), Biological Diversity – frontiers in measurement and assessment, p. 55-65. Oxford University Press, New York, US.

MCCUNE, B. AND M. J. MEFFORD. 1999. PC-ORD version 4.0, multivariate analysis of ecological data: User´s guide. MjM Software Design, Glaneden Beach, US.

MCGILL, B. J. 2003. A test of the unified neutral theory of biodiversity. Nature 422: 881-885.

MCGILL, B. J. 2006.Empirical tests of the neutral theory. Ecology 87: 1411-1423.

MCGILL, B. J. 2011. Species abundance distributions.*In* Magurran, A. E. and B. J. McGill (eds.), Biological Diversity – frontiers in measurement and assessment, p. 105-122. Oxford University Press, New York, US.

MCKANE, A. J., D. ALONSO, AND R. V. SOLÉ. 2000. A mean field stochastic theory for species-rich assembled communities. Phys Rev E 62: 8466-8484.

MCKANE, A. J., D. ALONSO, AND R. V. SOLÉ. 2004. Analytic solution of Hubbell´s model of local community dynamics. Theoretical Population Biology 65: 67-73.

MEIRA-NETO, J. A. A., F. R. MARTINS, AND A. L. SOUZA. 2005. Influência da cobertura e do solo na composição florística do sub-bosque em uma floresta estacional semidecidual em Viçosa, MG, Brasil. Acta bot bras 19: 473-486.

MULLER-LANDAU, H. C. 2008. Colonization-related Trade-offs in tropical forests and their role in the maintenance of plant species diversity. *In*CARSON, W. P., AND S. A. SCHNITZER (Eds.) Tropical Forest Community Ecology, p. 182-195. Blackwell Publishing Ltd, Chichester, West Sussex, UK.

NERI, A. V. 2007. Gradiente pedológico-vegetacional de Cerrado em Paraopeba, MG. Ph.D. thesis, Universidade Federal de Viçosa, Viçosa, BR.

NEWTON, A. C. 2007. Forest ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, UK, 454 p.

OLIVEIRA, F. F. AND M. A. BATALHA. 2005. Lognormal abundance distribution of woody species in a cerrado fragmento (São Carlos, southeastern Brazil). Rev Bras Bot 28: 39-45.

OLIVEIRA-FILHO, A.T. AND M. A. L. FONTES.2000. Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. Biotropica 32: 793-810.

PAULA, A. L., A. F. SILVA, P. MARCO-JR., F. A. M. SANTOS, AND A. L. SOUZA. 2004. Sucessão ecológica da vegetação arbóres em uma Floresta Estacional Semidecidual, Viçosa, MG, Brasil. Acta Bot Bras 18: 407-423.

PEEL, M. C., B. L. FINLAYSON, AND T. A. MCMAHON. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Sys Sci 11: 1633-1644.

PINTO. L. V. A., S. A. BOTELHO, A. T. OLIVEIRA-FILHO, AND A. C. DAVIDE. 2007. Estudo da vegetação como subsídio para propostas de recuperação das nascentes da Bacia hidrográfica do Riberão Santa Cruz, Lavras, MG. R Árvore 29: 775-793.

PRESTON, F. W. 1948. The commoness and rarity of species. Ecology 29: 254-283.

RIBAS, R. F., J. A. A. MEIRA-NETO, A. F. SILVA, AND A. L. SOUZA. 2003. Composição florística da dois trechos em diferentes etapas serais de uma Floresta Estacional Semidecidual em Viçosa, Minas Gerais. R Árvore 27: 821-830.

ROSINDELL, J., S. P. HUBBELL, AND R. S. ETIENNE. 2011. The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten. Trends Ecol Evol 26: 340-348. Doi:10.1016/j.tree.2011.03024

SOUZA, J. S., F. D. B. ESPÍRITO-SANTO, M. A. L. FONTES, A. T. OLIVEIRA-FILHO, AND L. BOTEZELLI. 2003. Análise das variações florísticas e estruturais da comunidade arbórea de um fragmento de Floresta Semidecídua às margens do Rio Capivari, Lavras-MG. R Árvore 27, 185-206.

TER BRAAK, C. J. F. 1988. CANOCO – A FORTRAN program for canonical community ordination. Technical report LWA-88-2, TNO, Institute of Applied Computer Science, Wageningen, BE.

TILMAN, D. 1980. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, UK, 360 p.

TOLENTINO, G. S. 2011. Composição e partição de nicho em gradiente de solo e luz no cerrado. Master thesis, Universidade Federal de Viçosa, Viçosa, BR.

VELOSO, H.P., A.L.R. RANGEL FILHO, AND J. C. A. LIMA. 1991. Classificação da vegetação brasileira, adaptada a um sistema universal. IBGE, Rio de Janeiro, BR, 123 p.

VOLKOV, I., J. R. BANAVAR, S. P. HUBBELL, AND A. MARITAN. 2003. Neutral theory and relative species abundance in ecology. Nature 424: 1035-1037.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Am Nat 156: 145-155.

WEBB, C. O., D. D. ACKERLY, M.A. MCPEEK, AND M. J. DONAGHUE. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475-505.

WEBB, C. O., D. D. ACKERLY, AND S. KEMBEL. 2011. Software for the analysis of phylogenetic community structure and character evolution (with Phylomatic and Ecovolve). Users Manual. Revised August 8, 2011, 39 p.

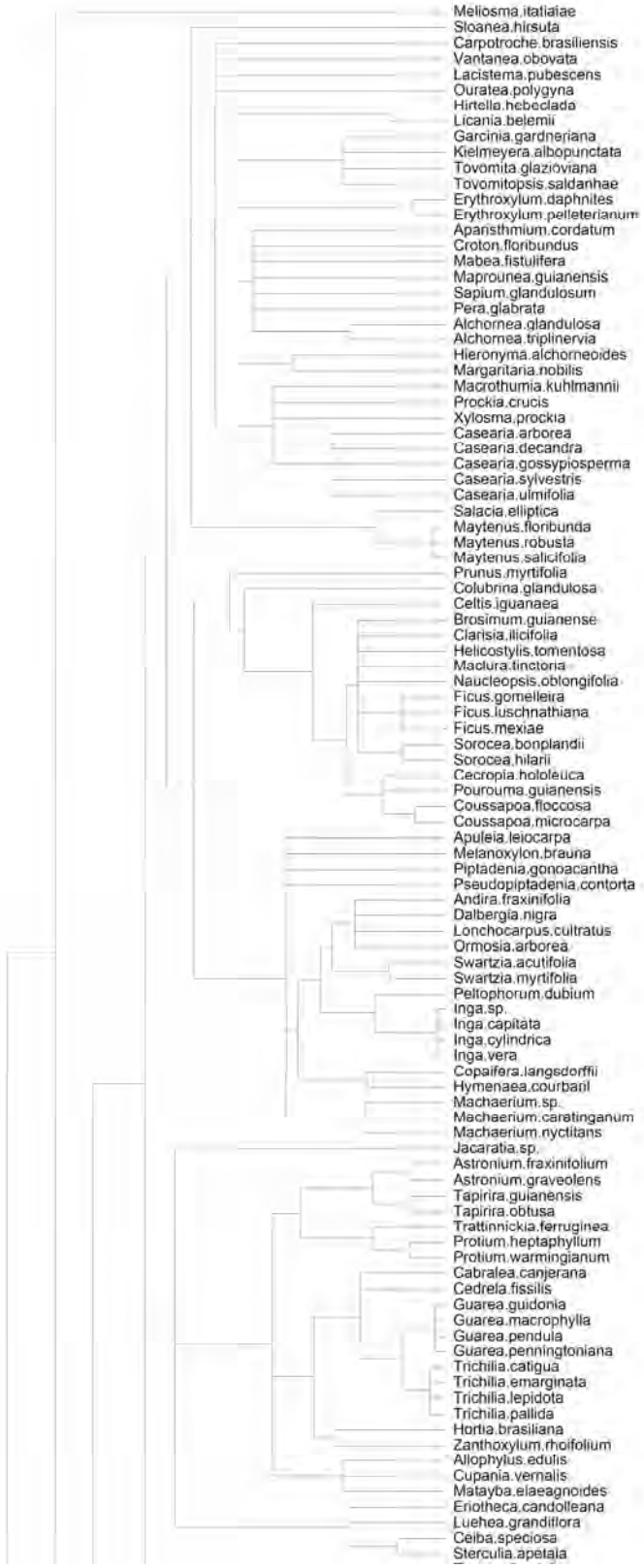
WEBB, C. O. AND M. J. DONOGHUE. 2005. Phylomatic: tree assembly for applied phylogenetics. Mol Ecol Not 5: 181-183.

WIKSTROM, N., V. SAVOLAINEN, AND M. W. CHASE. 2001. Evolution of angiosperms: Calibrating the family tree. Proceedings of the Royal Society of London, Series B – Biological Sciences 268: 2211-2220.

WILSON, J. B. 1995. Null models for assembly rules: the Jack Horner effect is more insidious than the Narcissus effect. Oikos 72: 139-144.

ZIMMERMANN, J. K., J. THOMPSON, AND N. BRAKOW. 2008. Large Tropical Forest Dynamics Plots: Testing Explication for the Maintenance of Species Diversity. *In*CARSON, P. C. AND A. S. SCHNITZER (Eds.). Tropical Forest Community Ecology, pp. 98-118. Blackwell Publishing Ltd, Chichester, West Sussex, UK.

Supplementary Material



Continued...

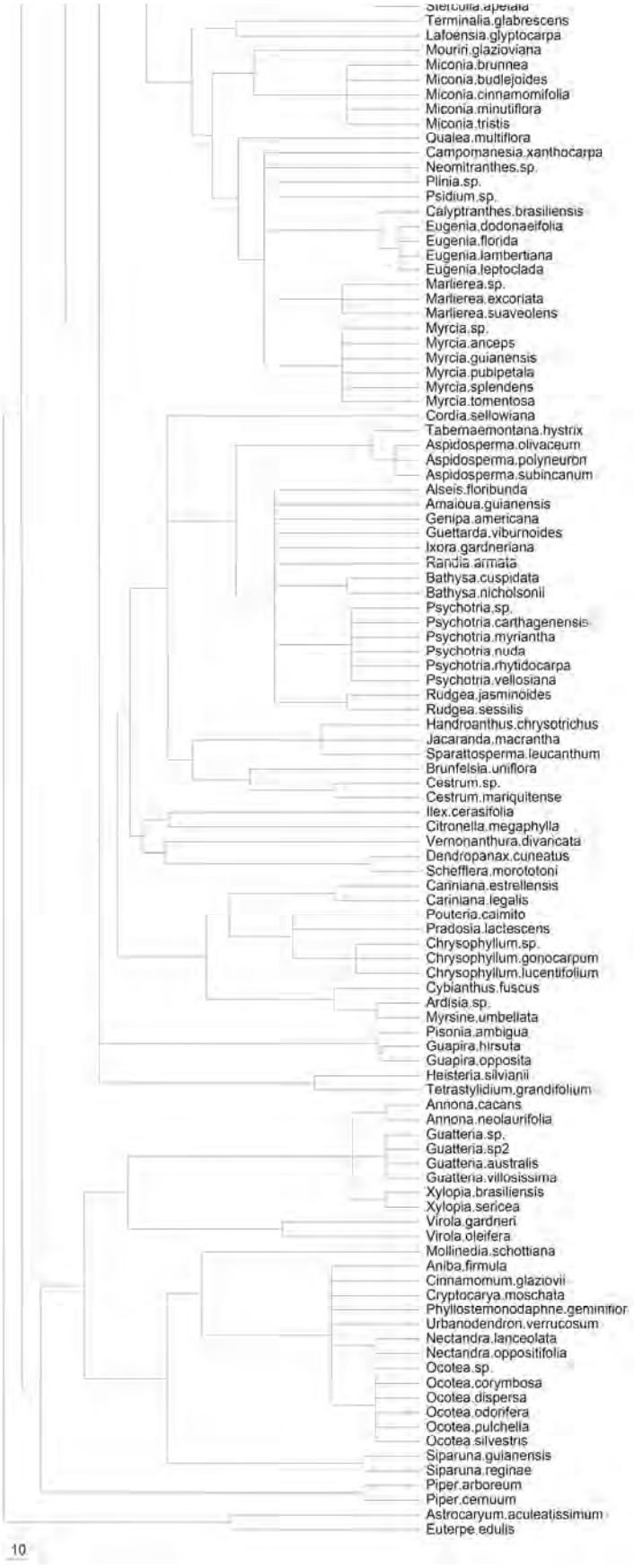


Figure S1. Final tree of the FSN tree community based on R200703050.bl.

MAIN CONCLUSIONS

Species richness and diversity are poor indicators for intactness of campo rupestre vegetation, because human disturbances may increase them as predicted by the hypothesis of intermediate disturbances. Other indicators like precentage of invasive, endangered or endemic species should be consulted.

Although suffered selective wood extraction and situated in a highly fragmentized landscape, the Forest of Seu Nico still maintained primary forest traits until 2010. Nevertheless, there are once evidences for an alarming species loss that mmight be due to logging and fragmentation of the surrounding areas. On the other hand, increase in basal area indicates higher resource availability, perhaps an early consequence of climate change.

Trying to explain species richness in a megadiverse tropical forest, this thesis gives evidence for both niche assembly and neutral theories. Species abundance distribution is best explained assuming stochastic ecological drift, while phylogenetic community composition highlights the role of interspecific competition and negative density-dependent factors of community organizing factors. Therefore, UNTBB should not be reduced to a pool of null hypothesis. Instead, further predictions from UNTBB like the role of dispersal limitations on broader spatial scales on local community composition should be examined. To synthesize both theories and explain species richness and community composition patterns in megadiverse tropical forests, further research activity should therefore focus on three subjects: First, the role of dispersal limitations should be highlighted. Then, it should be examined, why SAD models assuming ecological drift by chance do well to explain species abundance data. At last, the role of biotic factors influencing germination, seedling development and plant fitness should be analyzed.