UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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Comunidades arbóreas ao longo de um gradiente altitudinal na floresta atlântica sul-brasileira

Martin Molz

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Martin Molz

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Tese apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para a obtenção do Título de Doutor em Ciências: Botânica.

SUMÁRIO

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Um único padrão de formatação foi adotado ao longo desta tese, mas cada artigo atende aos parâmetros próprios das revistas escolhidas, a saber: *Ecological Management* e *Biotropica*.

RESUMO

Três comunidades arbóreas foram investigadas ao longo de um gradiente altitudinal em uma encosta montanhosa no Sul do Brasil, o qual se estende da floresta pluvial (clima subtropical) à floresta nebular (temperado úmido). Dados de altura total e diâmetro à altura do peito foram coletados em seis unidades amostrais de 20 × 20 m (0,24 ha) por comunidade ou elevação (≈ 220, 420 e 700 msnm), as quais receberam a denominação de “comunidade inferior”, “intermediária” e “superior”. Nas mesmas parcelas, amostras superficiais de solo (0–20 cm) foram coletadas e subsequentemente analisadas quanto a diferentes parâmetros. Um levantamento florístico foi realizado ao longo de todo o gradiente para observar a distribuição das espécies entre as comunidades e no seu entorno. As observações florísticas visaram à complementação do esforço amostral empreendido, bastante limitado pelas condições extremamente acidentadas do terreno na área de estudo. No primeiro artigo foi investigada a existência de tipos vegetacionais ao longo do gradiente altitudinal e, em caso positivo, como eles diferem entre si. Da mesma forma, a partir dos dados coletados foi realizada uma caracterização das florestas de encosta no limite sul da floresta atlântica costeira. Além dos métodos acima citados, utilizaram-se ANOVA e testes de Tukey para avaliar as diferenças entre os parâmetros estruturais e também entre os parâmetros de solo para cada comunidade. Para estimar a riqueza de espécies e o número mínimo de indivíduos adicionais (ou a área amostral) necessários para detectar a riqueza assintótica estimada foram utilizados dois métodos não-paramétricos, enquanto que para detectar a existência dos tipos vegetacionais foram utilizados agrupamento difuso (*fuzzy clustering*) e ordenação (PCoA). As diferenças mais marcantes na composição e estrutura foram percebidas entre a comunidade superior e as demais, onde foram encontradas

diferenças significativas na composição, na estrutura e nas variáveis ambientais analisadas. Os resultados indicaram a existência de dois tipos vegetacionais nítidos: “vegetação de terras baixas”, com espécies predominantemente associadas às porções inferiores do gradiente, e “vegetação montana”, onde predominam espécies características de regiões de altitude. Devido à maior parte das diferenças observadas ter ocorrido no interior da cobertura nebular, sugere-se que ela seja considerada como um limite natural que separa ambos os tipos vegetacionais. Entre as conclusões, sugere-se: (1) uma revisão da atual classificação das formações que compõem a floresta atlântica costeira (Veloso *et al.* 1991), porque os resultados encontrados demonstram que o limite altitudinal entre a formação “baixo montana” e “montana” (≈ 400 msnm) é claramente inconsistente; (2) que novos estudos sobre gradientes altitudinais na floresta atlântica costeira são urgentemente necessários, especialmente nas porções inferiores e superiores das encostas montanhosas; e (3) que as florestas nebulares também merecem uma atenção especial, visto que até o presente momento muito pouco se sabe a respeito delas. O segundo artigo da tese investigou a distribuição de abundâncias das espécies (DAEs) arbóreas nas comunidades amostradas. Para investigar os padrões de equabilidade e diversificação de nicho, bem como as possíveis influência de restrições ambientais sobre as DAEs ao longo do gradiente estudado, cinco modelos de distribuição de abundâncias foram ajustados aos dados, juntamente com diversas medidas de diversidade. Na seleção do melhor modelo foram utilizados o critério de Akaike (AIC), o critério de Akaike de segunda ordem (AIC_c) e o critério bayesiano (BIC), além dos pesos de Akaike e coeficientes de evidência. A amostragem resultou em um pico de riqueza específica na comunidade intermediária, mas a riqueza estimada apontou para a sua diminuição monotônica com o aumento da altitude. Em cada uma das comunidades ocorreu uma taxa regular de ≈ 30% de espécies raras (*singletons*), bem como uma substituição de espécies constante entre

as comunidades. A dominância aumentou monotonicamente com a elevação da altitude, mas a diversidade caiu drasticamente entre as comunidades intermediária e superior. Já a diversidade de nichos diminuiu com a elevação da altitude. Os aspectos das curvas de DAEs variaram ao longo do gradiente, resultando em diferentes modelos selecionados para cada uma das altitudes. Por fim, em comparação com a inferência baseada na ponderação de modelos, a estratégia de escolha do melhor modelo foi claramente superior. Como conclusão geral, levanta-se a hipótese de que a temperatura e a ocorrência de geadas sejam os principais fatores limitantes na distribuição de muitas das espécies tropicais que ocorreram ao longo do gradiente. Estes dois fatores seriam, juntamente com os efeitos produzidos pela cobertura nebular, os principais responsáveis pela drástica redução na diversidade entre a comunidade intermediária e a comunidade superior e também pela limitação no crescimento das espécies que ocorrem nesta última.

Palavras-chave: floresta atlântica costeira, floresta nebular; tipos vegetacionais, associações de espécies; agrupamento difuso, ordenação; DAEs; equabilidade e diversidade de nichos; raridade; seleção de modelos de DAEs; pesos de Akaike; coeficientes de evidência

INTRODUÇÃO GERAL

A floresta pluvial atlântica sustenta uma das taxas mais elevadas de riqueza de espécies e endemismos, sendo, além disso, considerada um dos cinco *hotspots* de diversidade mais ameaçados no mundo (e.g., Mittermeier *et al.* 1999, Myers *et al.* 2000, Ribeiro *et al.* 2009). Sua extensão latitudinal (em torno de 29º), abrangendo regiões tropicais e subtropicais, combinada com sua extensão altitudinal (nível do mar até > 2.000 msnm), favoreceu uma diversidade elevada e inúmeros endemismos, incluindo mais de 20.000 espécies de plantas e inúmeras outras de animais (Myers *et al.* 2000, Silva & Casteleti 2003, Ribeiro *et al.* 2009). Entretanto, devido à sua proximidade da costa Atlântica, a qual concentra as mais elevadas densidades populacionais no Brasil, a maior parte das florestas de terras baixas costeiras foi desmatada e ocupada. Desse modo, atualmente os remanescentes de floresta atlântica costeira se encontram concentrados principalmente nas encostas de algumas cadeias de montanhas próximas à costa.

No Sul do Brasil, a paisagem é fortemente marcada pelo Planalto Sul-Brasileiro, que compreende a Serra Geral e a Serra do Mar. A elevação de maior destaque é a Serra Geral, que no Paraná e em Santa Catarina aparece mais recuada em relação à da Serra do Mar, mas no Rio Grande do Sul termina junto ao litoral. As partes elevadas da Serra Geral abrigam um rico mosaico de florestas com araucária e campos (e.g., Teixeira *et al.* 1986, Veloso *et al.* 1991, IBGE 2004, Behling & Pillar 2007, Overbeck *et al.* 2007), além de segmentos de floresta nebular (Falkenberg & Voltolini 1995). Já a vegetação da planície litorânea é formada por florestas pluviais de terras baixas, restingas e campos (e.g., Rambo 1951, 1961; Teixeira *et al.* 1986).

Entre a planície litorânea e o platô da Serra Geral, estende-se um gradiente altitudinal de florestas de encosta que abriga elevada diversidade, com zonas de vegetação que variam de florestas de terras baixas e de encosta com porte elevado a florestas nebulares atrofiadas. Nas porções inferiores do gradiente (< 500 msnm) as árvores podem atingir até 30 m de altura, o sub-bosque é denso e diversificado e a abundância de palmeiras é elevada. Nas porções superiores (> 500 msnm) as árvores não passam de 20 m de altura, o sub-bosque também é denso, porém muito menos diversificado, e a abundância de palmeiras diminui progressivamente até que estas desaparecem. Com a elevação da altitude, as árvores se tornam cada vez mais baixas, com estratos cada vez menos evidentes e ocorre a substituição gradativa de palmeiras por samambaias arborescentes. Próximo aos picos dos morros mais elevados e às bordas do platô ocorrem verdadeiras florestas anãs, com árvores baixas (6–8 m), sem estratificação aparente, densamente cobertas de liquens e musgos e com incrível abundância de epífitos, além de densas populações de bambus do gênero *Chusquea* em alguns trechos.

Um dos aspectos mais marcantes em gradientes altitudinais é a tendência à formação de zonas de vegetação a baixas altitudes (< 1.500 msnm) em pequenas montanhas costeiras, o que tem perturbado os cientistas por longo tempo. Esse fenômeno é comumente conhecido como “efeito Massenerhebung”, “elevação da massa” ou “efeito telescópico” (e.g., Richards 1952, Van Steenis 1972, Grubb 1977, Proctor *et al.* 1989, Bruijnzeel *et al.* 1993, Whitmore 1998, Bruijnzeel 2002). Acredita-se que a enorme massa de grandes montanhas expostas a intensos níveis de radiação durante os períodos sem nuvens eleve a temperatura do ar sobrejacente, permitindo que as plantas ampliem a sua distribuição altitudinal. Provavelmente a mesma causa não se aplica a montanhas médias ou pequenas onde se observa o mesmo efeito. Ao invés disso, a contração de zonas de vegetação em muitas montanhas pequenas deve ser atribuída à elevada umidade do ar oceânico promovendo a formação de nuvens em elevações muito baixas, em vez de uma taxa de lapso de temperatura mais acentuada com a elevação associada a pequenas montanhas (Bruijnzeel 2002). Esse efeito é mais pronunciado em áreas com elevada pluviosidade e, portanto, elevada umidade atmosférica (Van Steenis 1972, Bruijnzeel *et al.* 1993).

Estudos sobre composição, estrutura e comunidades ecológicas em gradientes altitudinais remetem às origens da biogeografia. Contudo, não obstante os esforços de dois séculos em caracterizar gradientes ambientais de riqueza de espécies em busca de padrões universais, surpreendentemente poucos desses padrões têm sido amplamente reconhecidos (e.g., Nogués-Bravo *et al.* 2008). Nos últimos anos tem ocorrido um ressurgimento moderno do interesse em padrões de riqueza e diversidade ao longo de gradientes altitudinais, de modo que estudos de riqueza de espécies em gradientes altitudinais têm paulatinamente substituído o gradiente latitudinal como um modelo para estudos de larga escala em gradientes (Rahbek 2005). Para analisar a variação geral da riqueza e distribuição de espécies com a elevação, um requerimento mínimo para qualquer conjunto de dados é que inclua dados que abranjam todo o gradiente, embora se torne progressivamente difícil encontrar gradientes apropriados com hábitat natural contínuo ao longo de todo o gradiente (Rahbek 1995). Isto é um problema especialmente com relação a regiões de terras baixas e contrafortes, que são muitas vezes as zonas de elevação mais perturbadas. Entretanto, mesmo que não existam gradientes completos é fundamental que sejam efetuados estudos nos remanescentes existentes. Na floresta atlântica costeira, por exemplo, inexistem dados quantitativos de riqueza e distribuição de espécies arbóreas ao longo de gradientes altitudinais com métodos e análises atuais. A própria classificação atual da floresta atlântica costeira (Veloso *et al.* 1991, IBGE 2004) não apresenta a necessária fundamentação em dados numéricos, de modo que as cotas altitudinais sugeridas para as diferentes formações são baseadas em dados subjetivos e/ou empirismo.

Métodos de análises multivariadas sempre desempenharam um papel importante em detectar e sintetizar padrões em dados. Entre os métodos mais amplamente utilizados estão a classificação numérica, ou análise de agrupamento, e a ordenação, ou análise de gradiente (Kent 2006). Um dos métodos de análise de agrupamento mais interessantes, e, incrivelmente, pouco utilizado, é o agrupamento difuso (*fuzzy clustering*). Enquanto que nos métodos usuais um elemento é atribuído a um único grupo, no agrupamento difuso um elemento recebe um percentual de participação que pode variar de zero a um, correspondendo a uma participação de 0 a 100%. Trata-se, portanto, de um método mais realista do ponto de vista ecológico, pois na natureza não existem grupos rígidos como aqueles criados pelos métodos usuais de agrupamento.

Outro aspecto que recebeu novo alento foi a questão da distribuição de abundâncias de espécies (DAE), muito em especial a partir do surgimento da teoria neutra da biodiversidade (Hubbell 2001). A DAE é a descrição da abundância (número de indivíduos observados) para cada espécie diferente encontrada em uma comunidade e, como tal, é uma das descrições mais básicas de uma comunidade ecológica (McGill *et al.* 2007). A DAE segue uma das leis mais antigas e universais da ecologia, de que plotadas as espécies de uma comunidade em um histograma esta se apresenta como uma curva côncava com muitas espécies raras e apenas algumas poucas espécies comuns (e.g., McGill *et al.* 2007). A distribuição de abundâncias é uma exposição completa da informação sumarizada em uma medida de diversidade de espécies ou equabilidade (Wilson 1991). Assim, a criação de inúmeros modelos de distribuição de abundâncias representa diferentes tentativas de sintetizar informações relativas a padrões e processos ecológicos. E, apesar de mais insucessos do que sucessos até o momento (McGill *et al.* 2007), trata-se de uma área promissora.

Ainda mais promissora é a forma de analisar dados e fazer inferências conhecida como seleção de modelos, onde ao invés da abordagem tradicional de teste de hipóteses e conceitos associados (valores de p e níveis de α), diversas hipóteses que competem entre si são simultaneamente confrontadas com dados (Burnham & Anderson 2002, Johnson & Omland 2004). A seleção de modelos pode ser usada para identificar um único melhor modelo, levando assim ao suporte de uma hipótese em particular, ou pode ser usada para fazer inferências a partir de um conjunto de modelos, permitindo assim inferências a partir de múltiplos modelos (Burnham & Anderson 2002, Bolker 2008). Esta é certamente uma das áreas que mais tem recebido a atenção de ecólogos nos últimos tempos.

O presente estudo foi desenvolvido em um gradiente altitudinal de vegetação situado no município de Maquiné (RS), na divisa com o município de Terra de Areia, em altitudes que variam entre aproximadamente 200 e 720 msnm. Ali se investigou a possível existência de zonas de vegetação arbórea (ou tipos vegetacionais) e realizou-se um detalhamento da composição e estrutura das comunidades investigadas. Atenção especial foi dada às condições ambientais dentro e fora da cobertura nebular que se forma regularmente em torno de 550 msnm, e se as mudanças nas condições ambientais foram acompanhadas por alterações na composição das espécies. Em outra abordagem no mesmo gradiente altitudinal, averiguou-se a distribuição de abundâncias de espécies (DAE) arbóreas através de cinco modelos ajustados aos dados. Diferentes critérios baseados em máxima verossimilhança foram utilizados na escolha do melhor modelo para cada altitude. As comunidades foram também descritas utilizando medidas de diversidade e uma abordagem para enquadrar as espécies como comuns ou raras.

Com as abordagens acima descritas, esta tese procurou responder às seguintes questões:

1. Existem diferenças nas florestas ao longo do gradiente altitudinal que se estende da planície litorânea (clima subtropical) ao platô do Planalto Sul-Brasileiro (clima temperado) no limite sul da floresta atlântica costeira?
2. Se elas existem, como e quanto diferem entre si. Quais são as causas dessas possíveis diferenças?
3. Ao utilizar modelos de distribuição de abundâncias, seleção de modelos e medidas diversidade, é possível concluir algo a respeito dos padrões e possíveis causas da distribuição de espécies nas florestas estudadas? Quais são os padrões de equabilidade e diversidade de nichos ao longo do gradiente altitudinal?
4. E quais são as possíveis influências de fatores ambientais sobre a distribuição das espécies ao longo do gradiente altitudinal estudado?

Este estudo visa a ampliar o conhecimento sobre a formação mais diversa e também mais ameaçada no Brasil, a floresta pluvial atlântica costeira, pois, até onde se sabe, até o momento inexistem estudos que tenham analisado comunidades arbóreas em gradientes altitudinais no Sul do Brasil. Os métodos utilizados trazem abordagens distintas e até inovadoras frente ao que, em regra, vem sendo realizado, em especial no tocante à aplicação de critérios de seleção de modelos na área da ecologia. Duas abordagens muito distintas estão contidas nesta tese: uma empírica e outra de modelagem. Acredito que ambas são complementares e contribuem para uma melhor compreensão das questões levantadas.

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First Article

Vegetation types along an elevational gradient in the southern limit of the Brazilian Atlantic forest

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Abstract

The original cover of the subtropical Brazilian Atlantic coastal rain forest is characterized by historical degradation due to wood extraction, agriculture and livestock, along with urban areas ever larger. This led to the eradication of most of the lowland and also lower montane forests near to the coastal plain. In a context of forest restoration, natural vegetation composition and distribution patterns need to be known and included in a framework for site classification. Thus, we studied tree-species communities along an elevational gradient in the southern limit of the Atlantic coastal rain forest. Structural and floristic surveys along the complete gradient were made for comparison between the communities analyzed. Soil samples were collected for analyses, and ANOVA and Tukey's tests were used to evaluate differences between the structural parameters and the soil parameters at each elevation. Nonparametric methods were also used to estimate the species richness and the minimum number of additional individuals or sampling area required to detect the estimated asymptotic species richness. Fuzzy *c*-means clustering and ordination were used to analyze the optimum number of groups. All communities were species-rich, but observed and estimated richness showed dissimilar patterns. Communities most pronounced differences in composition and structure were perceived between the upper community and the others, where significant changes in climate and soil characteristics were found. Results showed that the cloud line represents a natural boundary that separates the vegetation types in lowland and montane, with many species associated to one type, most especially Myrtaceae.

Keywords Atlantic forest · elevational gradient · vegetation types · cloud forest · cluster analysis and ordination · species associations

Introduction

Elevational gradients are complex systems which usually consist of continued variations in climate, topography and soils (e.g., Baruch 1984; Austin and others 1996; Pendry and Proctor 1996), often accompanied by associations between species and vegetation zones (e.g., Ohsawa 1984; Ludwig and Cornelius 1987; Kessler 2000). In recent years, there has been a resurgence of interest in modern patterns of richness and diversity along altitudinal gradients, so that studies of species richness in the altitudinal gradients have gradually replaced the latitudinal gradient as a model for studies of large-scale gradients (Rahbek 2005). Regretfully this interest has not extended to Brazil, where the studies on altitudinal gradients are still rare.

Floristic composition and geographic and climatic variables shaped the current understanding of the Atlantic forest as a large biome (covering ≈ 1.5 million km^2) with many different formations and associated ecosystems (e.g., Oliveira-Filho and Fontes 2000, Galindo-Leal and Câmara 2003). Studies had associated elevation with the internal differentiation between the Atlantic forest formations (e.g., Oliveira-Filho and Fontes 2000, Scudeller and others 2001), but there are very few direct investigations of the associations between elevation and vegetation types in the Atlantic forest. According to current classification, the Brazilian Atlantic coastal rain forest is divided in lowland (< 30 m asl), lower montane (30–400 m asl), montane (400–1000 m asl), and upper montane (> 1000 m asl) vegetations types (Veloso and others 1991).

In the southern limit of the Atlantic coastal forest, a climate and vegetation gradient extends along the eastern border of the South Brazilian Plateau from the subtropical lowland rain forest to the humid temperate mosaic of *Araucaria* forest and grasslands (Campos). These highly diverse vegetation types were addressed concerning a number of issues for management and conservation purposes (e.g., Behling and Pillar 2007; Murray-Smith and others 2009), although the slope forests that lie between them remain poorly known.

Clustering provides a common means of identifying structure in complex data (Still and Bialek 2004), such as how many vegetation types exist in an elevational gradient. In recent years techniques of fuzzy classification are becoming more widely used (Kent 2006). There are large differences between ordinary set theory and fuzzy-set theory. In the former, if an element belongs to a particular set (i.e., is a member of that set), it can receive the value of 1, whereas otherwise it receives the value of 0. In fuzzy-set theory the elements have degrees of membership and the set, whose boundaries are no longer well defined, is termed ‘fuzzy’ (Equihua 1990). As a result the elements can receive any value within the interval [0,1], so that memberships close to unity indicate a high degree of similarity between a sample and a class (or community) whereas memberships close to zero indicate little similarity between a samples and a class (Foody 1999).

The objective of this study is twofold. First, by using fuzzy clustering, ordination, and environmental variables we aim to identify whether there are different natural vegetation types along an elevational gradient, and, if they exist, how they differ from each other. Secondly, with the aid of composition and structure data, we make a first characterization of the slope forests in the southern limit of the Brazilian Atlantic forest. With this e seek to contribute for the preservation and possible future restoration of the highly threatened Brazilian Atlantic coastal rain forest in its southern limit.

Methods

Study Area and Environmental Setting

The Atlantic forest occurs between latitudes 3º and 31º S of South America, mainly extending along the Brazilian coast (e.g., Ribeiro and others 2009). At its southern coastal limit, in the Brazilian state of Rio Grande do Sul, the Atlantic forest occurs as a 20–30 km broad belt on the coastal lowlands and the slopes of the South Brazilian Plateau up to 1000 m asl. The highland vegetation of the South Brazilian Plateau is composed by a mosaic of humid temperate *Araucaria* forests and grasslands (Campos), while the slopes inbetween are covered by a gradient that extends from tall rain forests to cloud forests.

The study area encompassed an elevational gradient ranging from lower montane rain forests, at ≈ 220 m asl, to cloud forests, at ≈ 700 m asl. Above 750 m asl the medium size forest gave way to a stunted forest with small trees up to 6–8 m and many bamboos, followed by shrubs and grasses until the peak (814 m asl), that is connected to a higher plateau (> 900 m asl) with a rich mosaic of cloud forests, tall *Araucaria* forests and grasslands.

The intensive use of the lowlands and submontane areas for cattle-raising and tropical cultures, such as pineapple and banana, along with vegetable plantings in the river valleys, led to the suppression of the largest part of the forests that once existed there. As a result, most of the remnants are on the slopes, and no more complete vegetation gradients can be found in the southern limit of the Atlantic coastal forest. The more rugged the topography, the more forests are conserved and more difficult it is to carry out studies on them.

Lithology varies from sedimentary rocks in the lowlands to igneous extrusive rocks above ≈ 180 m asl. The steep slopes in this region are full of cliffs and tall steps, where natural landslides occur regularly. These soils are acid, and podzolization and soil wetness are pronounced above 550 m asl.

All over the year, though not on a daily basis, a cloud cap forms starting from ≈ 550 m asl. The mean annual temperatures vary from 18.9ºC at 220 m to 16ºC at 700 m (with a lapse rate of 0.57 ºC /100 m), annual precipitation varies from 1,700 to 2,045 mm, and mean annual occurrences of frost are between 1(-3) to more than 10 in the upper elevation (Nimer 1990).

Field Data Collection

Between November 2008 and April 2010, six 20 × 20 m (0.04-ha) plots were appraised at three sites or elevations designated as “lower” (≈ 220 m — 29º38’49’’ S, 50º8’1’’ W), “middle” (≈ 420 m — 29º38’38’’ S, 50º8’12’’ W), and “upper” (≈ 700 m — 29º38’25’’ S, 50º8’18’’ W) communities. The diameters at breast height (dbh) and total heights (H) of all trees > 5 cm dbh in the plots were measured. Due to difficult access conditions to reach a larger sampling effort, we made a floristic survey and observations along the entire gradient to form a fuller picture on the distribution of the species. The classification followed APG III (2009) for angiosperms and Smith and others (2006) for ferns.

Surface soil samples (0–20 cm) were also collected at four points of each plot and then homogenized for subsequent analysis of the following parameters: clay content, pH, P, K, organic matter (OM), Al, Ca, Mg, cation exchange capacity (CEC), and base saturation (BS %).

Data Analysis

It has been noted that biodiversity sampling is labor intensive (e.g., Longino and Colwell 1997, Lawton and others 1998), and species with very low abundance are hard to detect (e.g., Gotelli and Colwell 2001, Magurran 2004), especially in communities with many rare species. Thus, to estimate the number of species for each community we used the Chao 2 nonparametric estimator of asymptotic richness (Chao 1987). For conservation purposes it is opportune to know the amount of sampling required to detect all of the species present in the area. A site which hosts a high number of rare species requires a larger area to be able to preserve biodiversity than sites that have few rare species. For that reason we used a nonparametric method recently developed by Chao and others (2009) to find the minimum number of additional individuals or sampling area required to detect any arbitrary proportion of the estimated asymptotic species richness.

According to the forest strata in which they were found in the surveys, personal observations and literature, species were classified as canopy, sub-canopy or understory species. In order to evaluate whether there is significant differences in community structure, the arithmetic mean of dbh and H average and maximum values were estimated, followed by a one-way ANOVA and a Tukey's pairwise comparison between communities performed with statistical software PAST (Hammer and others 2001). ANOVA and Tukey's tests were also used to analyze differences between the soil parameters at each elevation with 95% CI.

Cluster analysis and ordination were made using packages 'cluster' (Maechler and others 2005), and 'vegan' (v1.17.3, Oksanen and others 2010) from the statistical software R (v2.12.2, R Development Core Team 2011). First, data was partitioned into *c* clusters by using fuzzy clustering. Most clustering methods focus on discontinuities, resulting in "hard" classifications where a given object belongs to only one cluster. Fuzzy clustering, on the contrary, assigns degrees of membership to each object (e.g., Abonyi and Feil 2000; Fischer and Getis 2010; Borcard and others 2011), and hence it is a more realistic approach to gradient analysis. The method is based on the concept of partial truth-values between ‘completely true’ and ‘completely false’ (Fischer and Getis 2010), allowing a more nuanced interpretation of the relationships among sites and of the cluster limits (the potential vegetation types), which may not be so clear-cut as most clustering methods labels. Next, the Anderson and others (2006) variant of the Gower dissimilarity index (that omits double-zeros) was computed with logarithmic standardization, followed by a Principal Coordinates Analysis (PCoA) to display the dissimilarities between plots. The membership of the fuzzy clustering and the distance matrix were plotted as an ordination plot which shows the probability profile of the class membership, symbolized by the size of each sector.

Results

Composition and structure

A total of 109 species from 41 families were found at the three elevations (Table 1). The lower and middle communities shared a high number of species (56), the middle and upper a smaller number (37), whereas only 25 species occurred along the entire gradient. The main composition similarities occurred at the family level, so that with increasing taxonomic level (species to family), the number of taxa shared between communities along the gradient increased. Most families occurred in the complete gradient (17), and an expressive number of families (14) occurred only at the lower and middle communities. Families whose tree-species are largely or exclusively tropical, such as Araliaceae, Chrysobalanaceae, Clusiaceae, Fabaceae, Magnoliaceae (in South America), Myristicaceae, and Phyllanthaceae, were not found in the upper site. Myrtaceae and Lauraceae were by far the most species-rich families.

In all communities there were only a few very abundant species and a large number of rare species. *Euterpe edulis,* one of the most widespread palm-trees in the Brazilian Atlantic forest, was the commonest species at the lower and middle communities, while in the upper community 40% of the sampled individuals were of *Alsophila setosa*, a fern tree. Other abundant species were *Chrysophyllum inornatum*, very common in the lower and middle communities but very rare in the upper community, and, for example, *Cabralea canjerana, Chrysophyllum viride, Guapira opposita,* and *Sorocea bonplandii*, relatively abundant at all elevations.

The observed (S_{obs}) and estimated richness (S_{est}) were dissimilar (Table 2), with a mid-elevation peak for S_{obs}, and a drop from the lower to the upper community for S_{est}. The observed number of individuals and the S_{obs} had the same pattern, with a peak in the middle community. But compared to the middle and upper communities, attaining the asymptotic richness for the lower community would have required a much higher sampling effort in number of individuals or sampling area than was possible in this study.

Table 2 Observed and estimated species richness (*S*), number of individuals (*n*) and sampling area (in hectares) for the communities of the elevational gradient. Percentages represent the fraction of the estimated species richness, number of individuals and area that is desired

	Observed			Estimated (100%)			Estimated (95%)		
Community	***S***	***n***	**Area**	***S***	***n***	**Area**	***S***	***n***	**Area**
Lower (220 m)	71	564	0.24	137.1	11,123	4.73	130.2	3,675	1.56
Middle (420 m)	84	636	0.24	104.3	3,159	1.19	99.1	765	0.29
Upper (700 m)	47	521	0.24	57.9	1,987	0.91	55.0	537	0.25

The average and maximum tree height decreased significantly from the lower to the upper community (one-way ANOVA, $F = 50.4$, $P = <0.001$, and $F = 11.2$, $P = <0.001$, respectively). The differences in average height between the lower and middle communities were not statistically significant ($P = 0.18$), but both differed from the upper community ($P = <0.001$). Regarding the dbh, the average values did not differ between the elevations (one-way ANOVA, $F = 0.58$, $P = 0.57$), but the maximum values (one-way ANOVA, $F = 4.74$, $P = <0.02$) decreased between the middle and upper communities ($P = 0.02$).

Soils

The soil characteristics did not differ significantly between the lower and middle elevations, but greatly between those and the upper one. The only soil characteristic distinct at all elevations was pH (one-way ANOVA, $F = 41.73$, $P = <.001$; Table 3). The base saturation at the lower and middle communities indicates that the soils were eutrophic (BS ≥ 50%), while at the upper community they were dystrophic (BS < 50%), and had a high aluminum content (Al ≥ 4.0), i.e. were poor in nutrients and toxic. Concerning organic matter (OM), there were no significant differences between the elevations, although the increase in OM together with higher Al content and lower pH with the increasing elevation, pinpointed a growing podzolization towards the upper elevation.

Table 3 Characteristics of surface soil samples (0–20 cm) at the three elevations of the elevational gradient. Four samples per plot were taken and homogenized, and the mean for the six plots per elevation was computed for each parameter. All values are expressed as concentrations in oven dried (105ºC) soil. Significant differences between altitudes are indicated by letters and values of *F* and *P* are given in the two final rows

Elevation	**Clay**	**pH_{H2O}**	**P_{Total}**	**K**	**OM**	**Al**	**Ca**	**Mg**	**CEC**	**BS (%)**
Lower	20.17^{A}	5.72^{C}	5.18	222.0	6.03	0.03^{A}	12.32^{B}	4.65^{B}	22.33	77.0^{B}
Middle	16.5^{A}	5.05^{B}	6.22	159.0	7.65	0.77^{A}	10.07^{AB}	4.42^{B}	24.4	60.17^{B}
Upper	24.83^{B}	4.30^{A}	7.32	160.5	8.17	6.17^{B}	4.18^{A}	1.53^{A}	32.43	21.5^{A}
F	15.52	41.73	1.93	2.37	2.88	20.3	5.77	20.07	3.46	23.37
P	<0.001	<0.001	1.80	0.128	0.087	<0.001	0.014	<0.001	0.058	<0.001

Clustering and ordination

Fig. 1 shows the probability profile of each class membership, where the sizes of the sectors on the plot represent the possible association to a group. The only group with a clear dominant segment was the one established by the six plots of the upper elevation (mean coefficient membership and standard deviation = 91.5% ± 5.75%), alongside with plot number eight. Nonetheless, plot eight slightly larger sector related to the upper site (membership = 50%) was due to an unusually high number of individuals of the upper community most abundant species, *Alsophila setosa*. The distinction between the lower and middle communities' plots was not clear, but both were evidently distinct from the upper elevation.

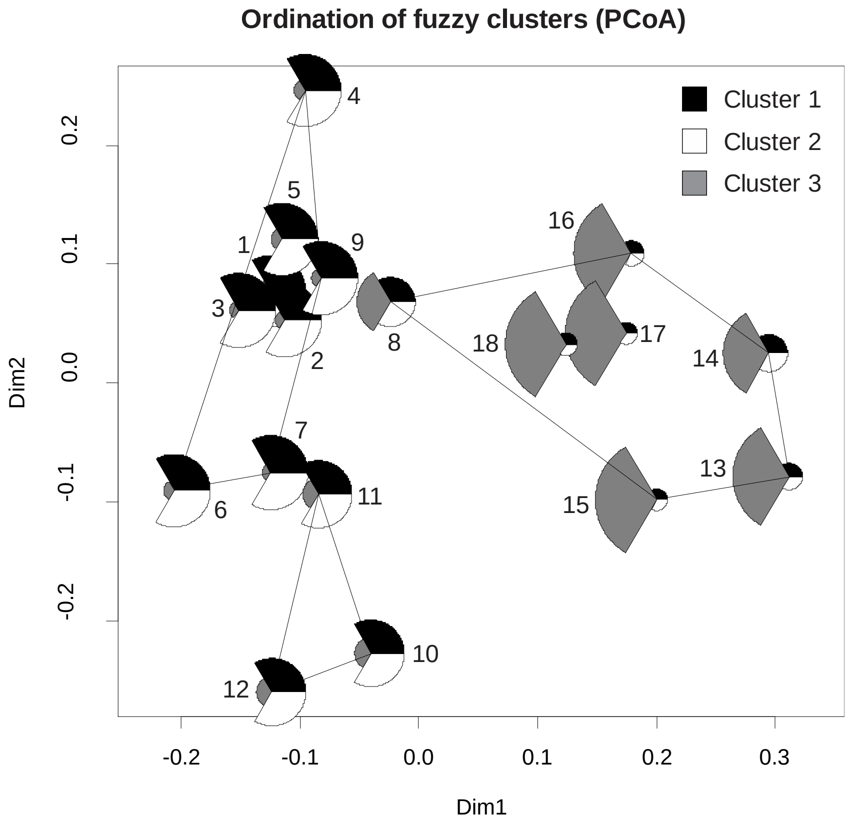

Fig. 1 Ordination of fuzzy clusters (PCoA) by means of Anderson and others (2006) variant of the Gower dissimilarity index. The size of each sector shows the probability profile of the class membership: lower community = plots 1–6; middle community = plots 7–12; upper community = plots 13–18

Two crisp groups or vegetation types emerged from our fuzzy *c*-means analysis, one associated to the lower community and other strongly connected to the upper community. Despite the middle community been partly connected to both communities, it was mostly associated to the lower one (Fig. 1). We suggest, therefore, that the cloud cap limit, which lies just about between the middle and upper communities (≈ 550 m asl), be used as a boundary between both types: the “lowland vegetation”, mainly associated to the lower segment of the gradient, and the “montane vegetation”, mainly associated to the upper segment of the gradient. Since most species associated to the lower portion occur as well in lowland forest fragments (pers. obs.), we prefer “lowland vegetation” instead of other expressions to designate this type.

Some species were related to one vegetation type but may potentially occur as infrequent or isolated individuals in other, while other species occur exclusively in one type. Canopy species strictly associated with the lowland vegetation, for instance, were *Aspidosperma olivaceum, Brosimum glaziovii, Hieronyma alchorneoides, Magnolia ovata, Pachystroma longifolium, Schefflera morototoni, Trichilia lepidota,* and *Virola bicuhyba*. *Hirtella hebeclada, Myrcia aethusa,* and *Myrcia pubipetala* were typical sub-canopy lowland vegetation species, while *Eugenia bacopari, Gymnanthes concolor, Ouratea parviflora,* and *Garcinia gardneriana* were characteristic understory species of the lowland vegetation. All these species are never found in the montane vegetation. Other typical lowland species, save for fortuitous occurrences in montane areas, were *Chrysophyllum inornatum* and *Meliosma sellowii*. Examples of tropical genera that occurred associated to the lowland vegetation were A*lchornea, Annona, Ficus, Nectandra,* and *Urera*. *Cecropia* and *Jacaranda* were other tropical genera found near the plots. Since it was less diverse, the montane vegetation had a lower number of associated species. *Cryptocarya aschersoniana, Ilex paraguariensis, Meliosma sinuata,* and *Roupala rhombifolia* were characteristic canopy species in the montane vegetation, while *Alsophila setosa* and *Casearia decandra* were typical understory species. Since the height of the trees was comparatively lower in the montane vegetation, species were not divided in canopy and sub-canopy ones.

Myrtaceae represented a special case because the family presented the highest diversity and several species were strongly associated to one vegetation type. *Myrcia aethusa, Myrcia grandifolia, Myrcia pubipetala, Myrciaria plinioides,* and *Neomitranthes gemballae* were exclusively associated to the lowland vegetation, while *Eugenia handroi, Myrceugenia oxysepala,* and *Myrciaria floribunda* occurred only in the montane vegetation. Although *Eugenia* *subterminalis* and *Myrceugenia miersiana* occurred in both middle and upper communities, the former was the most abundant Myrtaceae in the upper community and the latter is a distinctive species in the cloud and *Araucaria* forests. Thus, both can be considered strongly associated to the montane vegetation, next to the fact that they never occur in the lowland vegetation. *Myrceugenia myrcioides* is a very common species in the montane vegetation, but can also occur in the lowland vegetation.

Discussion

Even though remarkable differences in composition between the communities were noted all along the gradient, the most pronounced ones were perceived between the upper community and the others, where significant changes in structure and climate and soil characteristics were found. Visually the main sudden modifications were located next to the base of the cloud cap. With the elevation increase the crowns of the trees filled with epiphytes, trees gradually decreased in height, and tree ferns, like *Alsophila setosa* and *Dicksonia sellowiana*, became very abundant (though it did not occur in the sampled area, the latter species was abundant next to it). Approximately at 750 m the medium size forest gave way to a stunted forest with 6–8 m height and undifferentiated strata, and the last tropical palm-trees were replaced by dense populations of bamboos (*Chusquea mimosa*) and by a few individuals of *Geonoma schottiana*, a little palm characteristic in pioneer environments with high levels of organic matter (pers. obs.). Many of these characteristics were described as distinctive for the montane cloud forest in southern Brazil (Falkenberg and Voltolini 1995).

All these changes were found in the cloud cap within a few tens of meters of elevation and support the use of the cloud line as a natural boundary that separates the vegetation types as lowland and montane. Researchers have generally recognized three types of rainforest on wet tropical mountains: lowland rain forest, lower montane rain forest and upper montane rain forest (e.g., Richards 1952; Grubb 1971). Distinctive plant associations (Richards 1952) as well as altitudinal limits have been used to define these forest types (Grubb 1971). On small and isolated tropical mountains the upper limit of lowland rainforest is about 700−900 m (Grubb 1971). Based on our results we suggest that in the southern limit of the Brazilian coastal rain forests this limit lies between 500–700 m.

The occurrence of vegetation types on small, isolated coastal mountains that resembles the ones that occur on largest mountain ranges is called “mass elevation” (Massenerhebung effect) or “telescoping effect” (e.g., Van Steenis 1972; Grubb 1977; Proctor and others 1989; Bruijnzeel and others 1993; Whitmore 1998;). Bruijnzeel (2002) argued that the contraction of vegetation zones on many small coastal mountains has to be ascribed to the high humidity of the oceanic air promoting cloud formation at low elevations rather than to a steeper temperature lapse rate with elevation. Since mountain cloud caps are associated with a reduced amount of radiation and evaporation, higher rainfall and atmospheric humidity, and also wetter soils (e.g., Grubb 1974, 1977; Bruijnzeel and others 1993; Bruijnzeel 2002), the vicinity of the studied mountainous slope to the seashore (*ca.* 16.8 km away) and the low temperature lapse rate suggest that the contraction of vegetation zones was due to the high humidity from the Atlantic Ocean and that the change in species composition above the cloud line was due to changes in environmental conditions. The effect is most pronounced in areas with high rainfall and high atmospheric humidity (Van Steenis 1972; Bruijnzeel and others 1993), as was the case for the montane vegetation.

In tropical mountains decomposition is slowed at high altitude, soil acidity increases and nutrient supply decreases along with the productivity of the forest (Grubb 1977; Proctor and others 1988; Grieve and others 1990). The low pH values (< 4.5), poverty in certain macronutrients, high levels of aluminum and low percentage of base saturation pointed to dystrophic and toxic soils, indicating unfavorable conditions to plant growth in the upper community. Compared to the lower community, for instance, the maximum tree-height was 65% lower within the cloud cap, an evident decline. These aspects can explain part of the sharp diversity decrease from the lowland to the montane vegetation, but not all. The absence of one or few species from one site may be due to a variety of causes (e.g., Borcard and others 2011), but the absence of many species was probably due to non-optimal environmental conditions for these species. Investigating the causes of change in forest structure and species composition in a small mountain in Malaysia, Pendry and Proctor (1996) found no evidence that, relative to the lowland forest, the lower montane forest suffered from either high winds, drought or waterlogging, high soil acidity or nutrient limitation, and concluded that the changes were due to temperature reduction with altitude. The environmental characteristics within the cloud cap appeared to be sufficiently restrictive to prevent the establishment of many species, at least those tropical trees that were sensitive to small temperature alterations and frosts occurrences, and occur only within a very narrow range on the southern limit of the Atlantic coastal rain forest.

Regarding the species richness, the percentage of the S_{obs} represented only 55% of the S_{est} for the lower community. In order to find the rarest species and to reach the asymptote (100% S_{est}) in this community a larger sampling effort would be necessary. The sampling area would have to be increased by a factor of twenty, an unattainable task in the studied hilly area. To attain the asymptote for the middle and upper communities it would be necessary to increase the sampling area by a factor five and four, respectively. This leads to a problem raised by many studies (e.g., Nogués-Bravo and others 2008; Rahbek 1995, 2005), that of the scale effects and human impact on the elevational species richness gradients. Monotonic decline and hump-shaped patterns with peak richness at many altitudes are the most commonly reported patterns (e.g., Rahbek 1995, 2005; Lomolino 2001; McCain 2007), but there is not a uniform pattern on elevational gradients of species richness (Rahbek 1995). The S_{obs} shows a hump-shaped pattern, while the S_{est} predicts a monotonic decline in species richness with the increase in elevation. As lowland forests are absent and, therefore, the gradient is incomplete, it is impossible to determine the original true pattern of species richness. Because lowlands are in fact more diversified in the Brazilian Atlantic coastal rain forest, we suppose that the center of the complete original gradient (taking into consideration sea-level lowlands to plateau highlands) was located closer to the lowlands or in fact on them.

Concerning species associations with the vegetation types, Myrtaceae were the family with the greatest diversity and also with highest number of species associated to one type. Myrtaceae are the most species-rich family in the southern limit of the Atlantic rain forest (Sobral 2003; Sobral and others 2006) and the fourth largest plant family in Brazil (Giulietti and others 2005). A recent work used the distributions of endemic and endemic-threatened species of Myrtaceae to indicate areas of rich plant diversity and conservation importance within the Brazilian Atlantic coastal forests (Murray-Smith and others 2009). Twelve areas were identified, one of them in the southern limit of the Atlantic forest (in the Serra Geral National Park and the Aparados da Serra National Park). Based on Sobral and others (2006) and personal observations, *Calyptranthes lucida, Calyptranthes rubella, Campomanesia guaviroba, Eugenia ternatifolia, Marlieria eugeniopsoides, Marlieria parviflora, Myrcia anacardifolia, Myrcia dichrophylla, Myrcia pubiflora, Myrcia pulchra, Myrcia splendens, Neomitranthes cordifolia, Plinia edulis,* and *Psidium longipetiolatum* can be also considered inherently linked to lowland vegetation. In montane vegetation (specifically cloud forest) *Eugenia dimorpha, Eugenia neomyrtifolia, Myrcia retorta,* and *Siphoneugena reitzii* can be added as species characteristically associated to this vegetation type.

As our study represents an incomplete elevational gradient, it is hard to make assumptions, nevertheless we assume some feasible conclusions. First, that composition, structure and environmental data shows a markedly separation between the upper community and the other communities. As the main differences occurred within the cloud cap, we suggest that it represents a natural boundary between two vegetation types, one more associated with the lowland vegetation and the other strongly associated with montane vegetation. This inevitably leads to the subject that at least one of the proposed limits for the Brazilian Atlantic coastal rain forest current classification (Veloso and others 1991) should be revised, because according to our results the boundary between the "lower montane" and the "montane" vegetations types (≈ 400 m asl) is clearly inconsistent. It should also be taken into account that the present study was conducted near the higher latitude of the Brazilian Atlantic coastal rain forest and, therefore, it is expected that at lower latitudes the altitudinal boundary between these vegetation types to be even higher. Finally, we suggest that more studies on elevational gradients are urgently needed in the Brazilian Atlantic coastal forest, especially in the lower and upper portions of mountainous slopes. The Brazilian cloud forests also deserve special attention, since to date very little is known about them.

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Second Article

Abundance Models of Tree-Species along an Elevational Gradient in the Brazilian Atlantic Forest

Submitted to *Biotropica*

ABSTRACT

We investigated tree-species abundance distributions (tree-SADs) along an elevational gradient on a mountainous slope in Southern Brazil that ranges from the Atlantic coastal rain forest (subtropical) to the cloud forest (humid temperate). Six plots (0.24-ha per site) were established at each elevation (≈ 220, 420 and 700 m asl), and structural features of the trees were measured. Five models were fitted to the data and communities were described using diversity measures and one approach to evaluate commonness and rarity. To select the best model we used three criteria (AIC, AIC_c, and BIC) along with Akaike weights and evidence ratios. There was a mid-elevation peak in tree-species richness, but total richness estimation indicated that the lower elevation is still richer in species. There was a continuous average of 30 ± 3 percent of rare species for each site over the complete gradient, but dominance increased monotonically with the increase in elevation. β-diversity values revealed constant species turnover rates throughout the gradient, though a strong drop in diversity occurred between the middle and upper sites. SADs shapes varied greatly along the gradient, and the selection criteria picked different models for all elevations as the best. Compared to model-averaged inference, best-model strategy was superior.

Key words: SADs; elevation; evenness; commonness and rarity; model selection; Akaike weights; evidence ratio.

RESUMO

Investigamos a distribuição de abundâncias de espécies (DAEs) arbóreas ao longo de um gradiente altitudinal em uma encosta montanhosa no Sul do Brasil, o qual se estende da floresta pluvial (clima subtropical) à floresta nebular (temperado úmido). Seis parcelas (0,24 ha por comunidade) por elevação (≈ 220, 420 e 700 m.s.n.m.) foram estabelecidas e a altura e o diâmetro das árvores mensurados. Cinco modelos de DAEs foram ajustados aos dados e as comunidades foram descritas usando medidas de diversidade e uma abordagem para avaliar a frequência de espécies comuns e raras. Para selecionar o melhor modelo foram utilizados três critérios (AIC, AIC_c e BIC) juntamente com pesos de Akaike e coeficientes de evidência. Foi encontrado um pico riqueza de espécies na elevação intermediária, mas a estimativa total de riqueza indicou que a elevação inferior é ainda mais rica em espécies. Foi encontrada uma média contínua de 30% ± 3% de espécies raras para cada comunidade ao longo do gradiente, mas a dominância aumentou monotonicamente com a elevação da altitude. Os valores de diversidade β revelaram uma taxa de substituição de espécies constante entre as comunidades, embora uma queda acentuada na diversidade tenha sido registrada entre as comunidades intermediária e a superior. As feições das DAEs variaram ao longo do gradiente, e os critérios de seleção indicaram diferentes modelos como o melhor para cada uma das elevações. Em comparação com a inferência com base na ponderação de modelos, a estratégia de melhor modelo foi superior.

SPECIES RICHNESS AND SPECIES ABUNDANCE DISTRIBUTIONS (SADs) comprise the two essential elements of biodiversity (Hubbell 2001). However, SADs enable more subtle comparisons and answers such as which community has a higher proportion of common or rare species rather than just informing which community is richer in species (McGill *et al.* 2007). When plotted as a rank-abundance plot on arithmetic scale (Whittaker 1965), SADs produce a specific hollow curve pattern in which most species are rare and relatively few species are abundant. This appears to be a universal pattern in multispecies communities (*e.g.*, Hanski 1982, Gaston 1994, McGill *et al.* 2007), and confirms earlier observations that most species are rare (*e.g.*, Preston 1948).

Environmental gradients provide a natural experiment or comparative basis for testing SADs theories about communities (McGill *et al.* 2006). Analyses of SADs along elevational (Whittaker 1960, 1975) and latitudinal gradients (Hubbell 1979), for example, have revealed a pattern of increasing evenness with productivity. McGill *et al.* (2007) pointed out that after these initial investigations few studies attempted to examine SADs models along environmental gradients. Communities across space commonly exhibit more or less marked β-diversity or species turnover rates, here defined as the rate or magnitude of change in species composition along predefined spatial or environmental gradients (Vellend 2001). Species turnover rate is an interesting feature because it allows insights on the mechanisms which structure communities; on the other hand, communities with few or no species in common are hard to compare. SADs, in contrast, allow for comparison of communities that have few or no species in common as in environment gradients, because abundance does not depend on the identity of the species (Wilson *et al.* 1996, McGill *et al.* 2007). Furthermore, assuming that the abundance of species reflects niche partitioning and competition for limited resources, SADs may help to shed light on the determining factors of biological diversity of a community (Magurran 2004).

Several models have been developed attempting to describe SADs, but their fit to empirical distributions varies greatly due to differences in types of organisms and ecological communities, variation in species abundances, and incomplete sampling. In a recent review, McGill *et al.* (2007) identified five main families of SADs models with over 40 members. From these, we selected broken-stick (MacArthur 1957), geometric series or niche preemption (Motomura 1932), lognormal (Preston 1948), Zipf (Zipf 1949) and Zipf-Mandelbrot (Mandelbrot 1977, 1982; Gray 1987).

The niche preemption model (hereafter "preemption") suggests that the first species is limited by the abiotic environment and subsequent species are limited mainly by competition (Wilson 1991). In the broken-stick the abundances reflect the partitioning of resources among competing species, by random divisions along a one-dimensional gradient. Lognormal distribution has been associated with communities in equilibrium (*e.g.*, May 1975, Sugihara 1980, Ugland & Gray 1982, Gray 1987, Tokeshi 1993), and it also predicts a low proportion of very rare species. The Zipf-Mandelbrot model applied to plant communities predicts that the presence of a species can be seen as dependent on previous physical conditions and previous species presences, the costs. Pioneer species have low cost, requiring few prior conditions, while late successional species have a high cost of energy, time, and organization of the ecosystem before they can invade (Wilson 1991). These cost differences between species result in Zipf or Zipf-Mandelbrot (hereafter "Mandelbrot") distribution (Frontier 1985).

Altitudinal gradients are among the most powerful 'natural experiments' for testing ecological responses of biota to environmental influences, such as low temperature (Körner

2007). Despite the advantages of testing SADs models along elevational gradients, since Whittaker's (1960, 1975) landmark studies few additional research has been done with SADs. In Brazil, studies with SADs are scarce (*e.g.*, Scudeller *et al.* 2001, Cielo Filho *et al.* 2002), and to our knowledge no study exists about SADs models along elevational gradients in the Brazilian Atlantic forest. By fitting the above named models to empirical data, we employed models that range from extreme dominance (preemption) to extreme evenness patterns (broken-stick), along with various diversity measures, to investigate evenness and niche diversification patterns and the possible influences of environmental constraints over SADs along an elevational gradient in the Brazilian Atlantic coastal rain forest.

METHODS

STUDY SITE. — The study was carried out on the eastern slope of the South Brazilian Plateau, which consists of the Serra Geral and Serra do Mar mountain ranges. Serra Geral is an interior mountain range that approaches the seashore in the southernmost Brazilian state (Rio Grande do Sul), where altitude varies from sea-level to more than 1,000 m asl on lateral displacements of only a couple of kilometers. The slopes therein represent an edge between the sea-level coastal plain and the inland plateau, exhibiting an elevational gradient of vegetation that ranges from the Atlantic coastal rain forest (subtropical) to a mosaic of *Araucaria* forest and grasslands (humid temperate). Between these two vegetation types there is also a discontinuous range of cloud forest that ranges from narrow belts to spots with variable width (Falkenberg & Voltolini 1995). There, on a mountainous slope (814 m asl) whose base is about 16.8 km away from the seashore, we studied a vegetation gradient ranging from the rain forest to the cloud forest.

The moist and bland subtropical climate of the coastal plain resulted in large occupation of the lowlands and submontane areas with tropical cultures, mainly banana and pineapple, leading to a drastic reduction of the forested areas near to the coast. As a result, there is probably no complete, natural and untouched gradient ranging from sea-level to mountaintops in subtropical Brazil, and the last slope forests remain precisely due to the very hard access to the areas where they are located.

Lithology is not uniform, varying from sedimentary (up to 180 m asl) to igneous extrusive rocks (≥ 180 m asl). The weathering of lava flows that originated the Serra Geral produced cliffs with nearly vertical faces, tall steps, and steep slopes, where natural landslides frequently occur. Soils are acid along the entire gradient, and podzolization and soil wetness increase markedly with elevation.

Although not daily, there is a frequent cloud cap whose lower limit is at ≈ 550 m. Below the cloud line trees are as high as 30 m, while above are not higher than 17 m. Above ≈ 750 m the medium stature forest gave way to a stunted cloud forest (6–8 m), and above 790 m there were only shrubs and grasses, albeit the slope top is connected to a massif that presents tall forests even at higher altitudes. With less individuals and species, trunks and crowns full of epiphytes and hemiepiphytes, the upper elevation (lower montane forest) is structurally and floristically distinct from the other elevation forests.

CLIMATE. —The mean annual temperatures are 18.9ºC at 220 m, 17.3ºC at 420 m, and 16ºC at 700 m, with a lapse rate of 0.57 ºC /100 m; annual precipitation increases with elevation from 1,700 to 2,045 mm, with no dry seasons; estimated mean annual occurrences of frost oscillate between 1(–3) events in lowland areas and up to 30 in highland areas (Nimer 1990).

DATA SET. —The survey was conducted from November 2008 to April 2010. Eighteen plots of 20 × 20 m, with minimum distance of 20 m between each other, were established on a ridge of the mountain for all elevations, six at each one (0.24-ha per site): lower (≈ 220 m — 29º38’49’’ S, 50º8’1’’ W), middle (≈ 420 m — 29º38’38’’ S, 50º8’12’’ W) and upper site (≈ 700 m — 29º38’25’’ S, 50º8’18’’ W). All trees > 5 cm diameter at breast height (dbh) were enumerated and dbh and total height of the trees were measured.

DIVERSITY MEASURES. —Communities were described under eight measures: (1) observed richness for each elevation (S_{obs}); (2) number of restricted species in each elevation (S_{restr}); (3) Chao 2 non-parametric richness estimator (S_{est}, Chao 1987); (4) Shannon index H’ converted to its effective numbers (${}^{q}D$, Jost 2006, 2007),

$$ {}^{q}D = \exp(H') $$

where *q* is the ‘‘order’’ or value of the exponent in the basic sum underlying the diversity index — order *q* determines a diversity measure’s sensitivity to rare or common species (Keylock 2005), and the point that weighs all species by their frequency, without favoring either common or rare species, occurs when *q* = 1, that corresponds to the H’ index; (5) shared richness for pooled pair of elevations (S_{shared}); (6) total richness for pooled pair of elevations (S_{pooled}); (7) β-diversity (β_{sim}, Lennon *et al.* 2001),

$$ \beta_{sim} = \frac{\min(b, c)}{\min(b, c) + a} $$

where *a* comprises the total number of species that occur in both quadrats (communities), *b* is the total number of species that occur in the neighboring quadrat but not in the focal one, and *c* is the total number of species that occur in the focal quadrat but not in the neighboring one (Koleff *et al.* 2003); and (8) the drop ratio in diversity between communities (${}^{q}D_{ratio}$),

$${}^{q}\mathrm{D}_{\mathrm{ratio}} = \exp(\mathrm{H}') \,/ \exp\,(\mathrm{H}')$$

where ${}^{q}D_{ratio}$ is the ratio of drop in diversity ${}^{q}D$ for pooled pairs of elevations.

The shape of SADs curves contains information on the commonness and rarity of species, but since these are relative concepts and there is no sharp boundary between them, it is necessary to apply some definition to provide a boundary. We selected the Novotný and Basset (2000) approach, where singletons were regarded as rare, the same number of species from the upper end of the SAD as common, and the remainder as intermediate. The values obtained for each class were used to assess the proportion of individuals pertaining to each class.

THEORETICAL MODELS. —Rank/abundance data were plotted for each community using packages *BiodiversityR* (Kindt & Coe 2005) and *vegan* (v1.17.3, Oksanen *et al.* 2010) of the statistical software R (v2.11.1, R Development Core Team 2010). Broken-stick, preemption, lognormal, Zipf, and Mandelbrot models were fitted, mainly following Wilson (1991).The main features of the fitted models are described below, according to Oksanen *et al.* (2010). The Broken-stick gives a null model where the individuals are randomly distributed among observed species, and there are no fitted parameters. The preemption model estimates only one parameter, the preemption coefficient α, which gives the decay rate of abundance per rank. The lognormal model assumes that the logarithmic abundances of species are distributed according to a normal curve. The Zipf model has two parameters, p1 (the fitted proportion of the most abundant species) and γ (a decay coefficient). The Mandelbrot model adds the p2 (β) parameter to the Zipf model, that substitutes p1 changing it into a scaling constant c.

SELECTION CRITERIA. —Extensive discussions result from the attempt to decide which should be the best model selection criterion, especially between the two most commonly used, the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) (*e.g.,* Weakliem 1999, Burnham & Anderson 2002, 2004). However, useful information for model selection can be obtained from using AIC and BIC together, particularly when attempting to find models favored by both (Kuha 2004). We used both criteria and also AIC second-order bias correction (AIC_c), because sample size influences AIC values so that AIC_c compensates for bias due to small sample size (Burnham & Anderson 2002, 2004). As sample size affects the values of the criteria, we assessed sample size influence on the fittings by calculating the AIC_c values for each model using 2, 3, 4, 5, and 6 plots for each community, and afterward plotting the values against increasing sample sizes.

Models were analyzed with the data at hand and it was expected that the results would tend to support one or more hypotheses while providing less support for others. Models were compared to each other and the one with the lowest value was considered the best fit to the data. The individual AIC, AIC_c and BIC values are not interpretable as they contain arbitrary constants and are largely affected by sample size (Burnham & Anderson 2002). Thus, when evaluating models, differences between criteria values (Δ_i) is the determining factor (Burnham & Anderson 2002, Bolker 2008). Accordingly, AIC, AIC_c and BIC individual values were rescaled to

$$\Delta_i(C) = C_i - C_{min}$$

where C_i corresponds to the criterion and C_{min} is the minimum of the set of models for each C_i values, so that the model with the minimum value has $\Delta_i = 0$ (Burnham & Anderson 2002, 2004; Bolker 2008). The larger Δ_i, the less plausible the fitted model *i* as best approximation in the candidate set (Burnham & Anderson 2004). There are similar rules of thumb for AIC and BIC: Models having $\Delta_i \leq 2$ are more or less equivalent; Δ_i between 4 and 7 are clearly distinguishable; and $\Delta_i \geq 10$ are categorically different (Raftery 1996, Burnham & Anderson 2004, Bolker 2008). To a practical purpose, $\Delta_i < 2$ can be viewed as a threshold of improvement in fit.

The ranking of the candidate set of models suggests a primary inference level using the model with the minimum value or a small number of models with an essential tie for the minimum value (*i.e.*, $\Delta_i < 2$). When there was model selection uncertainty, AIC_c weights (ω_i) and evidence ratio provided a second inference level. To extract the ω_i values we used the *qpcR* Package (Ritz & Spiess 2008) from the statistical software R. The ω_i provide a ranking of the models and allow determining which model is best, which are tied for best, and which models are clearly inferior (Burnham & Anderson 2002). The bigger Δ_i, the smaller ω_i, and the less plausible model *i*. When the selected model was not convincingly best, evidence ratios allowed a formal chain of evidence for alternative hypotheses. The ratio was obtained dividing the higher ω_i value by the second higher ω_i value in the ranking, resulting in an evidence ratio between the best fit against the second ranked model.

The set of models were fitted specifically for each data set (*i.e.*, for each community), and selection criteria were compared within each data set because the inference depended on the available data. Models were computed starting with the simpler model and proceeding to the more complex ones (more parameters).

RESULTS

All forests were relatively tree-species rich (Table 1), but there was a mid-elevation peak in species richness corresponding to 77 percent of the richness for the entire gradient (S_{obs} = 109 spp.). Despite the mid-elevation peak, the S_{est} values confirm that if we had captured the total richness for the gradient, species richness would decrease monotonically with the increase in elevation. Diversity values (^{q}D) were similar between the lower and middle elevations, but decreased greatly in the upper elevation. An appraisal of pooled pairs of communities showed that the richness shared by the lower and middle sites was around twice as big then the richness for the lower and upper sites pooled. β-diversity (β_{sim}) values were analogous for contiguous elevations, but much higher between the extremes of the gradient. While β_{sim} relies on the difference in species composition and reflects gains and losses between sites, $^{q}D_{ratio}$ captures the true percentage of diversity decrease between sites. The greatest drop, as expected, occurred between the richest and the poorest sites, *i.e.*, the middle and upper sites.

TABLE 1. *Diversity measures along the elevational gradient in the Serra Geral mountain range, Southern Brazil.* S_{obs} *= observed richness;* S_{restr} *= number of restricted species;* S_{est} *= estimated richness given by Chao2;* ^{q}D *= diversity as effective numbers of species (Jost 2006);* S_{shared} *= shared species richness;* S_{pooled} *= species richness for pooled pairs;* β_{sim} *= beta diversity; and* $^{q}D_{ratio}$ *= drop ratio in diversity (%).*

	Single community				**Pooled pairs of communities**				
Elevation	S_{obs}	S_{restr}	S_{est}	^{q}D	**Pair**	S_{shared}	S_{pooled}	β_{sim}	$^{q}D_{ratio}$
Lower[1]	71	15	137.1	36.0	**1–2**	56	99	0.211	6.0
Middle[2]	84	16	104.3	38.3	**1–3**	25	93	0.468	63.8
Upper[3]	47	10	57.9	13.0	**2–3**	37	94	0.213	66.0

A total of 23% of the 109 species occurred along the entire gradient, while a portion of 20.5 ± 1.3 percent of the S_{obs} for each community were restricted to one site (S_{restr}). There were no shared species between the lower and upper forests that did not occur at the middle forest, and we found a low variation in the total richness for pooled pairs of elevations (S_{pooled}).

The 27 most abundant species (≥15 individuals) represented 80 percent of the 1,721 sampled individuals and 25 percent of the total richness. From these, 13 species were abundant along the entire gradient, 11 occurred only in the lower and middle communities or presented only one occasional individual in the upper community (four species), and three were limited to the middle and upper communities.

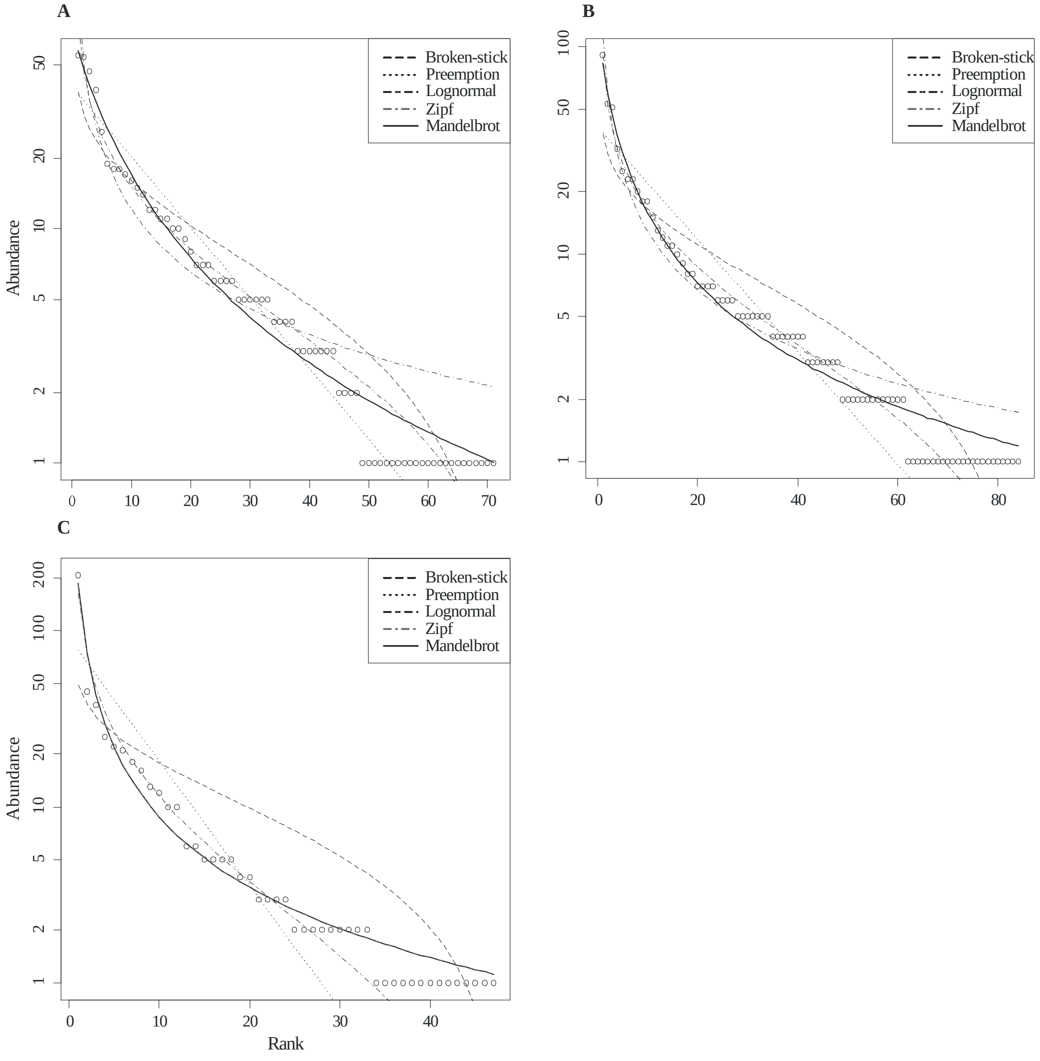
The commonness and rarity approach seemed natural because singletons, by definition, were all included as rare (Table 2). Each community had many singletons and hence many rare and common species, but because all communities were species-rich, the species included in the intermediate abundance class resulted more numerous for all elevations. The lower and upper limits of the intermediate class were quite equal for the communities, but the upper limit for the common species class (maximum abundance) showed an increasing dominance with the increase in elevation. Taking into account S_{obs} for each community, there was a continuous average of 30 ± 3 percent of rare species all over the gradient.

SADs shapes varied greatly along the gradient, with hollower curves and an expanding tendency toward a long tail of successively minor species with increasing elevation (Fig. 1). There was a negative correlation between elevation and evenness. Mandelbrot parameter β revealed this reduction in equality from the lower ($\beta = 9.88$), middle ($\beta = 2.72$), to the upper elevation ($\beta \leq 0$), visually represented by a more shallow slope on the rank-abundance plot for higher β values (Fig. 1).

TABLE 2. *Commonness and rarity of species along an elevational gradient in Serra Geral mountain range, Southern Brazil, following Novotný and Basset (2000). S = species richness in each class; Interval = number of individuals comprising each class.*

	Lower		Middle		Upper	
Class	S	Interval	S	Interval	S	Interval
Rare	23	1	23	1	14	1
Intermediate	25	2–6	38	2–6	19	2–5
Common	23	7–55	23	7–91	14	6–207
Total	**71**	**564**	**84**	**636**	**47**	**521**

FIGURE 1. Species abundance distributions (SADs) along an elevational gradient in Serra Geral mountain range, Southern Brazil, and fitted models: Broken-stick, preemption, lognormal, Zipf, and Mandelbrot. (A) Lower elevation, (B) middle elevation, and (C) upper elevation.



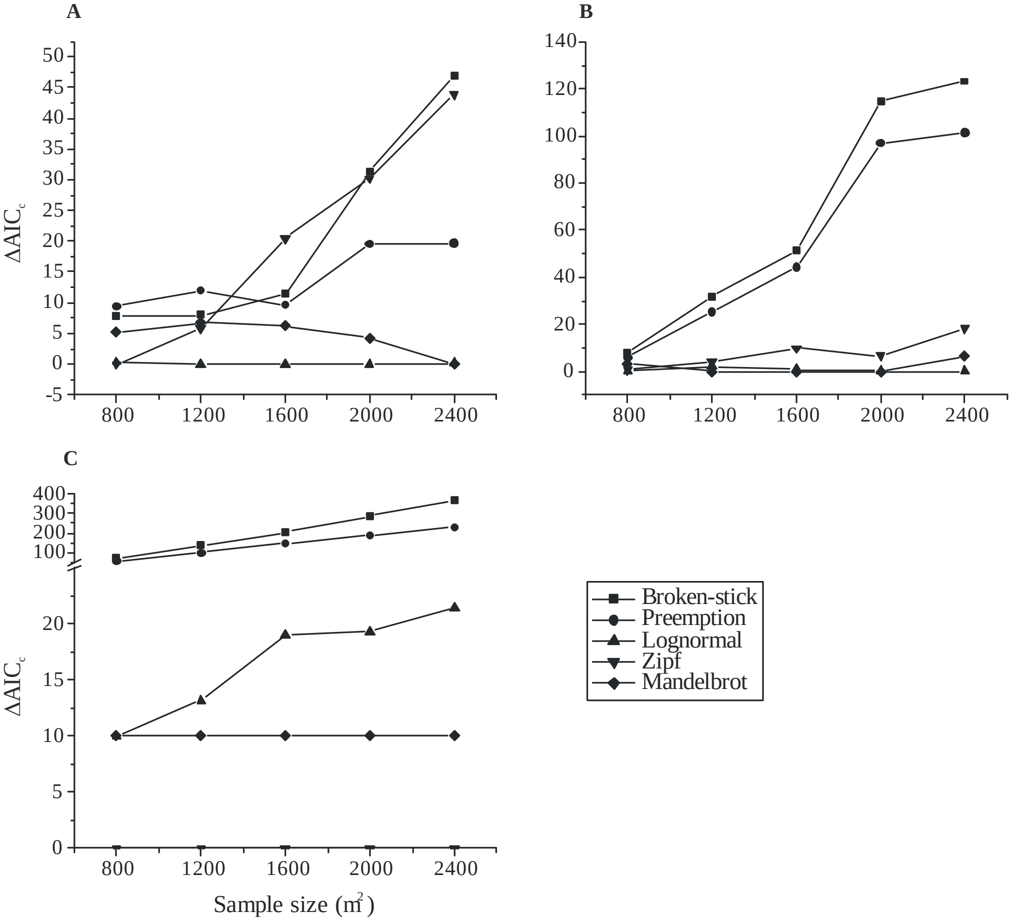
When attempting to select the best model, AIC, AIC_c and BIC picked different ones (Δ_i) (Table 3). Broken-stick and preemption models clearly did not fit the data, independently of the criteria used, while the other models showed distinct quality of fit to the communities. In general, AIC_c results were dissimilar from those of AIC and BIC. For the middle and upper sites, for instance, AIC_c was the only criterion which presented values that put all models as clearly distinguishable ($\Delta AIC_c > 4$), while for the lower site the opposite was true. High model selection uncertainty resulted in both lognormal and Mandelbrot selected for the lower site. Lognormal was the best fit for the middle site, whereas Zipf resulted as the best model under all criteria for the upper site.

TABLE 3. *Akaike's Information Criterion (AIC), Akaike's second-order corrected Information Criterion (AIC_c), and Bayesian Information Criterion (BIC) minimum values (Δ_i) for the set of models fitted, along with Akaike weights (ω_i) extracted from AIC_c values. df = degrees of freedom, who match the number of parameters of each model; Δ_i correspond to the differences, were each criteria value is subtracted from the smallest respective criteria value in the set of models.*

		Lower elevation				**Middle elevation**				**Upper elevation**			
Model	df	ΔAIC	ΔAIC_c	ΔBIC	ω_i	ΔAIC	ΔAIC_c	ΔBIC	ω_i	ΔAIC	ΔAIC_c	ΔBIC	ω_i
1. Broken-stick	0	58.89	46.89	52.1	0.000	128.78	123.19	122.33	0.000	371.38	367.38	367.68	0.000
2. Preemption	1	30.67	19.67	26.14	0.000	105.93	101.34	101.91	0.000	232.96	229.96	231.11	0.000
3. Lognormal	2	8.14	0.14	5.88	0.483	1.6	0.00	0.00	0.961	21.49	21.49	21.49	0.000
4. Zipf	2	51.93	43.93	49.67	0.000	19.87	18.27	18.27	0.000	0.00	0.00	0.00	0.982
5. Mandelbrot	3	0.00	0.00	0.00	0.518	0.00	6.40	0.83	0.039	0.00	8.00	3.85	0.018

Sample size influenced on the fittings of the models, as represented by the ΔAIC_c values calculated for increasing sample sizes (Fig. 2). The lower site gave a good example on how the best fit model changed with increasing sample size. It began giving support to the Zipf and lognormal models, while others were rejected. With increasing sample size Zipf deviated while lognormal continued as the best model until the last plot was added, when Mandelbrot converged and they became equivalent. Fig. 2b and 2c show the sample size influence on the fittings of the models for the middle and upper sites.

FIGURE 2. Sample size (m^2) vs. ΔAIC_c values for the fitted models: Broken-stick, preemption, lognormal, Zipf, and Mandelbrot. As plots were added one by one, ΔAIC_c values were calculated for the fitted models and the resulting values were plotted against sample size (m^2). (A) Lower elevation, (B) middle elevation, and (C) upper elevation.



Evidence ratios assisted to shed light on differences in the ΔAIC_c values (Table 3). For Mandelbrot vs. lognormal, evidence ratio was about 1 for the lower site (*i.e.*, $\omega_5/\omega_3 = 1.07$), a relatively weak support for the best model. Evidence ratio for the best model (lognormal vs.

Mandelbrot) in the middle site was relatively high ($\omega_3/\omega_5 = 24.6$). In the upper site the Zipf vs. Mandelbrot evidence ratio was convincingly strong against the latter ($\omega_4/\omega_5 = 54.55$), also corroborated by Fig. 1c.

DISCUSSION

Evidence suggests that although diversity may decrease with increasing elevation (*e.g.*, Beals 1969, Vázquez & Givnish 1998), this pattern is not uniform (Rahbek 1995). Several papers present a well-documented mid-elevation peak in species richness (*e.g.*, Terborgh 1977, McCoy 1990). Rahbek (1995) suggested that this mid-elevation peak lacking in many other studies may be due to a failure to study complete gradients or to account for sampling effort or sample area. We have found a mid-elevation peak, but S_{est} for each community suggests a pattern of decreasing richness with increasing elevation. Considering that there are no more complete gradients in the eastern border of the Serra Geral mountain range, Rahbek's proposition, despite not supported, is not contradicted either. But if the lowland forests, currently lacking, were taken into account, the middle of the gradient would coincide with some point of the lowlands, thus corroborating Rahbek's suggestion in our study.

β_{sim} seized how different each elevation was, in terms of species composition, from the other elevations, and ${}^{q}D_{ratio}$ captured the true percentage of drop in diversity between sites. The related values of β_{sim} between neighboring sites indicate a continuous species turnover along the gradient, but the index did not capture the drop in diversity, which was even greater between the middle and upper sites (${}^{q}D_{ratio} = 66\%$) than between both tails of the gradient (${}^{q}D_{ratio} = 63.8\%$). This great drop in diversity between middle and upper sites will be discussed subsequently.

Brown (1984) proposed that the abundance of most species is greatest near the center of the range of its distribution and declines toward the boundaries. He interpreted this as the result that the more abundant and widespread species have broader range of resources. Widespread species have also greater tolerance to a wider range of environmental conditions, such as on elevational gradients (*e.g.*, Whittaker 1956, 1960, 1965). In our study, only half of the most abundant species had such a broad range of resources and of tolerance to the environmental changes throughout the gradient. The species that can tolerate wide variation in one factor (we suppose it would be mainly temperature) also tend to be tolerant of other factors, and hence to be both locally abundant and spatially widespread (Brown 1984). The remnant of the most abundant species was restricted chiefly to the lower and middle communities. There were four times more abundant species in the lower and middle communities than in the upper one, and hence it is suggested that the environmental conditions in the lower/middle communities are less constraining than those in the last. Moreover, possibly the center of true original gradient (considering lowlands at the sea-level to the highlands) was located closer to the lowlands or in fact on them.

We found two important constants over the entire gradient, the average percentages of rare species (singletons) and of species restricted to one elevation (S_{restr}). Nevertheless, we do not suppose that these species are rare or restricted in a regional scale. Instead, we suppose they are rare and have a restricted distribution along the gradient since seemingly only narrow ranges of environmental conditions meet the conditions they require to survive and reproduce.

As climate variables seem to be the major ones to describe differences in species richness with elevation (*e.g.*, Körner 1995, Pendry & Proctor 1996), we suggest some factors that would help to explain the SADs we found. Pendry and Proctor (1996), studying a small mountain with evergreen rain forest in Brunei, found that the lower montane forest, relative to the lowland, was not adversely affected by winds, drought or water logging, high soil acidity or nutrient limitation, and concluded that the observed changes in forest structure and species composition were due to the lower temperatures at the higher altitude. Even though temperature differences were not great, they concluded that at least some tropical trees were very sensitive to this factor. As most tree-species that occur in the Brazilian subtropical region are tropical species (*e.g.*, Rambo 1961), and more than half of the species were restricted to the lower and middle communities, possibly some of these species could also be very sensitive to lower temperatures in the Serra Geral gradient.

Frosts represent an additional biologically meaningful climate parameter (Holdridge *et al.* 1971, Grubb 1974). Torres *et al.* (1997), for instance, found a floristic differentiation between coastal and interior regions in the Brazilian state of São Paulo and concluded that it resulted mainly from the number of frost occurrences and precipitation level. The variation in the number of frost occurrences between the areas they studied (> 600 km between the extremes) is lesser then the variation between the lower and upper communities in the gradient where our study was located (< 2 km). Frost occurrences are very rare in the lowlands and submontane areas of our investigated region, as evidenced by the presence of tropical cultures that are very sensitive to frosts and low temperatures. Differently, in some points of the South Brazilian Plateau frosts can exceed 30 events per year (Falkenberg & Voltolini 1995).

Additional aspects that need to be taken into account are the reduced amount of radiation available for photosynthesis, the high atmospheric humidity, and the excessive soil wetness within the cloud cap, conditions that might depress the growth of some species (Grubb 1974, 1977). Within the cloud cap (in the upper site), compared to the lower community, the maximum tree-height was 65% lower. It seems plausible that the cloud cap effects, along with the high number of frosts and lower temperatures, could be operating as strong environmental constraints for many tropical species and could thus be the main cause of the great drop in diversity from the middle to the upper site.

The regular lower limit of abundance for common species at all sites roughly coincided with the steepness point where the SAD curves became smoother (Fig. 1; Table 2). This steepness with which abundances decline from the most abundant species to the least abundant ones within a community has attracted much attention (Tokeshi 1993). Novotný and Basset (2000) "singleton-based definition" accurately identified the point at which the SAD curves become steeper, at least in our sites. Since there are no absolute definitions for commonness and rarity (Magurran 2004), this approach offers helps to analyze SADs.

The model fittings provided some general information on the degree of equality and niche diversification along the elevational gradient. Broken-stick and preemption represented extremes of evenness and dominance which did not fit the data. Despite the fact that dominance increased with elevation, the ruling out of these models proved that extremes of dominance and evenness did not occur along the gradient. Different studies demonstrated that more complex habitats produced SADs with higher evenness (*e.g.,* Cotgreave & Harvey 1994, Cielo Filho *et al.* 2002). In our data, the Mandelbrot parameter β, which represents the degree of niche diversification (Frontier 1985, Wilson *et al.* 1996) and a measure of evenness, decreased from the lower toward the upper community. As the lower site had the lesser degree of dominance by the most abundant species, it is also probably the more niche-diversified site, followed by the middle and then by the upper site. To some extent, we associate Mandelbrot and lognormal, which represented the best fit for the lower (both models) and middle sites (lognormal), with higher levels of evenness and niche diversification, while we relate Zipf, which was the best fit for the upper site, with lesser levels of the same parameters.

When there is high ambiguity in the model selection, as was the case for the lower elevation, Burnham and Anderson (2002) suggest that one should expect a lot of variation from sample to sample in the selected best model when multiple independent samples were possible. Although our samples were not indeed independent, the more samples we added, the greater the uncertainty in model selection for this particular data set (Fig. 2a). This inability to detect a single best model was an indication that at least the data of the lower community were inadequate for a strong inference (Burnham & Anderson 2002, 2004).

Lognormal and Mandelbrot are set by contrasting assumptions; the former is seen as the result of many factors acting simultaneously on the species, and the later as the result of many factors acting sequentially (Wilson 1991). The lower community had higher evenness and higher niche diversification. Total richness estimation (S_{est}) for this site predicted that we had found only half of the species richness (relatively, the S_{obs} stands for ≈ 80 percent of the S_{est} for the middle and upper sites), which meant that several rare species were not sampled. As the lognormal distribution predicts a low proportion of very rare species, it would be expected that a sample size increase would result in a Mandelbrot distribution. On the other hand, in several situations the lognormal distribution gave a very good approximation to Zipf's law, implying that stochastic processes can lead to a zipfian distribution (Silagadze 1997). Further studies are necessary to elucidate this issue.

Frontier (1985) assumed that it is possible to connect the shape of SAD curves with the degree of "maturity" of an ecosystem, where higher levels of energy, time, and organization of the ecosystem mean more mature (or structured) communities. As a consequence of the steeper

SADs curve and, therefore, of the greater dominance than the other sites, the upper site, fitted by a Zipf distribution, seemed “less mature”. As we argued above, there are probably stronger environmental constraints influencing the upper community. Accordingly, we conjecture that the Zipf model would fit well in those communities where environmental constraints play an important role, but only in the absence of extremes of dominance.

CONCLUSIONS

A mid-elevation peak of S_{obs} was found in the studied area, but the S_{est} indicated that as observed in evenness it would reach its peak in the lower elevation, or possibly below, if we had studied the complete gradient. As no complete gradients are available in the eastern border of the Serra Geral anymore, the hump-shaped pattern envisioned by Rahbek (1995) for these situations is not contradicted either.

Environmental constraints apparently were responsible for the great drop in diversity from the middle to the upper community. On the other hand, our data suggest that the SADs with higher evenness in the lower and middle communities resulted from weaker environmental constraints and higher niche diversification. We suggest also that many tropical species are very sensitive to little temperature changes and to frost occurrences.

With respect to model selection, Burnham and Anderson (2004) pointed that the use of AIC when AIC_c really should be used is a pervasive mistake in the literature. We concluded that AIC_c provided better responses than AIC, and BIC too. When models were selected by good or bad fit using the ΔAIC_c values, Akaike weights and evidence ratios the SADs allowed establishing a relationship between some assumptions of the models and the observed patterns.

This does not mean the assumptions of the models can be accepted, but instead that the models cannot be discarded and empirical and/or experimental analysis on niche apportionment and environmental constraints are necessary for a better understanding of the shape of the SADs patterns along the gradient.

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CONCLUSÃO GERAL

Muitas são as questões levantadas ao longo desta tese, e outras tantas surgiram ou poderão surgir a partir dela. Todo aquele que já subiu a pé pelas florestas das encostas orientais do Planalto Sul-Brasileiro (Serra Geral), desde o nível do mar até os mosaicos de campos e florestas com araucária, pôde observar diferenças notáveis na composição e na estrutura das florestas ao longo do gradiente altitudinal. As diferenças existem, não restam dúvidas, mas o difícil é separá-las e caracterizá-las.

Acredito que o primeiro artigo respondeu à questão se existem tipos vegetacionais. Através da análise de agrupamento difuso e da ordenação confirmou-se a existência de dois grupos, um mais associado às terras baixas e áreas de encosta próximas a elas, e outro mais fortemente associado às áreas de encosta montanas e ao platô. Contudo, surge a questão: E se fossem amostradas mais faixas ao longo do gradiente e com um esforço amostral maior (mais parcelas), manter-se-iam os mesmos grupos? Arrisco dizer que provavelmente sim, pois os dados e as evidências sugerem que a cobertura nebular produz de fato condições diferenciadas e que são limitantes para o crescimento de grande parte das espécies arbóreas registradas ao longo do gradiente. No curto trecho entre 550 e 800 msnm é possível perceber como a floresta tropical vai dando lugar a uma floresta cada vez mais baixa e menos estratificada, até se converter apenas em arbustos e gramíneas (vide figuras em anexo). A substituição dos palmiteiros (*Euterpe edulis*) pelos samambaiaçus (*Alsophila setosa*), xaxins (*Dicksonia sellowiana*) e bambus (*Chusquea mimosa*) é outra característica muito marcante. As diferenças mais marcantes entre a vegetação que denominei de “terras baixas” e a vegetação “montana” foram as seguintes:

1. Uma diminuição brusca na diversidade, que cai quase pela metade da comunidade intermediária (≈ 420 msnm) para a comunidade superior (≈ 700 msnm);
2. Diferenças significativas na H média;
3. Diferenças significativas no DAP máximo;
4. Diferenças significativas em boa parte dos parâmetros de solo analisados;
5. Presença de solos eutróficos nas comunidades inferior e intermediária e de solos distróficos e tóxicos na comunidade superior.

Com relação às medidas de diversidade, os estudos mais suscitaram dúvidas do que contribuíram para elucidar os padrões de riqueza e abundância ao longo do gradiente. Os dados amostrados indicaram um pico de riqueza na comunidade intermediária, enquanto que a riqueza estimada indicou uma riqueza mais elevada para a comunidade inferior. Visto que deve se considerar a totalidade do gradiente como aquele compreendendo as florestas de terras baixas até as florestas no alto do platô, é possível, e até provável, que as estimativas de riqueza estejam corretas. Contudo, essa discussão e a falta de consenso permeiam toda a literatura sobre gradientes altitudinais, mas o que tem se dito é que é possível que os mecanismos que controlam as variações altitudinais se devam amplamente a efeitos de escala.

Quanto aos raros gradientes completos, o que se observa no limite sul da floresta atlântica costeira no Brasil é o mesmo que se observa em outras áreas montanhosas no mundo, onde as regiões mais baixas são afetadas pela colonização e exploração dos recursos naturais, e as zonas mais elevadas com campos estão sujeitas ao pastejo e às práticas antropogênicas de usar fogo para manter a vegetação campestre e assim impedir o crescimento da vegetação florestal. Desse modo, os extremos dos gradientes na maioria das vezes estão ausentes das análises simplesmente por não existirem mais.

A simples constatação ao longo deste estudo de que as áreas de florestas de terras baixas ou de encosta próximas a estas compreendem os segmentos com a diversidade mais elevada no limite sul da floresta atlântica mostra uma necessidade premente de conservação e também de restauração de alguns trechos nestas áreas. Uma alternativa interessante, por exemplo, seria aumentar os limites da Reserva Biológica da Serra Geral, de modo a incluir algumas das encostas voltadas para o oceano. Estas florestas, incluindo boa parte da área do presente estudo, encontram-se atualmente desprotegidas. Programas de conservação e de restauração dos remanescentes de terras baixas e das porções inferiores das encostas de floresta atlântica costeira deveriam estar entre as medidas mais urgentes nas atuais políticas públicas. Mas o que verdadeiramente se observa é que as áreas com menor diversidade (no presente estudo a comunidade superior) são aquelas mais isoladas e protegidas, enquanto que as áreas mais diversas (comunidade intermediária e inferior) são as mais próximas a áreas populosas e, portanto, mais desprotegidas. Levando em consideração que comunidades com muitas espécies raras requerem áreas maiores para preservar a diversidade local, esse é um problema que merece mais atenção. Resumindo, é urgente criar unidades de conservação de floresta atlântica de terras baixas no limite sul desta formação, ou seja, no Litoral Norte do Rio Grande do Sul e no Litoral Sul do Estado de Santa Catarina.

Relativo aos padrões de equabilidade e diversidade de nichos ao longo do gradiente altitudinal foi observado um decréscimo monotônico tanto na equabilidade como na diversidade de nichos com a elevação da altitude. Os resultados sugerem que isso se deva a fatores ambientais restritivos, em especial temperatura e ocorrência de geadas. As características internas na cobertura nebular também produzem condições desfavoráveis ao desenvolvimento das plantas. As condições mais restritivas e homogêneas encontradas na comunidade superior sugerem de fato uma menor diversificação de nichos e, daí, a menor equabilidade, as quais se refletiram no ajuste das curvas de DAEs e também no melhor modelo para esta comunidade. Os modelos selecionados para as demais comunidades também corroboram os aspectos acima mencionados.

O uso de seleção de modelos e de critérios de seleção em trabalhos de ecologia tem se mostrado cada vez mais amplo. Neste trabalho espero ter contribuído para difundir esse método que se mostra muito promissor para todas as áreas, da ecologia à evolução. O mesmo pode ser dito do método de agrupamento difuso, que merece mais atenção por ser muito mais realístico e promissor do que os demais métodos de agrupamento. O que ambos têm em comum, seleção de modelos com base em critérios de informação e agrupamento difuso, é que tratam de aproximações da realidade e não respostas “certas” e “erradas” como em testes de hipóteses e em métodos de agrupamento rígidos.

Por fim, sugerem-se tópicos que podem representar rumos na continuação desta pesquisa:

1. Faltam estudos sobre a composição, a estrutura e as variáveis ambientais que caracterizam a floresta nebular. Não existe nenhum consenso ou qualquer tipo de delimitação do que exatamente diferencia uma floresta nebular no Brasil das demais florestas de encosta ou das florestas com araucária.

2. São necessários estudos mais completos e amplos em gradientes altitudinais, com mais faixas amostrais e com um esforço amostral mais elevado, para daí corroborar, complementar ou mesmo refutar os dados por ora apresentados.

3. É preciso que se faça uma investigação baseada em dados quali-quantitativos que preencha as lacunas e problemas relativos à atual classificação da vegetação brasileira, a começar pelas florestas sul-rio-grandenses, em especial a mata atlântica. Algumas críticas têm sido feitas, mas até o momento não há nenhum estudo específico que tenha confrontado a classificação existente com dados quantitativos e análises adequadas. Trata-se de um aspecto fundamental.

ANEXOS

TABLE 1. Species abundances along the elevational gradient in Maquiné (RS), with their respective families, distributions, and forest strata in which they occurred. **Forest strata: CAN** = Canopy; **SUB** = Sub-canopy; **UND** = Understory. **Distribution: L** = Lower community; **M** = Middle community; **U** = Upper community; **LM** = Lower and Middle communities; **MU** = Middle and Upper communities; **LMU** = Lower, Middle and Upper communities.

Family	**Species**	**Abundance**				
		220 m	**420 m**	**700 m**	**Distr.**	**Strata**
Annonaceae	*Annona cacans*	0	2	0	M	CAN
	Annona rugulosa	1	1	0	LM	UND
Apocynaceae	*Aspidosperma olivaceum*	1	0	0	L	CAN
Aquifoliaceae	*Ilex paraguariensis*	0	2	5	MU	CAN
Araliaceae	*Oreopanax fulvus*	0	2	0	M	UND
	Schefflera morototoni	4	1	0	LM	CAN
Arecaceae	*Euterpe edulis*	55	91	12	LMU	UND
Bignoniaceae	*Handroanthus pulcherrimus*	1	0	0	L	SUB
Boraginaceae	*Cordia ecalyculata*	0	0	2	U	CAN
Cardiopteridaceae	*Citronella paniculata*	3	0	0	L	SUB
Celastraceae	*Maytenus glaucescens*	1	1	0	LM	CAN
Chrysobalanaceae	*Hirtella hebeclada*	15	3	0	LM	SUB
Clusiaceae	*Garcinia gardneriana*	10	10	0	LM	UND
Cunoniaceae	*Lamanonia ternata*	1	7	2	LMU	SUB
Cyatheaceae	*Alsophila setosa*	0	53	207	MU	UND
Elaeocarpaceae	*Sloanea monosperma*	5	5	0	LM	CAN
Euphorbiaceae	*Alchornea triplinervia*	1	4	0	LM	CAN
	Gymnanthes concolor	39	15	0	LM	UND
	Pachystroma longifolium	7	0	0	L	CAN
	Sapium glandulosum	0	4	2	MU	SUB
	Tetrorchidium rubrivenium	0	4	0	M	CAN
Fabaceae	*Albizia edwallii*	0	1	0	M	CAN
	Erythrina falcata	1	1	0	LM	CAN
	Inga marginata	1	0	0	L	UND
	Inga sessilis	5	0	0	L	SUB
	Lonchocarpus cultratus	0	1	0	M	CAN
	Ormosia arborea	4	0	0	L	SUB
Lauraceae	*Aiouea saligna*	4	1	1	LMU	SUB
	Cinnamomum glaziovii	5	2	3	LMU	CAN
	Cryptocarya aschersoniana	0	0	1	U	CAN
	Endlicheria paniculata	0	2	1	MU	UND
	Nectandra megapotamica	5	11	1	LMU	CAN
	Nectandra oppositifolia	3	5	0	LM	CAN
	Ocotea catharinensis	0	2	3	MU	CAN

Family	**Species**	**Abundance**			**Distr.**	**Strata**
		220 m	**420 m**	**700 m**		
	Ocotea indecora	2	3	10	LMU	SUB
	Ocotea silvestris	1	7	5	LMU	SUB
	Ocotea urbaniana	0	2	2	MU	CAN
Magnoliaceae	*Magnolia ovata*	6	3	0	LM	CAN
Malvaceae	*Luehea divaricata*	1	1	0	LM	CAN
Melastomataceae	*Leandra dasytricha*	1	0	0	L	UND
	Miconia latecrenata	0	1	0	M	UND
	Miconia pusilliflora	0	1	2	MU	UND
Meliaceae	*Cabralea canjerana*	18	13	38	LMU	CAN
	Guarea macrophylla	0	1	0	M	UND
	Trichilia claussenii	17	4	0	LM	SUB
	Trichilia lepidota	3	5	0	LM	CAN
Monimiaceae	*Hennecartia omphalandra*	19	3	0	LM	SUB
	Mollinedia schottiana	18	18	6	LMU	UND
Moraceae	*Brosimum glaziovii*	7	0	0	L	CAN
	Ficus cestrifolia	1	1	0	LM	CAN
	Ficus luschnathiana	0	0	1	U	CAN
	Sorocea bonplandii	47	20	13	LMU	UND
Myristicaceae	*Virola bicuhyba*	11	1	0	LM	CAN
Myrtaceae	*Calyptranthes grandifolia*	11	6	18	LMU	SUB
	Eugenia bacopari	2	0	0	L	UND
	Eugenia handroi	0	0	2	U	CAN
	Eugenia multicostata	3	6	6	LMU	SUB
	Eugenia rostrifolia	6	7	0	LM	CAN
	Eugenia subterminalis	0	2	21	MU	SUB
	Eugenia verticillata	2	6	22	LMU	UND
	Myrceugenia foveolata	0	1	0	M	UND
	Myrceugenia glaucescens	0	3	0	M	UND
	Myrceugenia miersiana	0	1	2	MU	UND
	Myrceugenia myrcioides	0	0	1	U	UND
	Myrceugenia oxysepala	0	0	1	U	UND
	Myrcia aethusa	16	5	0	LM	SUB
	Myrcia glabra	0	1	0	M	SUB
	Myrcia tijucensis	14	25	1	LMU	SUB
	Myrcia pubipetala	12	18	0	LM	SUB
	Myrciaria delicatula	0	1	0	M	SUB
	Myrciaria floribunda	0	0	3	U	CAN
	Myrciaria plinioides	9	5	0	LM	UND
	Neomitranthes gemballae	6	2	0	LM	SUB
	Plinia brachybotrya	1	2	2	LMU	SUB
Nyctaginaceae	*Guapira opposita*	26	32	10	LMU	SUB
	Pisonia zapallo	7	2	0	LM	SUB

Family	**Species**	**Abundance**			**Distr.**	**Strata**
		220 m	**420 m**	**700 m**		
Ochnaceae	*Ouratea parviflora*	1	0	0	L	UND
Phyllanthaceae	*Hieronyma alchorneoides*	1	6	0	LM	CAN
Primulaceae	*Myrsine guianensis*	3	4	0	LM	SUB
	Myrsine hermogenesii	1	2	0	LM	SUB
	Myrsine loefgrenii	1	0	0	L	UND
	Myrsine lorentziana	1	5	5	LMU	SUB
Proteaceae	*Roupala brasiliensis*	5	2	0	LM	CAN
	Roupala rhombifolia	0	0	1	U	CAN
Rosaceae	*Prunus myrtifolia*	4	4	0	LM	CAN
Rubiaceae	*Coutarea hexandra*	0	1	0	M	SUB
	Faramea montevidensis	12	23	5	LMU	UND
	Posoqueria latifolia	0	3	1	MU	SUB
	Psychotria suterella	5	12	25	LMU	UND
Rutaceae	*Esenbeckia grandiflora*	0	1	0	M	UND
	Zanthoxylum astrigerum	1	3	0	LM	SUB
Sabiaceae	*Meliosma sellowii*	8	9	1	LMU	UND
	Meliosma sinuata	0	0	4	U	CAN
Salicaceae	*Casearia decandra*	0	7	16	MU	UND
	Casearia obliqua	1	8	0	LM	SUB
	Casearia silvestris	3	5	1	LMU	SUB
	Xylosma pseudosalzmannii	1	0	0	L	SUB
Sapindaceae	*Allophylus edulis*	1	1	2	LMU	UND
	Allophylus guaraniticus	0	1	0	M	UND
	Cupania vernalis	0	1	3	MU	SUB
	Matayba guianensis	6	8	4	LMU	CAN
Sapotaceae	*Chrysophyllum inornatum*	54	51	1	LMU	UND
	Chrysophyllum viride	10	23	45	LMU	CAN
Solanaceae	*Cestrum bracteatum*	1	0	0	L	UND
	Solanum sanctaecatharinae	0	1	0	M	UND
Thymelaeaceae	*Daphnopsis fasciculata*	0	0	1	U	UND
Urticaceae	*Coussapoa microcarpa*	3	4	0	LM	CAN
	Urera baccifera	2	0	0	L	UND
Verbenaceae	*Verbenoxylum reitzii*	0	11	0	M	SUB
TOTAL		**564**	**636**	**521**		

Figura 1. Gradiente altitudinal na Serra Geral, Maquiné, RS, visto da planície costeira em Morro Alto, RS 407.

Figura 2. Gradiente altitudinal na Serra Geral visto da planície costeira em Terra de Areia, RS 486.

Figura 3. Gradiente altitudinal na Serra Geral visto da BR 101, na divisa entre Maquiné e Terra de Areia, RS. A encosta à direita da calha d'água, no centro da figura em direção ao pico, é onde foram realizadas as amostragens.

Figura 4. A encosta montanhosa oculta pela cobertura nebular que se forma frequentemente.

Figura 5. O interior da floresta na comunidade inferior, a aproximadamente 220 msnm.

Figura 6. Outra vista do interior da floresta na comunidade inferior, a aproximadamente 240 msnm.

Figuras 7a-b. À esquerda, palmiteiros remanescentes próximos à comunidade inferior (≈ 250 msnm). À direita, um dos muitos paredões rochosos instransponíveis que necessitavam ser contornados para acessar as áreas de estudo.

Figura 8. Área próxima à comunidade intermediária (≈ 380 msnm) com solos rasos e recoberta por densa vegetação herbácea composta por *Calathea monophylla* e *Heliconia farinosa*.

Figura 9. Aspecto da floresta na comunidade intermediária (≈ 440 msnm).

Figura 10. Aspecto da floresta na comunidade superior (≈ 720 msnm).

Figura 11. Sub-bosque de samambaiaçus (*Alsophila setosa*) próximo a comunidade intermediária (≈ 730 msnm).

Figura 12a-b. Troncos retorcidos muito característicos na comunidade superior. À esquerda *Myrciaria floribunda* e à direita *Eugenia subterminalis*.

Figura 13a-b. Aspecto da vegetação próximo ao pico da encosta (≈ 814 msnm). À esquerda vegetação herbáceo-arbustiva característica e à esquerda transição da floresta nebular para a vegetação herbáceo-arbustiva.

Figura 14. Município de Terra de Areia visto a partir do pico da encosta, com destaque para a BR 101, que cruza a cidade, a lagoa Itapeva ao norte e as áreas de terras baixas completamente ocupadas por atividades antrópicas.

Figura 15. Planície costeira ocupada por lavouras, pastagens e plantios de eucaliptos, com alguns raros remanescentes degradados de florestas de terras baixas.

Figura 16. Plantações de banana nas florestas de terras baixas próximas ao sopé da encosta do presente estudo.

Figura 17a-b. Vistas do pico: à esquerda, vista da BR 101, Terra de Areia e ao norte a lagoa Itapeva; à direita, vista da planície com destaque para a lagoa dos Quadros e o Oceano Atlântico ao fundo.

Figura 18a-b. Vistas do pico: à esquerda, avanços da Serra Geral, a BR 101 na beira da lagoa dos Quadros, e ao fundo a lagoa da Pinguela e o Oceano Atlântico; à direita, vale e Município de Maquiné, e patamares da Serra Geral.