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Dissertação de Mestrado

Comunidades herbáceas terrícolas em floresta atlântica primária e secundária no sul do Brasil

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Porto Alegre, março de 2014

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Resumo

As espécies herbáceas terrícolas têm papel fundamental nas interações bióticas que ocorrem no interior de florestas. Entender as relações ecológicas que envolvem este grupo de plantas é essencial para a compreensão da dinâmica de florestas tropicais, sobretudo em ambientes perturbados e complexos, como a floresta tropical atlântica brasileira. O objetivo deste estudo foi avaliar como as comunidades herbáceas terrícolas se relacionam com as características ambientais de floresta tropical atlântica primária e secundária, no sul do Brasil. Nós coletamos dados sobre composição e estrutura (riqueza, cobertura e altura média) de comunidades herbáceas em 16 parcelas de 36m² em cada habitat florestal. Nós analisamos a variação da composição herbácea nos dois habitats através de Análise de Variância Multivariada por Permutação (PerManova) e executamos uma análise de caminhos, utilizando a abordagem PLS-PM (*Partial Least Square Path modeling),* para testar efeitos diretos e indiretos da estrutura do componete arbóreo, fertilidade do solo, luminosidade e do componente lenhoso regenerativo na estrutura das comunidades herbáceas. Os resultados da PerManova mostraram que as comunidades herbáceas foram diferentes entre floresta primária e floresta secundária; as variáveis ambientais que significamente contribuiram para essa variação foram a abertura da copa, o pH e o teor de matéria orgânica. A análise de caminhos mostrou que na floresta primária a estrutura da comunidade herbácea foi afetada direta e positivamente pela fertilidade do solo e indireta e negativamente pela estrutura do componente arbóreo através de sua influência direta no componente lenhoso regenerativo; na floresta secundária a estrutura da comunidade herbácea foi afetada diretamente, tanto positivamente pela disponibilidade de luz, quanto negativamente pelo componente lenhoso regenerativo. De uma forma geral, as variáveis consideradas explicaram bem a variação nos dados das comunidades herbáceas. As comunidades herbáceas de florestas primárias e secundárias são diferentes em resposta ao ambiente biótico e abiótico peculiar de cada habitat florestal. A interação entre espécies herbáceas e o componente lenhoso regenerativo

parece aumentar na floresta secundária, reforçando a ideia de que as relações entre esses grupos de plantas são intensificadas em ambientes perturbados.

Abstract

Terrestrial herbs play a fundamental role in biotic interactions occurring inside forests. The study of the ecological relationships involving this plant group is essential for the understanding of the dynamics of tropical forests, especially in complex and disturbed environments, as the Brazilian Atlantic forest. The objective of this study was to evaluate how herb communities are related to environmental characteristics of old-growth and secondary tropical Atlantic Forest in southern Brazil. We collected data on composition and structure (cover, richness and average height) of herbaceous communities in 16 plots with 36 m² in each forest habitat. We used a permutation multivariate analysis of variance (PerMANOVA) to evaluate the variation in composition of herb communities in old-growth and secondary forest and performed a path analysis to test direct and indirect effects of tree component structure, canopy openness, soil fertility and understory woody component on herb community structure. PerMANOVA results showed that composition of herb communities were different between old-growth and secondary forest; the environment variables canopy openness, organic matter, and pH significantly explained a proportion of the variability of the composition of herb communities. Path analysis indicated that in old-growth forest the herb community structure was affected direct and positively by soil fertility and indirect and negatively by the structure of tree component structure as above mediated by its influence on understory woody component. In secondary forest the herb community structure was affected directly and positively by light availability and negatively by the understory woody component. In general, the analysed variables explained well the variation in the herbaceous community data. Herb

communities in old-growth and secondary forests respond differently to biotic and abiotic variables. Interactions between woody regeneration and herbaceous communities seem to increase in secondary forest, reinforcing the idea that relations between these plant groups are intensified in disturbed environments.

Sumário

Introdução geral

As comunidades vegetais de florestas tropicais são compostas por um amplo espectro de formas de vida, arranjadas em diferentes estratos no interior dessas formações. O estrato inferior das florestas tropicais úmidas, do qual fazem parte às espécies herbáceas terrícolas, contribui de maneira significativa tanto para a diversidade de formas de vida, como para a diversidade de espécies (Tchouto *et al.* 2006). Do ponto de vista ecológico, as plantas herbáceas terrícolas participam de diversos processos interativos e, portanto, do funcionamento do ecossistema florestal como um todo (Roberts 2004; Verstraeten et al. 2013).

O estrato herbáceo pode ser definido como o conjunto de plantas que ocorre até certa altura no interior da floresta (Gilliam 2007), englobando árvores e lianas juvenis, pequenos arbustos, herbáceas terrícolas propriamente (autotróficas) e saprófitos (aclorofilados). Por outro lado, alguns autores definem o estrato herbáceo como sendo composto somente pelas plantas herbáceas propriamente ditas, ou seja, aquelas que completam seus ciclos de vida obrigatoriamente enraizadas no solo, não possuem tecido lenhoso, são clorofiladas e mecanicamente independentes (Cestaro et al. 1986; Costa 2004). Esta última definição, foi adotada neste estudo.

Embora estudos com comunidades herbáceas venham sendo realizados em florestas tropicais, ainda existem em quantidade relativamente pequena e ainda não possuem a importância que é dada em estudos direcionados a florestas temperadas e boreais (Gilliam 2007; Barbier et al. 2008). No Brasil ja foram desenvolvidos importantes estudos voltados a este grupo de plantas, sobretudo na região sul (Citadini-Zanette et al. 2010). Entretanto, a grande maioria destes estudos tiveram um cunho florístico e/ou fitossociológico. Estudos que analisem os fatores ambientais envolvidos na abundância e distribuição das espécies herbáceas são mais raros, como, por exemplo, o de Costa et al. (2005) e Costa (2006) na Floresta Amazônica e de Inácio & Jarenkow (2008) e Lima & Gandolfi (2009) na Floresta Atlântica *sensu lato*. Pode-se dizer que a composição florística e a estrutura quantitativa das comunidades herbáceas são bem conhecedidas,

mas pouco se sabe sobre os mecanismos que controlam a estrutura e a dinâmica das comunidades herbáceas nas diferentes formações das florestas tropicais, visto a grande complexidade ambiental inerente a estas florestas.

Muitos estudos são direcionados à compreensão de florestas bem preservadas, no entanto sabe-se que entender os processos ecológicos que ocorrem em florestas secundárias e fragmentadas é importante para avaliar como acontece a recuperação da floresta ou qual impacto dessas modificações na diversidade e no ecossistema. O estudo de comunidades herbáceas florestais é uma parte fundamental para se entender a dinâmica dessas florestas, pois é um grupo de plantas que responde intensamente a alterações ambientais (Richards 1996).

O objetivo principal deste estudo foi avaliar como comunidades herbáceas terrícolas se relacionam com as características ambientais de floresta atlântica primária e e secundária, no sul do Brasil (Apêndice 4). Para isso, nós analisamos a variação da composição das comunidades herbáceas e testamos efeitos causais diretos e indiretos da estrutura do componete arbóreo, fertilidade do solo, luminosidade e do componente lenhoso regenerativo na riqueza, cobertura e altura média das comunidades herbáceas terrícolas em cada habitat. Os resultados do estudo foram estruturados na forma de um artigo científico, escrito em inglês, visando a publicação em uma revista de circulação internacional.

Article: Effects of biotic and abiotic factors on terrestrial herb communities in old-growth and secondary south Brazilian Atlantic Forest

Introduction

One goal of community ecology is to understand how vegetation patterns are generated as a result of multiple environmental influences. In fact, interactions between several factors generally represent the most common case and they mostly explain the variations of a particular group of organisms better than the effects of a single factor (Laughlin & Abella 2007; Russo *et al.* 2012). Some ecological studies search an integrated analysis of the many aspects composing an ecosystem or biological community, incorporating both biotic and abiotic effects in these analyses, or additionally taking in account the anthropic impacts in a particular system under study (Verheyen *et al.* 2003; Both *et al.* 2011; Bartels & Chen 2013). Such studies are essential for the understanding of the dynamics of tropical forests, which are well known for their high complexity and diversity, and also for their great variety of distinct vegetation types, showing different physiognomies and ecological processes (see Carson & Schnitzer 2008).

Terrestrial herbs are an important component of the complex interaction net occurring inside tropical forests. Composition and structure of herb communities vary strongly in relation to environmental gradients along large spatial scales (Montgomery 2004; Cicuzza *et al.* 2013). At a local scale, these plants can perform an essential role in the forest regeneration, such as inhibiting or facilitating the establishment of woody species through resource utilization, both underground and aboveground (Benítez-Malvino 2006, Griffiths *et al.* 2007). Thus, in some natural forest systems, herbaceous species may function as a potential filter of tree diversity (George & Bazzaz 1999). From the perspective of the herb layer, this interaction may be considered a "bottom up" control (Both *et al.* 2011). On the other hand, a wide range of variables may directly and indirectly affect the structure of herb communities. For instance, the structural characteristics of the tree layer, as height and cover of the upper tree, may have a direct negative effect on herb

species abundance (Both *et al.* 2011) or otherwise an indirect effect by changing light availability, litter accumulation and quantity of soil nutrients (Barbier *et al.* 2008). In this sense, the tree layer has an influence on the herb communities in a "top down" direction (Both *et al.* 2011). Moreover, studies indicate that light availability (Lee 1989, Jones *et al.* 2006; Lima & Gandolfi 2009), topographic gradients and associated soil and litter properties (Gentry & Emmons 1987; Costa 2006; Rodrigues & Costa 2012) are important direct abiotic factors conditioning the spatial arrangement of herb communities in local scale.

It is important to point out that much of the present ecological knowledge of herbaceous communities comes from temperate forests, which have been a traditional subject for the study of these plants (see Gilliam 2007). Studies focusing tropical and subtropical forests are, in contrary, still much more scarce. This reality seems contradictory in face of the well-known high contribution of this plant group to the total diversity of tropical forests (Gentry & Dodson 1987; Linares-Palomino *et al.* 2009). Even in subtropical latitudes, as indicated by a large scale floristic inventory carried out in Santa Catarina state, in south Brazil, 25% of all species in Atlantic slope forests resulted to be terrestrial herbs (Sevegnani *et al.* 2013).

The study of herbaceous communities becomes still more important in a presently widespread context of fragmented landscapes, formed by mosaics of old-growth and secondary forests. The physical characteristics in secondary patch forests are quite different from those inside old-growth forests, resulting in great part from a modified structure of the tree component, mostly regarding light incidence and soils proprieties (Guariguata & Ostertag 2001; Tabarelli *et al.* 2004). Additionally, forest patches are susceptible to edge effects, which generate significant changes in the abiotic and biotic characteristics (Tabarelli *et al.* 1999), favoring the establishment of herbaceous species which are more characteristic of open environments (Costa & Magnusson 2002). Moreover, herbaceous cover generally becomes higher in secondary forests in comparison to old-growth forests and alternatively abundance decreases at late successional stages

(Behera & Misra 2006; Jules *et al.* 2008). As a consequence, resource competition with other plant groups increases, and the interactions between herbs and woody regeneration may become crucial for the structural characteristics found in future forests (Gilliam 2007).

In this study we evaluated the variation of the composition of herbaceous plant communities in relation to the environmental characteristics (i.e. structure of tree component, light availability, soil fertility and understory woody component) of old-growth and secondary tropical Atlantic Forest, and we also analyzed direct and indirect causal effects of these environmental characteristics on structure (i.e. total cover, richness and average height) of herb communities in both forest habitats. To achieve this latter objective we performed a path analysis to test our *a priori* hypothesized multifaceted model (Fig. 1). This model follows a hierarchical order of interactions based on a "top-down" effect (Both *el al.* 2013), that is, we evaluated direct and indirect effects of structure of tree component, light availability and soil fertility, and the direct effect of the understory woody component on community structure. We expected that the composition and structure of herb communities will differ between old-growth and secondary forest, with the latter presenting higher cover and richness of herb species due to the distinct environments in both forests (Guariguata & Ostertag 2002; Jules *et al.* 2008). We expected to find stronger effects of soil fertility in old-growth forest (Gentry & Emmons 1987) and stronger effects of light availability and of understory woody component in secondary forest, due to a higher light availability and thus an accentuated competition between the woody understory and the herb species (Benítez-Malvido 2006; Gilliam 2007). In both forest habitats we expected to find direct and indirect effects of structure of tree component on herb community structure, both in space and the influence through of other factors (Barbier *et al.* 2008; Both *et al.* 2011), forming a cascade effect of canopy structure on herb community structure.
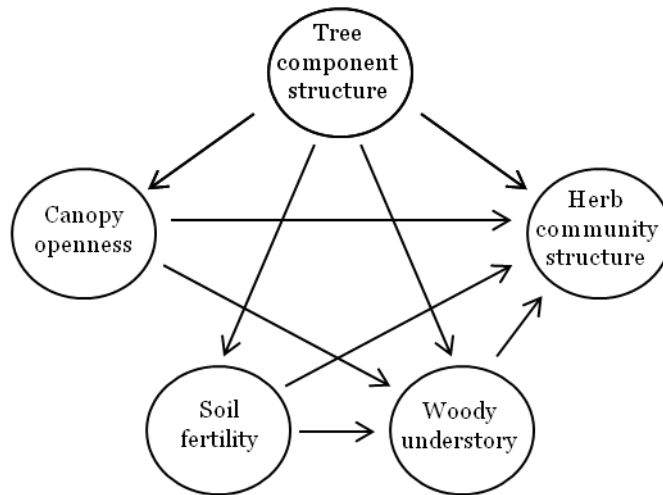
Figure 1. A priori model assumed in our hypothesis on the relationships between environmental factors and herbaceous community structure. Arrows indicate the directions of the causal effects expected.

Methods

STUDY AREA

The study was conducted in an old-growth forest within the conservation unit Serra Furada State Park (SFSP) and in non-protected secondary forest patches in the surrounding area, located in southern Santa Catarina State, Brazil (28°11'30.52"S and 49°23'33.18"W at the Park headquarters). The study region covers an area of about 2700 ha mostly covered with evergreen tropical rain forest vegetation, commonly known as tropical Atlantic forest *sensu strictu* (Oliveira-Filho & Fontes 2000). Although the region is located in the subtropical zone both the forest physiognomy and the floristic composition are similar to tropical regions of the Atlantic forest, as elsewhere in coastal Santa Catarina (Negrelle 2002). The extension of this forest to subtropical latitudes is mainly due to the orographic rainfall regime in this region (Oliveira Filho & Fontes 2000). The climate of the region is humid subtropical, with a mean annual temperature of 18.7 °C and mean annual precipitation of 1700 mm. Soil types are strongly related to topography and elevation, and so Cambisols occur on the rounded relief at lower elevations (350 to 650 m), while Neosols occur on the steep slopes at higher altitudes (above 650 m) (EMBRAPA 2009; FATMA 2010).

The SFSP shows a very good state of environmental conservation, with many characteristic species of regional climax forests (Veloso & Klein 1957) and the predominance of large tree species, some of them rare and endangered (e.g. *Ocotea catharinensis* Mez). The vegetation around the SFSP in contrast has suffered significant changes along time. The great environmental heterogeneity of the region imposed a diversification in the land colonization and multiple uses of the natural resources. The exploitation of these resources comprised mainly the selective extraction of timber and non-timber forest products, such as palm-heart (*Euterpe edulis* Mart.), complete suppression of forest land for cattle pasture and agriculture or and forestry with exotic *Eucalyptus* species. The anthropic interference thus resulted in a highly fragmented forest environment composed of secondary forest patches in different sucessional stages, characterized by different pioneer tree species (FATMA 2010).

SAMPLING DESIGN

Overall 32 plots were established, 16 in each forest type, in order to examine the relationships between the herb community and environmental factors. Sampling sites were previously selected on satellite images. We avoided sites near streams and forest gaps, keeping a distance of at least 100 m. In the SFSP old-growth forest the distance between plots was at least 200 m and the distance from the forest edges was at least 500 m. In the surrounding areas of secondary forest plots were at least 370 m distant from each other and the distance from the forest edge was at least 40 m. In secondary forest, plots were located in isolated forest patches, always greater than 3 ha, and in larger continuous areas, sometimes connected through a narrow forest corridor. Due to the size and shape of patches of secondary forests, edge effects could not be avoided because the plots were established at a distance where the influence of edge effect may be considered effective (Laurance *et al.* 2002). All plots were distributed at elevations between 430-650 m above sea level, which are associated to "montane forests" in subtropical latitudes, according to the Brazilian Vegetation System (IBGE 2012).

In each of the 32 selected sites, 10 x 10 m plots were established for a quantification of tree structure. All trees with ≥ 5 cm diameter at breast height were measured. We assessed density, total basal area, and mean height per plot. In the center of each plot we took hemispherical photographs to quantify light availability, using a Canon EOS Rebel XT camera equipped with a fisheye lens directed upright to the sky and positioned at 1.00 m above the ground in a tripod. Photographs were taken in the early morning and late afternoon. We estimated canopy openness as an indirect measure of light availability using Gap Light Analyzer software version 2.0 (Frazer *et al.* 1999). This measure is strongly related with the amount of light reaching the forest floor (Lima & Gandolfi 2009). Within each plot we also took four topsoil (5-20 cm) samples and mixed them to produce a composite sample. We analyzed soil fertility considering the clay content, pH, amount of organic matter, the sum of exchangeable bases and base saturation (Ronquim 2010). The soil chemical analyses were carried out at the Soil Analysis Laboratory of the Federal University of Rio Grande do Sul (UFRGS). Fertility parameters were generally low in our study, probably resulting from the high aluminum content (Ronquim 2010). All these variables were used as potential prediction variables for the composition and structure of herb communities.

The herb community was assessed in 6 x 6 m subplots centered in the larger plots for tree sampling. As herbaceous species we considered all self-supporting plants without evident woody structures spending their entire life cycle near the forest floor. We evaluated herb structure measuring height, cover and species richness. Cover for each herb species was estimated using the logarithmic scale proposed by Causton (1988). In order to improve visual estimation of herb species' covers through this scale, we divided each subplot in nine 2 x 2 m quadrates. In the subplots we also estimated the total cover of the understory woody component, defined as shrubs and recruits of trees and lianas up to 1 m height, using the same procedure as for the herb community. The understory woody

component was also used as a predictor of herb community parameters. Vouchers of the sampled herb species were deposited in ICN Herbarium, UFRGS, Porto Alegre, Brazil.

DATA ANALYSIS

We used a permutation multivariate analysis of variance (PerMANOVA) (Anderson 2001) to evaluate the variation in composition of herb communities in old-growth and secondary forest. The quantitative measure for this comparison was the cover of each species per plot. Additionally, we used the log-transformed predictor variables as covariates in this analysis (Oksanen *et al.* 2013). PerMANOVA was performed with the 'adonis' function in the 'vegan' package (Oksanen *et al.* 2013), in software R, using Bray–Curtis dissimilarities and 999 permutations. This analysis is a powerful method for ecological data because multivariate normal distribution is not required and because it is possible to perform the analysis with more variables than sampling units (MacArdle & Anderson 2001).

We used partial least squares path modeling (PLS-PM) (Tenenhaus *et al.* 2005) to assess the direct and indirect effects of biotic and abiotic factors on herb community structure. PLS-PM is considered a "soft modeling" approach to structural equation models, where no strong assumptions on distribution, sample size and the measurement scale are required (Esposito-Vinzi *et al.* 2010). In this analysis a network of causal relationships between latent variables (LVs) is assessed. The LVs are unobserved or conceptual variables, estimated through a block of observable or manifest variables (MVs). The relationships among the LVs are specified in a structural or inner model and the relationships between the block of MVs and their own LV are specified in a measurement or outer model. PLS-PM algorithm follows a sequential procedure: first, LVs scores are calculated as weighted sums of their MVs through an iterative process (outer and inner weight relations); second, the relationships between LVs (path coefficients) are calculated; and third, the correlations (loadings) between a LV and its MVs are calculated. This

procedure is carried out through a system of interdependent equations based on simple and multiple regressions (Esposito-Vinzi *et al.* 2010).

We performed PLS-PM with the statistical software R version 2.14 using the "plspm" package (Sanchez *et al.* 2013) for each forest environment. We conceptualized five LVs: 1) tree component structure, 2) canopy openness, 3) soil fertility, 4) woody understory, and 5) herb community structure. Each conceptual LV was estimated using the values of measured MVs (the LVs and its MV blocks are shown on Tab. 2). The MVs measured in different units were standardized (mean zero, unit variance) before running the analysis. LVs scores were estimated using "path scheme" (for obtaining inner weights) and "reflective way" (for obtaining outer weights). The idea behind the reflective way is that the MVs are consequences or effects of their LVs and each MV is related to its LV by a simple regression (Esposito-Vinzi *et al.* 2010). Path coefficients were estimated by ordinary least squares multiple regressions. The direct effects are given by the path coefficients and indirect effects are the product of the path coefficients, that is, the paths whereby one LV influence another LV by taking an indirect path.

Before interpreting the results in PLS-PM it is necessary to assess the quality of both the structural and the measurement model. Primarily, we evaluated the quality of the measurement model. For reflexive way a block of MVs must to be unidimensional. To check the unidimensionality we used the Dillon-Goldstein's rho index. Index more than 0.7 is considered a unidimensional block (Esposito-Vinzi *et al.* 2010). The loyalty of MVs with its LV was assessed by cross-loadings and the contribution of each MV for their LV by loadings. Variables with loadings less than 0.7 were removed of the final model (Tenenhaus *et al.* 2005). Subsequently we evaluated the structural model taking into account the coefficients of determination R^2 that indicates the amount of variance in the endogenous (dependent) LV explained by its exogenous (independent) LV and Goodness of Fit (GoF), a global criterion to assess the overall prediction performance of the model. The validity of the model parameters (i.e. loadings, R^2, path coefficients) were tested with bootstrapping, using a 95 % confidence interval and 200 resamples. Lower percentiles and

upper percentiles of bootstrap confidence interval of all parameters are shown on Appendix 1.

Results

COMPOSITION AND STRUCTURE OF HERB COMMUNITIES AND ENVIRONMENTAL HETEROGENEITY

Overall, 38 herbaceous species were sampled in our study. In the old-growth forest we found 18 species and in the secondary forest 26 species. Only six species were common to both environments: *Calathea monophylla, Heliconia farinosa* (both locally abundant), *Nidularium innocentii, Pleurostachys urvillei, Sauroglossum nitidum* and the fern *Pteris decurrens*. Among the most abundant species, the fern *Blechnum brasiliense* (Blechnaceae) was exclusive for secondary forest, whereas another fern, *Didymochlaena truncatula* (Hypodematiaceae), only occurred in old-growth forest. Following these species, grasses stand out as exclusive and abundant species in secondary forest. In both forests, angiosperms presented more families and cover than ferns. In secondary forest the richness of angiosperms was greater than ferns (20/6 species), but in old-growth richness it was the same for both plant groups (9/9 species). Ferns were more abundant in old-growth forest than in secondary forest (134/98 total cover), whereas angiosperms were more abundant in secondary forest than in old-growth forest (407/170 total cover). The complete list of families and species with cover values is given in Appendix 2. The herb species cover in secondary forest was greater than in old-growth forest, 70% and 42% of the sampled area, respectively.

The PerMANOVA results (Tab. 1) showed that composition of herb communities were different between old-growth and secondary forest (F = 8.28, P = 0.001). The environment variables canopy openness (F = 2.25, P = 0.032), organic matter (F = 3.60, P = 0.006) and pH (F = 4.62, P = 0.001) significantly explained a proportion of the variability of the composition of herb communities. The full models (including the factor "forest type" and the environmental variables) explained 59% of the variability of the composition of herb communities.

Table 1. PerManova results for herb composition data of old growth and secondary Atlantic forest and biotic and abiotic factors used as covariables in the analysis. SS = sum of squares, F = F statistic and P value. Significance: (*) P ≤ 0.05; (**) P ≤ 0.01; (***) P ≤ 0.001.

Variables	SS	F	R²	P
Forest type	1.70	8.28	0.17	0.001***
Basal area	0.23	1.10	0.02	0.362
Density	0.30	1.47	0.03	0.196
Average height	0.35	1.70	0.04	0.097
Canopy openness	0.46	2.25	0.05	0.032*
Clay	0.25	1.22	0.03	0.277
Ph	0.95	4.62	0.10	0.001***
Organic matter	0.74	3.60	0.07	0.006**
Sum bases	0.26	1.26	0.03	0.243
Base saturation	0.31	1.50	0.03	0.193
Woody understory	0.31	1.53	0.03	0.142
Residuals	4.11	-	0.41	-
Total	9.99	-	1	-

QUALITY OF MEASUREMENT MODELS

The initial measurement models were not satisfactory, because some MVs presented low contribution to their estimated LVs (Tab. 2). In old-growth forest we removed tree basal area, tree average height, clay, organic matter and sum of bases because these variables showed loadings less than 0.7. In the same way, in secondary forest we removed tree basal area, tree density, clay, organic matter, and herb average height. In face of these results we run the PLS-PM again without these variables. As a result the Dillon-Goldstein's rho index - DG. (rho) - was considered satisfactory for all LVs (Tab. 3). The cross-loadings also improved after the removal of the low MVs and were considered these values excellent, indicating loyalty of the MVs with their own LVs (Appendix 3).

Table 2. Initial and final measurement model loadings of PLS-PM performed in old-growth and secondary forest with latent variables and respective manifest variables.

Variables (*)	Old-growth forest Loadings		Secondary forest Loadings	
	Initial	Final	Initial	Final
Tree component structure				
Basal area	0.21	*Removed*	0.20	*removed*
Density	0.97	1.00	0.28	*removed*
Average height	0.53	*removed*	-0.93	1.00
Canopy openness				
Canopy openness	1.00	1.00	1.00	1.00
Soil fertility				
Base Saturation	0.95	0.97	0.90	0.94
Clay	-0.34	*removed*	-0.01	*removed*
Organic matter	0.08	*removed*	-0.65	*removed*
PH	0.88	0.96	0.92	0.95
Sum bases	0.63	*removed*	0.88	0.96
Woody understory				
Understory woody component	1.00	1.00	1.00	1.00
Herb community structure				
Cover	0.93	0.93	0.89	0.95
Height	0.88	0.89	-0.64	*removed*
Richness	0.72	0.70	0.96	0.94

(*) Latent variables are in bold type and manifest variables in normal type.

Table 3. Initial and final Dillon-Goldstein's rho index, determination coefficients R^2 for endogenous variables and initial and final Goodness of Fit (GoF) for evaluation of global model PLS-PM secondary forest and old-growth forest. Values in bold type are significant with a 95% bootstrap confidence of interval.

Latent variables	Old-growth forest DG. (rho)		R^2	Secondary forest DG. (rho)		R^2
	Initial	Final		Initial	Final	
Tree component structure	0.77	1.00		0.66	1.00	
Canopy openness	1.00	1.00	0.02	1.00	1.00	0.03
Soil fertility	0.81	0.96	0.23	0.69	0.96	0.04
Woody understory	1.00	1.00	**0.54**	1.00	1.00	**0.48**
Herb community structure	0.89	0.89	**0.64**	0.57	0.94	**0.89**
GoF	0.42	0.53		0.45	0.57	

STRUCTURAL MODEL IN OLD-GROWTH FOREST

In the evaluation of the structural model, where relations between LVs are presented, the coefficients of determination R^2 for the endogenous variables woody understory and herb community structure were significant, but not significant for canopy openness and soil fertility (Tab. 3). For the LV herb community structure, the exogenous variables explained 64% of their variance. The GoF index improved from 0.42 to 0.53 with the refinement of the measurement model. The LV soil fertility was the only variable that affected directly and significantly the herb community structure (0.64) and the LV tree

component structure, well explained by tree density, showed a strong indirect negative effect (-0.68) on herb community structure mediated by their influence on the LVs soil fertility and woody understory (Tab. 4, Fig. 2a). The LV tree component structure also affected strongly the woody understory, having a significant direct positive effect (0.78). Thus, in old-growth forest, richness, total cover and average height of herb community increased with soil fertility and decreased with tree density, which affected mainly and positively the woody understory cover. The LV canopy openness showed a weak effect on herb community structure (Tab. 4, Fig. 2a).

STRUCTURAL MODEL IN SECONDARY FOREST

Similarly to the PLS-PM performed in old-growth forest, in secondary forest the structural model showed that the coefficients of determination R^2 for the endogenous variables woody understory and herb community structure were significant, but not significant for canopy openness and soil fertility (Tab. 3). For the LV herb community structure, the exogenous variables explained 89% of their variance. The GoF index changed from 0.45 to 0.57 after the refinement of the measurement model. The LVs canopy openness and woody understory had a strong significant direct effect on herb community structure, the first with a positive effect (0.89) and the second with a negative effect (-0.78) (Tab. 4, Fig. 2b). So, in secondary forest, total cover and richness of the herb community increased with canopy openness and decreased with increasing cover of the understory woody component. The LV tree component structure had a direct positive effect on woody understory, but not significant to produce a strong indirect effect on herb community structure in secondary forest (Tab. 4, Fig. 2b).

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Table 4. Direct and indirect effect estimated by PLS-PM in old-growth and secondary forest. Values in bold type are significant with 95% bootstrap confidence interval

	Tree component structure	Canopy openness	Soil fertility	Woody understory
Old-growth forest				
Direct effect				
Tree component structure				
Canopy openness	0.12			
Soil fertility	-0.48	-		
Woody understory	**0.76**	-0.34	0.13	
Herb community structure	0.19	-0.05	**0.58**	-0.59
Indirect effect				
Tree component structure				
Canopy openness	-			
Soil fertility	-	-		
Woody understory	-0.10	-	-	
Herb community structure	-0.67	0.20	-0.08	-
Secondary forest				
Direct effect				
Tree component structure				
Canopy openness	0.18			
Soil fertility	0.20	-		
Woody understory	0.54	0.36	-0.32	
Herb community structure	0.10	**0.89**	0.15	**-0.73**
Indirect effect				
Tree component structure				
Canopy openness	-			
Soil fertility	-	-		
Woody understory	0.00	-	-	
Herb community structure	-0.20	-0.27	0.23	-
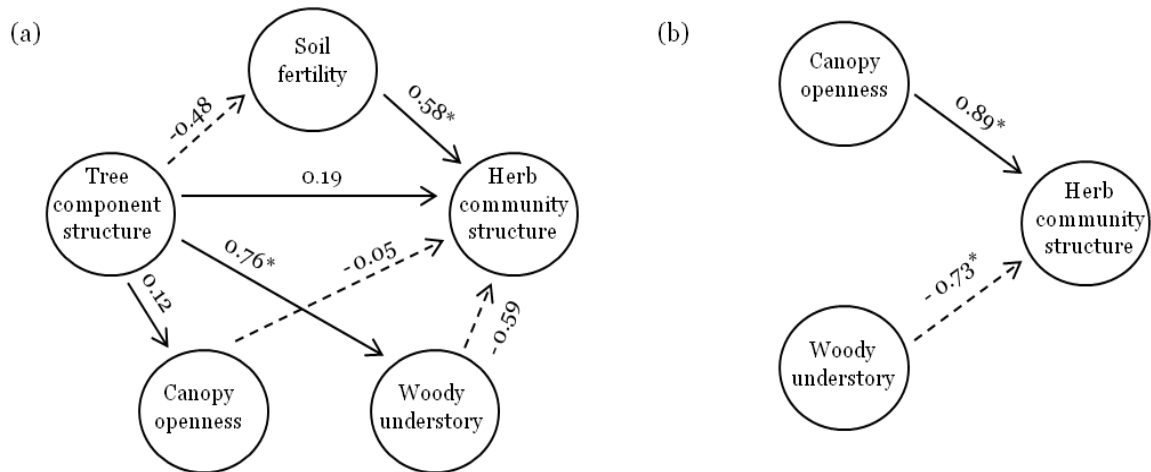
Figure 2. Path diagrams showing the main pathways which influence herb community structure in old-growth (a) and secondary (b) tropical Atlantic forest. Path coefficients are the direct effect of one latent variable (LV) on another LV. Values assigned with asterisks were significant at a 95% bootstrap confidence interval. The solid lines are positive effects and dashed lines are negative effects. In old-growth forest non-significant paths were also placed to view the paths traced by LV tree component structure that had strong indirect effect on herb community structure.

Discussion

We verified that herb communities are quite different between old-growth and secondary forests, with the later showing higher species richness and higher plant cover. Herbaceous communities in tropical old-growth forests are expected to be less dense and more scarcely distributed (Richards 1996). Alternatively, a higher richness and cover is expected in secondary and fragmented forests (Behera & Misra 2006). For herb communities, these results followed an expected pattern found between old-growth-forest and secondary forests (Jules *et al.* 2008; Both *et al.* 2011).

In disturbed environments, such as secondary forests, the light incidence is relatively high in the understory (Costa & Magnusson 2002; Lima & Gandolfi 2009). This characteristic allows the invasion of species adapted to environments with higher light incidence, as non-forest species and with a strong colonization power, as grasses and *Blechnum* species (Costa & Magnusson 2002, Paciencia & Prado 2005; Manninen *et al.* 2009), and thus increasing the herb cover and richness. The strong direct effect of canopy openness on herb community structure found in PLS-PM reinforces the idea that the incidence of light seems to be a decisive factor for arrangement of herb community structure in secondary forest. This result also agrees with the general concept that light availability is more correlated with herbaceous community structure in secondary forests than in old-growth forests (Jules *et al.* 2008). Moreover, these same species seem to be less susceptible to poor soil fertility, unlike of old-growth herb species (Gentry & Emmons 1987). This susceptibility to poor soils may be evidenced by the strong direct effect of soil fertility on herb community structure in old-growth forest and by a weak relationship between these variables in secondary forest.

In secondary forest the herb community structure was also negatively affected by the cover of the understory woody component. The woody understory is commonly abundant in tropical secondary forests, where the lower heights of trees allow a greater light input (Denslow & Gusman 2000; Rigueira *et al.* 2012). In fact, the tree component structure in secondary forest was well explained by the average height of trees, as

demonstrated by PLS-PM results. It is important to point out that the competition between woody understory and terrestrial herbaceous species appears to increase in secondary forests, favored by the weedy nature of some herbaceous species and the greater abundance of woody regeneration (Benítez-Malvido 2006). According to Harms *et al.* (2004), resource availability, as light in our study, may enhance interspecific competition, and this idea reinforces the intensified competitive interactions in disturbed environments (Gilliam 2007).

Otherwise, canopy openness showed to be non-significant for the herb community in old-growth forest. This result was unexpected since studies demonstrated strong correlations between canopy openness and herb community structure (Jones *et al.* 2006; Lima & Gandolfi 2009). This lack of relation in old-growth forests may be due to species characteristics. Shade-tolerant herbaceous species, as those occurring in forests with closed canopies and heterogeneous light environment, require low amounts of light, and so the increase in light availability will not necessarily increase the number of species (Härdtle *et al.* 2003).

In the old-growth forest, the effect of tree component structure, which was well explained by tree density, was a fundamental factor for herb community structure variation. The importance of this factor was principally manifested as an indirect negative effect, mediated through its influence on soil fertility and on woody understory. These interactive influences were also previously shown to occur in herbaceous communities in forests under different climates (Barbier *et al.* 2008; Mölder *et al.* 2008; Both *et al.* 2011). We have some potential explanations for these interactions. First, the tree component structure may have a profound influence on the soil nutrient supply (Barbier et 2008; Verstraten *et al.* 2013). Second, abundance of the overstory may be strongly correlated with the woody cover of the understory (Bartes & Chan 2013). Moreover, our sampling criterion allowed the inclusion of many lower trees, and this fact may explain the strong positive effect of the tree component structure on the woody understory (Both *et al.* 2011). Finally, several effects originating from overstory characteristics, like physical and

chemical properties of litter and space competition with understory vegetation may have inhibiting influences on the establishment and abundance of herbaceous species (Benítez-Malvido 2006; Mölder *et al.* 2008; Albrecht & Mccarthy 2009; Rodrigues & Costa 2012), and in this way explaining the negative effect of tree component structure on herb community structure.

Although we did not include all the variables that may influence the herb community structure in both forests, our predictive models had a great explanation power, indicating that the tested biotic and abiotic variables are responsible for most of the variation on the herbaceous in our study system. Altogether, our results suggest that herbaceous communities of old-growth and secondary forests respond in a quite different way to the biotic and abiotic variables analyzed, as canopy openness and understory woody component in secondary forest and soil fertility and tree component structure in old-growth forest. Moreover, our results suggest that change in the biotic and abiotic environmental conditions in a forest starts a strong shift in the composition and structure of the herb community. We hypothesized that these changes in environmental conditions may cause changes in functional traits and consequently impacts on ecosystem processes (Díaz *et al.* 2004), and may exclude those herbaceous species that are more sensible and do not support stressful environments and high competition for resources, as found in disturbed environments. In these environments, herb community structure can affect forest succession, as the increased abundance of herbs also increases competition of these plants with the understory woody component (Benítez-Malvido *et al.* 2001).

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Appendices

Appendix 1. Outcomes of bootstrapping 95% confidence interval provided by the lower percentiles and upper percentiles for Loadings, R², direct and total effects in old-growth and secondary forest. Significant values do not contain the zero in bootstrap confidence intervals.

Loadings and R²

Manifest variables	Secondary forest			Old-growth forest		
	Loadings	Percentiles *0.025*	*0.975*	**Loadings**	Percentiles *0.025*	*0.975*
Basal area	*removed*			*removed*		
Density	*removed*			1.00	1.00	1.00
Height	1.00	1.00	1.00	*removed*		
Canopy openness	1.00	1.00	1.00	1.00	1.00	1.00
Base saturation	0.94	0.85	0.99	0.97	0.95	0.99
Clay	*removed*			*removed*		
Organic matter	*removed*			*removed*		
pH	0.95	0.41	0.99	0.96	0.92	0.99
Sum bases	0.96	0.84	0.99	*removed*		
Understory woody component	1.00	1.00	1.00	1.00	1.00	1.00
Cover	0.95	0.90	0.98	0.93	0.74	0.98
Height	*removed*			0.89	0.67	0.96
Richness	0.94	0.82	0.98	0.70	0.03	0.97
Latent variables	**R²**			**R²**		
Canopy openness	0.03	0.00	0.35	0.02	0.00	0.35
Soil fertility	0.04	0.00	0.41	0.23	0.00	0.67
Woody understory	0.48	0.24	0.87	0.54	0.33	0.86
Herb structure	0.89	0.84	0.98	0.64	0.52	0.92

Total and direct effects

Old-growth forest	Direct effect	Percentiles *0.025*	*0.975*
Tree component structure -> Canopy openness	0.12	-0.27	0.59
Tree component structure -> Soil fertility	-0.48	-0.82	0.34
Tree component structure -> Woody understory	0.76	0.30	1.07
Tree component structure -> Herb community structure	0.19	-0.66	1.13
Canopy openness -> Woody understory	-0.34	-0.68	0.25
Canopy openness -> Herb community structure	-0.05	-0.57	0.37
Soil fertility -> Woody understory	0.13	-0.41	0.50
Soil fertility -> Herb community structure	0.58	0.10	1.08
Woody understory -> Herb community structure	-0.59	-1.17	0.13
Secondary forest			
Tree component structure -> Canopy openness	0.18	-0.35	0.59
Tree component structure -> Soil fertility	0.20	-0.55	0.64
Tree component structure -> Woody understory	0.54	-0.02	0.89
Tree component structure -> Herb community structure	0.10	-0.22	0.32
Canopy openness -> Woody understory	0.36	-0.09	0.71
Canopy openness -> Herb community structure	0.89	0.61	1.20
Soil fertility -> Woody understory	-0.32	-0.74	0.09
Soil fertility -> Herb community structure	0.15	-0.28	0.45
Woody understory -> Herb community structure	-0.73	-1.25	-0.25

Appendix 2. List of herb species found in old-growth and secondary forest of the studied tropical atlantic forest and their respective total covers absolut in each forest type. The scientific names were updated according to "The Plant List" database (www.theplantlist.org).

Family	Species	Secondary	Old-growth
Anemiaceae	Anemia phyllitidis (L.) Sw.	8	_
Aspleniaceae	*Asplenium brasiliense* Sw.	_	3
	Asplenium kunzeanum Klotzsch ex Rosenst.	_	3
	Asplenium triquetrum N. Murak. & R.C. Moran	_	1
	Asplenium uniseriale Raddi	_	2
Asteraceae	*Chaptalia nutans* (L.) Polák	5	_
	Elephantopus mollis Kunth	1	_
	Podocoma notobellidiastrum (Griseb.) G.L.Nesom	6	_
Athyriaceae	*Diplazium cristatum* (Desr.) Alston	3	_
Blechnaceae	*Blechnum brasiliense* Desv.	79	_
Bromeliaceae	*Nidularium innocentii* Lem.	4	19
Cyperaceae	*Pleurostachys gaudichaudii* Brongn.	_	4
	Pleurostachys urvillei Brongn.	22	10
Dennstaedtiaceae	*Dennstaedtia globulifera* (Poir.) Hieron.	_	4
Dryopteridaceae	*Lastreopsis amplissima* (C. Presl) Tindale	_	28
	Megalastrum connexum (Kaulf.) A.R. Sm. & R.C. Moran	_	18
Heliconiaceae	*Heliconia farinosa* Raddi	80	31
Hypodematiaceae	*Didymochlaena truncatula* (Sw.) J. Sm.	_	73
Marantaceae	*Calathea monophylla* (Vell.) Körn.	145	97
Melastomataceae	*Bertolonia mosenii* Cogn.	_	3
Orchidaceae	*Aspidogyne fimbrillaris* (B.S.Williams) Garay	_	4
	Liparis nervosa (Thunb.) Lindl.	14	_
	Malaxis excavata (Lindl.) Kuntze	2	_
	Prescottia stachyodes (Sw.) Lindl.	_	1
	Psilochilus modestus Barb.Rodr.	1	_
	Sauroglossum nitidum (Vell.) Schltr.	8	1
Poaceae	*Homolepis glutinosa* (Sw.) Zuloaga & Soderstr.	4	_
	Ichnanthus pallens (Sw.) Munro ex Benth.	31	_
	Panicum surrectum Zuloaga & Morrone	9	_
	Panicum laxum Sw.	45	_
	Paspalum sp.	1	_
Pteridaceae	*Pteris decurrens* C. Presl	5	2
	Pteris denticulata Sw.	1	_
Rubiaceae	*Coccocypselum geophiloides* Wawra	18	_
	Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	6	_
	Coccocypselum sp.	1	_
	Diodia sp.	4	_
Thelypteridaceae	*Thelypteris rivularioides* (Fée) Abbiatti	2	_

Appendix 3. Outcomes from PLS-PM in old-growth and secondary forest, showing final cross-loadings beetwen latent variables (LV) and manifest variables (MV). Cross-loadings are the loadings of a MV with all LVs. Values in bold type (diagonal) show that loadings of a MV with their own LV is greater than when compared to the loadings with others LVs.

Old-growth forest

Variables	Tree component structure	Canopy openness	Soil fertility	Woody understory	Herb community structure
Density	**1.00**	0.12	-0.48	0.65	-0.48
Canopy openness	0.12	**1.00**	0.13	-0.23	0.19
Base saturation	-0.51	0.08	**0.97**	-0.26	0.62
pH	-0.41	0.18	**0.96**	-0.28	0.62
Woody understory	0.65	-0.23	-0.28	**1.00**	-0.62
Cover	-0.38	0.25	0.47	-0.67	**0.93**
Height	-0.54	0.07	0.77	-0.53	**0.89**
Richness	-0.15	0.20	0.23	-0.22	**0.70**

Secondary forest

Variables	Tree component structure	Canopy openness	Soil fertility	Woody understory	Herb community structure
Height	**1.00**	0.18	0.20	0.54	-0.10
Canopy openness	0.18	**1.00**	0.21	0.39	0.65
Base saturation	0.21	0.24	**0.94**	-0.02	0.43
pH	0.24	0.26	**0.95**	-0.14	0.46
Sum bases	0.10	0.08	**0.96**	-0.22	0.40
Woody understory	0.54	0.39	-0.14	**1.00**	-0.35
Cover	-0.10	0.61	0.49	-0.35	**0.95**
Richness	-0.10	0.61	0.36	-0.30	**0.94**

Apêndice 4. Localização do Parque Estadual da Serra Furada no estado de Santa Catarina, nos municípios de Orleans e Grão-Para. A ortofoto mostra os limites do Parque (linha amarela) e parte do entorno. As demais linhas delimitam zona de amortecimento (verde), floresta primária (laranja) e floresta secundária (preto).
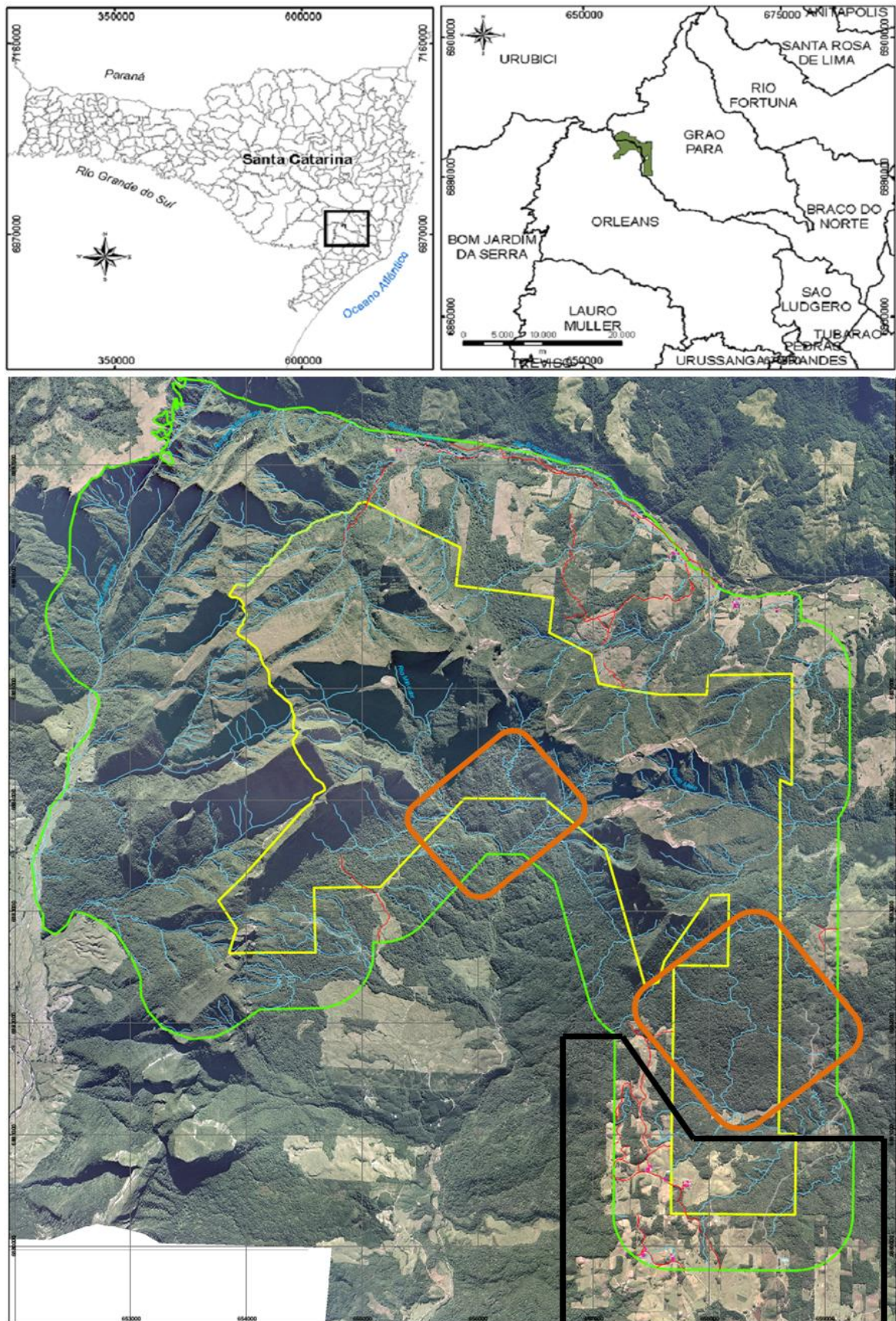
Fonte: FATMA (2010)

Considerações finais

Com este estudo nós identificamos alguns fatores responsáveis pela variação das comunidades herbáceas de florestas primárias e secundárias na floresta atlântica do sul do Brasil. Nossas variáveis explicaram grande parte da variação das comunidades herbáceas. Vimos que a variação é decorrente das interações entre diversos fatores bióticos e abióticos.

Comprovamos que as espécies herbáceas são sensíveis ao ambiente onde estão. A mudança no ambiente físico de uma floresta desencadeia uma forte mudança na estrutura da comunidade herbácea. Estas mudanças podem ser afetar tanto a sucessão da floresta como para a manutenção de espécies herbáceas. Por exemplo, o incremento de espécies herbáceas ruderais pode modificar o andamento sucessional da floresta, já que estas competem diretamente por recursos com juvenis arbóreos. Como consequência, espécies herbáceas autóctones podem extinguir-se localmente, pois não suportam ambientes estressantes e de alta competição por recursos como encontrado nas bordas de floresta.

Nosso estudo deixa em aberto outras questões a serem respondidas, como: quais espécies herbáceas são indicadoras de floresta primária e secundária; qual a relação das espécies herbáceas com mecanismos de polinização e dispersão nestes ambientes. Estudos que analisem como a diversidade específica e funcional das comunidades herbáceas varia em ambientes espacialmente amplos e altamente fragmentados, com a floresta atlântica, também são importantes. Assim, poderemos identificar quais mecanismos são responsáveis pela distribuição das espécies em amplos gradientes ambientais.