UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Tese de Doutorado

Padrões ecológicos do estrato herbáceo em florestas costeiras no sul do Brasil

Ronaldo dos Santos Junior

Porto Alegre, março de 2019

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Tese apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como um dos requisitos para obtenção do título de Doutor em Ciência Botânica.

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No setor entre Osório e Torres, as lagoas maiores batem diretamente contra o sopé da serra Geral [...]. Isto tem por consequência uma total diferença entre no lado atlântico e continental: No lado atlântico há os juncais, o campo seco, os parques de jerivás, figueiras, cedros, louros, timbaúvas, a mata brejosa; no lado continental há a mata virgem da fralda da serra, completamente diferente em caráter e composição. A vegetação do lado Atlântico, em nenhum lugar, penetra o domínio da serra; a da serra, pelo contrario, desce a planície enquanto a fertilidade do solo lhe permite, chegando a imprimir o seu cunho a certos trechos entre as lagoas, como entre Capão da Canoa e a extremidade norte da Lagoa dos Quadros [...]. (RAMBO, 1956, p. 25).

RESUMO

As planícies costeiras brasileiras compreendem tipos florestais geralmente diferenciados pelas condições do solo. Atualmente, estas florestas encontram-se altamente fragmentadas, proporcionando um cenário interessante para o estudo dos efeitos da fragmentação de habitat e de fatores ecológicos sob as comunidades vegetais. Neste sentido, o estrato herbáceo pode contribuir para a compreensão destes efeitos, pois é sensível a alterações ambientais e pode responder de forma diferente a fatores ecológicos, haja vista as diferentes formas de vida que o compõe. Nesta tese, é apresentado o primeiro estudo realizado em ampla escala geográfica que explora a diversidade e a diferenciação florística do estrato herbáceo em florestas atlânticas da planície costeira. Os resultados foram estruturados na forma de dois artigos científicos. O primeiro artigo teve como objetivo avaliar a diversidade e variação florística das formas de vida vegetal presentes no estrato herbáceo entre os três principais tipos de florestas costeiras – Floresta Arenosa, Turfosa e Pluvial, e investigar se as características de diversidade e composição florística contribuíam para a distinção entre estas florestas, comumente distinguidas com base no componente arbóreo adulto. O segundo artigo teve como objetivo investigar os fatores ecológicos que controlam a diversidade alfa e beta do estrato herbáceo em um ecossistema altamente fragmentado como as florestas costeiras. O estudo foi realizado em 23 fragmentos florestais localizados na planície costeira do nordeste do Rio Grande do Sul e sudeste de Santa Catarina, incluindo cinco florestas arenosas, oito florestas turfosas e 10 florestas pluviais. O estrato herbáceo (≤ 1-m altura) incluiu as seguintes formas de vida: trepadeira, herbácea terrícola (incluindo angiospermas e samambaias), palmeira, arbusto (incluindo arbustos e sub-arbustos) e árvore (incluindo arvoretas). Os resultados encontrados mostraram que as distinções entre esses tipos de florestas são complexas quando se leva em consideração o estrato herbáceo. As diversidades alfa e beta são governadas por processos determinísticos, principalmente relacionados às condições do solo, mas outras causas ecológicas podem ser importantes para determinadas formas de vida. Embora a fragmentação do habitat possa impor mudanças na diversidade e composição do estrato herbáceo, as condições do solo e as variáveis climáticas ainda contribuem para explicar a variação da diversidade, apesar dos efeitos de fragmentação.

Palavras chave: floresta de dunas, vegetação do solo, floresta turfosa, floresta pluvial, restinga, métricas de fragmentação, floresta subtropical, diversidade beta, diferenciação florística, diversidade alfa, formas de vida, teoria do Nicho.

ABSTRACT

The Brazilian coastal plains comprise very different forest types commonly distinguished by soil conditions. Nowadays, these lowland formations occur in a highly fragmented landscape, providing an interesting scenario for the study of fragmentation effects and ecological drivers on plant communities. In this sense, the herb layer can contribute to the understanding of these effects, since it is highly sensitive to environmental changes and may respond differently to ecological factors, given the different life-forms occurring in the forest understory. Here, we present the first study on a broad geographic scale that explores diversity and floristic differentiation of the herb layer in the coastal plain of Brazilian Atlantic Forest. The results were organized in two scientific papers: In the first, we assessed the contribution of herb layer life-forms to diversity and floristic variation in the three main coastal forest types: Dune forest, Peat forest and Rain forest. In addition, we investigated if herb layer characteristics match coastal forest distinctions made commonly on the basis of the tree layer. In the second paper, we investigated the ecological factors driving alpha and beta diversity in the herb layer of forest fragments scattered across the coastal plain. Herb layer (plants ≤ 1 m in height) was sampled in 23 forest fragments, distinguishing species according to distinct life-forms: herbs, shrubs, palms, trees, and climbers. The results evidenced that the distinctions among forest types are complex when taking into account the herb layer. We showed that herb layer life-forms are shaped by deterministic processes mostly related to soil conditions, but other ecological drivers may be important when disentangling these life-forms. Although habitat fragmentation can impose changes on forest herb layer assemblages, especially herbaceous species, soil and climate conditions overwhelm the contribution in explain alpha and beta diversity along a short but steep environmental gradient, as the one here analysed in coastal plain Atlantic forests.

Keywords: dune forest, ground vegetation, peat forest, rain forest, *restinga*, fragmentation metrics, subtropical forest, beta diversity, floristic differentiation, alpha diversity, life-forms, niche theory.

SUMÁRIO

1. INTRODUÇÃO GERAL

A diversidade de depósitos geológicos que originaram as planícies costeiras brasileiras e a consequente formação pedológica associada a estes depósitos geraram condições ambientais que permitiram o estabelecimento de uma variedade de tipos de formações vegetais (Waechter 1990, Menezes & Araujo 2005), como campestres, arbustivas e florestais, arranjadas na forma de um mosaico de vegetação, comumente chamado de "complexo de restinga" (Araujo et al. 2004, Lima et al. 2011). As diferenças fisionômicas e ambientais relacionadas à variação edáfica possibilitaram a distinção de três tipos principais de florestas na planície costeira (Waechter 1990, Scarano 2006, Marques et al. 2015): i) Floresta arenosa, também referenciada como floresta psamófila, floresta de restinga, mata alta de restinga, capões de dunas, etc. (Dorneles & Waechter 2004a, Lima et al. 2011), desenvolvendo-se em solos arenosos não inundados; ii) Floresta turfosa, também conhecida como floresta paludosa, floresta brejosa, floresta inundada, etc., estabelecida em solos orgânicos e permanentemente alagados (Waechter 1990, Menezes & Araujo 2005, Scarano 2006); iii) Floresta pluvial (Floresta Atlântica *stricto sensu* - Oliveira Filho e Fontes 2000), desenvolvendo-se na parte mais interna da planície costeira onde os solos são mais antigos e ricos em nutrientes e não inundados (Marques et al. 2015). Embora o caráter estrutural e fisionômico seja distinto, estes tipos florestais foram colonizados, sobretudo, por espécies provindas das associações vegetais adjacentes, como a floresta atlântica de encosta (Rambo 1956).

As comunidades vegetais de florestas tropicais e subtropicais são compostas por amplo espectro de formas de vida, arranjadas espacialmente em diferentes estratos. O estrato inferior contribui de maneira significativa tanto para quantidade de formas de vida, quanto para a diversidade total dessas florestas (Gentry & Dodson 1987, Tchouto et al. 2006). Existem diferentes terminologias e definições para qualificar este estrato. Gilliam (2007) apresenta diferentes termos, entre os quais, o mais comumente citado na literatura é o estrato herbáceo (Ingl. *Herb layer*). Segundo este mesmo autor, o estrato herbáceo pode ser definido como o conjunto de plantas que ocorre até certa altura no interior da floresta, englobando árvores e lianas juvenis, pequenos arbustos, herbáceas terrícolas propriamente (autotróficas) e saprófitos (aclorofilados). Nesta definição, estão presentes plantas residentes, ou seja, que permanecerão neste estrato durante todo seu ciclo de vida e plantas transientes, que permanecem temporariamente no estrato herbáceo e completarão seu ciclo de vida em estratos superiores. Por outro lado, a definição de estrato herbáceo pode enfatizar formas de vida. Neste sentido, alguns autores definem o estrato herbáceo sendo composto somente pelas plantas herbáceas propriamente ditas, ou seja, aquelas que completam seus ciclos de vida obrigatoriamente

enraizadas no solo, que não possuem tecido lenhoso, são clorofiladas e mecanicamente independentes (Cestaro et al. 1986, Costa 2004).

As formas de vida vegetal que habitam o estrato herbáceo estão ligadas a importantes processos interativos e, portanto, ao funcionamento do ecossistema florestal como um todo (Roberts 2004, Verstraeten et al. 2013). O estrato herbáceo apresenta grande importância na dinâmica de regeneração das florestas, onde espécies arbóreas podem ter seus crescimentos inibidos por competição com outras formas de vida, pela redução da luz que chega ao solo ou pela transferência de patógenos para os regenerantes (Gilliam 2007, Griffiths et al. 2007). Esta interação pode funcionar como potencial filtro da diversidade arbórea adulta (George & Bazzaz 1999). De modo geral, estudos têm demonstrado relações positivas entre a disponibilidade de luz no sub-bosque e abundância e diversidade do estrato herbáceo (Lima & Gandolfi 2009, Both et al. 2011). Gradientes topográficos e propriedades pedológicas também contribuem localmente para a variação na composição e diversidade deste estrato (Costa 2004, 2006). Em escalas maiores, a variação florística do estrato herbáceo está fortemente relacionada com as variações pedológicas e climáticas (Cicuzza et al. 2013, Jones et al. 2013).

Apesar da importância do estrato herbáceo para as florestas (e.g. no estado de Santa Catarina 25% das espécies da Floresta Ombrófila Densa são herbáceas terrícolas) (Sevegnani et al. 2013), o que se sabe atualmente sobre a ecologia deste estrato provém, sobretudo, de estudos realizados em florestas temperadas e boreais, na Europa e na América do Norte, com poucos estudos realizados em florestas tropicais e subtropicais, como os de Costa (2006) na Amazônia, Jones et al. (2006, 2013) na América central e Both et al. (2011) na floresta subtropical chinesa. Na Mata Atlântica foram desenvolvidos importantes estudos voltados a este grupo de plantas, sobretudo na região sul e sudeste do Brasil (Citadini-Zanette 1984, Cestaro et al. 1986, Polisel et al. 2014). Entretanto, a grande maioria destes estudos teve um cunho florístico e/ou fitossociológico. Estudos analisando fatores ambientais locais envolvidos na abundância e distribuição das espécies herbáceas (Inácio & Jarenkow 2008, Lima & Gandolfi 2009, Santos-Junior et al. 2017) ou ainda, padrões biogeográficos (Vieira et al. 2015) são raros. Além disso, a grande maioria destes estudos consideraram somente plantas herbáceas terrícolas compondo o estrato herbáceo ou ainda somente grupos específicos como as samambaias (Jones et al. 2006), com pouquíssimos estudos considerando outras formas de vida como integrantes deste estrato (Dorneles & Negrelle 1999, Polisel et al. 2014).

O entendimento dos fatores que determinam a distribuição de espécies é um dos focos da ecologia de comunidades (Leibold et al. 2004). As variações na estrutura e composição de espécies podem estar relacionadas a filtros ambientais (Jones e al. 2006), a limitação de dispersão associada à distância geográfica ou ainda a eventos históricos (Condit et al. 2002). Estes processos determinísticos e estocásticos podem simultaneamente influenciar a estruturação das

comunidades e variarem em importância relativa conforme a escala espacial ou temporal analisada (Costa et al. 2005, Jones et al. 2006, Laliberté e al. 2009). Além disso, os processos ecológicos que modulam as comunidades vegetais podem ser alterados de maneira substancial pela fragmentação do habitat, decorrente da atividade humana (Laurance et al. 2006). Essas alterações ocorrem tanto em níveis bióticos quanto abióticos (Tabanez & Viana 2000). Fragmentos florestais, quando comparados a uma área de floresta contínua, podem apresentar aumento da temperatura e diminuição da umidade do solo próximo às bordas (Tabanez & Viana 2000), facilitando a colonização de espécies generalistas, que muitas vezes se tornam muito abundantes na comunidade, e a extinção local de espécies mais sensíveis a alterações abióticas (Lôbo et al. 2011). Geralmente, este processo resulta em uma redução da diversidade de espécies e em uma homogeneização taxonômica entre comunidades (Lôbo et al. 2011). A alteração na composição específica ou ainda funcional das comunidades vegetais em decorrência dos efeitos da fragmentação afeta direta ou indiretamente os processos ecossistêmicos (Díaz et al. 2004, Girão et al. 2007, Carrenõ-Rocabado et al. 2012).

Neste sentido, o estudo do estrato herbáceo é essencial para o entendimento dos processos que modulam as comunidades florestais, pois é um grupo de plantas sensível a alterações ambientais (Richards 1996, Benítez-Malvido 2006) e pode apresentar diferente respostas a fatores ecológicos, devido à variedade de formas de vida que o compõe (Benítez-Malvido & Martínez-Ramos 2003, Both et al. 2011, Pasion et al. 2018). Tendo em vista a grande variação ambiental encontrada na planície costeira e o caráter fragmentado das florestas, este cenário pode ser interessante para mensurar a importância relativa da fragmentação e dos fatores ambientais na estruturação do estrato herbáceo. Além disso, a florestas costeiras são diferenciadas e classificadas de acordo com as características estruturais do componente arbóreo adulto, sendo que pouco se sabe sobre a contribuição do estrato herbáceo para esta diferenciação. Desta maneira a presente tese teve como objetivo principal caracterizar os padrões de diversidade e composição florística do estrato herbáceo das formações florestais que ocorrem na planície costeira no sul do Brasil e avaliar os fatores ecológicos que determinam tais padrões.

Os resultados desta tese foram estruturados na forma de dois artigos científicos. O primeiro artigo, intitulado "**Diversity and floristic differentiation of South Brazilian coastal plain Atlantic forests based on herb layer life-forms**", teve como objetivo avaliar a diversidade e variação florística das formas de vida vegetal presentes no estrato herbáceo entre os três principais tipos de florestas costeiras - Floresta arenosa, turfosa e pluvial – e investigar se as características de diversidade e composição florística contribuíam para a distinção entre estas florestas, comumente distinguidas com base no componente arbóreo adulto. Já o segundo artigo, intitulado "**Ecological drivers of alpha and beta diversity in the herb layer of South Brazilian Atlantic Forest fragments"**, teve como objetivo investigar os fatores ecológicos que controlam a

diversidade alfa e beta do estrato herbáceo em um ecossistema altamente fragmentado como as florestas costeiras.

1.1. Área de estudo e delineamento amostral

O estudo foi realizado em 23 fragmentos florestais localizados na planície costeira do nordeste do Rio Grande do Sul e sudeste de Santa Catarina (Figura 1, Apêndice B), incluindo cinco florestas arenosas, oito florestas turfosas e 10 florestas pluviais. No centro de cada fragmento florestal, foram estabelecidas três parcelas de 10 × 4 m, espaçadas pelo menos a 100 m uma da outra. Estas parcelas foram subdivididas em subparcelas de 2 × 2 m para estimativas de cobertura e densidade de cada espécie do estrato herbáceo. O estrato herbáceo foi considerado incluindo todas as plantas vasculares ≤ 1-m altura, excluindo plantas lenhosas menores que ≤ 10 cm de altura e incluindo espécies herbáceas terrícolas > 1 m altura. As plantas foram classificadas em uma das seguintes formas de vida: trepadeira, herbácea terrícola (incluindo angiospermas e samambaias), palmeira, arbusto (incluindo arbustos e sub-arbustos) e árvore (incluindo arvoretas). A definição e o critério de seleção das áreas de amostragem bem como os critérios de inclusão das plantas, estão melhores detalhados nos artigos a seguir.
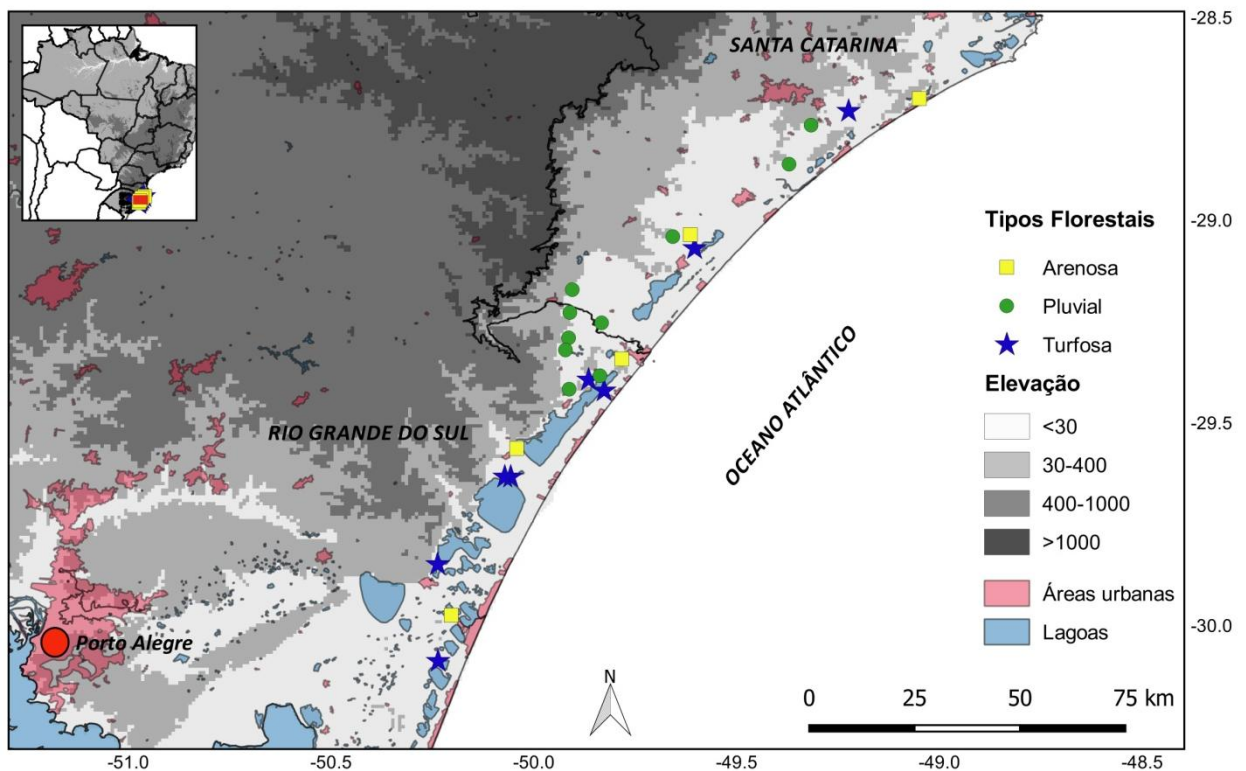
Figura 1. Região de estudo e localização dos fragmentos florestais utilizados na amostragem do estrato herbáceo.

1.2. Padrões florísticos e fitossociológicos

Foram amostrados 10.394 indivíduos, distribuídos em 342 espécies, 203 gêneros e 89 famílias (73 angiospermas e 16 samambaias) (Apêndice A). Cerca de 90% das espécies foram identificadas em nível de espécie (306 espécies). O restante foi identificado ao nível genérico (10 morfoespécies), ao nível de família (duas morfoespécies), ou não puderam ser identificadas (24 morfoespécies). Foram amostradas duas espécies exóticas, a herbácea terrícola *Hedychium coronarium* e a árvore *Syzygium jambos*, ambas originalmente paleotropicais (Ásia tropical).

As 10 famílias com as maiores riquezas foram Myrtaceae com 38 espécies, seguida de Rubiaceae com 22, Lauraceae e Piperaceae 12, Orchidaceae e Poaceae 11, Bignoniaceae e Fabaceae 10, Apocynaceae e Melastomataceae nove. Estas famílias compreenderam 42% das espécies amostradas. Myrtaceae e Rubiaceae foram as famílias com as maiores riquezas em todos os tipos florestais (Tabela 1). Orchidaceae, Bignoniaceae, Piperaceae e Apocynaceae estão entre as 10 famílias mais ricas comuns a todas as florestas, alternando-se em número de espécies de acordo com o tipo florestal.

Tabela 1. Gêneros e famílias com os maiores números de espécies (*S*) do estrato herbáceo de três tipos florestais da planície costeira no sul do Brasil. N = número de fragmentos amostrados em cada tipo florestal.

Arenosa (N = 5)	*S*	Turfosa (N = 8)	*S*	Pluvial (N = 10)	*S*
Total de espécies	194	Total de espécies	158	Total de espécies	208
Myrcia	8	*Mikania*	6	*Myrcia*	8
Eugenia	7	*Myrcia*	6	*Psychotria*	7
Ocotea	7	*Miconia*	5	*Eugenia*	6
Psychotria	6	*Piper*	5	*Piper*	5
Miconia	4	*Psychotria*	5	*Mikania*	4
Mikania	4	*Blechnum*	4	*Ocotea*	4
Piper	4	*Peperomia*	4	*Blechnum*	3
Erythroxylum	3	*Coccocypselum*	3	*Amphilophium*	2
Amphilophium	2	*Eugenia*	3	*Calyptranthes*	2
Annona	2	*Myrsine*	3	*Campomanesia*	2
Myrtaceae	24	Myrtaceae	17	Myrtaceae	23
Rubiaceae	15	Rubiaceae	11	Rubiaceae	14
Lauraceae	10	Piperaceae	9	Não identificadas	14
Orchidaceae	9	Asteraceae	7	Bignoniaceae	9
Poaceae	8	Melastomataceae	7	Fabaceae	8
Bignoniaceae	6	Não identificadas	7	Lauraceae	8
Piperaceae	6	Arecaceae	5	Orchidaceae	7
Apocynaceae	5	Orchidaceae	5	Dryopteridaceae	6
Asteraceae	5	Polypodiaceae	5	Piperaceae	6
Sapindaceae	5	Apocynaceae	4	Apocynaceae	5
Não identificadas	5	Bignoniaceae	4	Arecaceae	5

Os 10 gêneros com as maiores riquezas foram *Eugenia* e *Myrcia* com 11 espécies, *Ocotea* e *Psychotria* com oito cada, *Piper* sete, *Miconia* e *Mikania* com seis cada, *Blechnum* cinco e

Coccocypselum e *Peperomia* com quatro espécies cada. Estes gêneros contribuíram com 21% das espécies amostradas. *Myrcia* foi o gênero mais rico na floresta pluvial e na arenosa e o segundo na floresta turfosa (Tabela 1). *Eugenia*, *Psychotria*, *Mikania* e *Piper* figuraram entre os 10 gêneros mais ricos em todos os tipos florestais, exibindo diferentes riquezas conforme o tipo.

A floresta pluvial exibiu a maior riqueza de espécies, de gêneros e de famílias (208, 158 e 74, respectivamente), seguida da floresta arenosa (194, 134 e 62) e floresta turfosa (158, 102 e 57). Cerca de 17% das espécies amostradas são comuns a todos os tipos florestais (Figura 2). As florestas que compartilharam o maior número de espécies exclusivas foram a floresta arenosa e pluvial, com 17% das espécies comuns a ambas as florestas. A floresta pluvial foi a formação que apresentou o maior número de espécies exclusivas (34%), embora tenha sido também a com a maior riqueza.
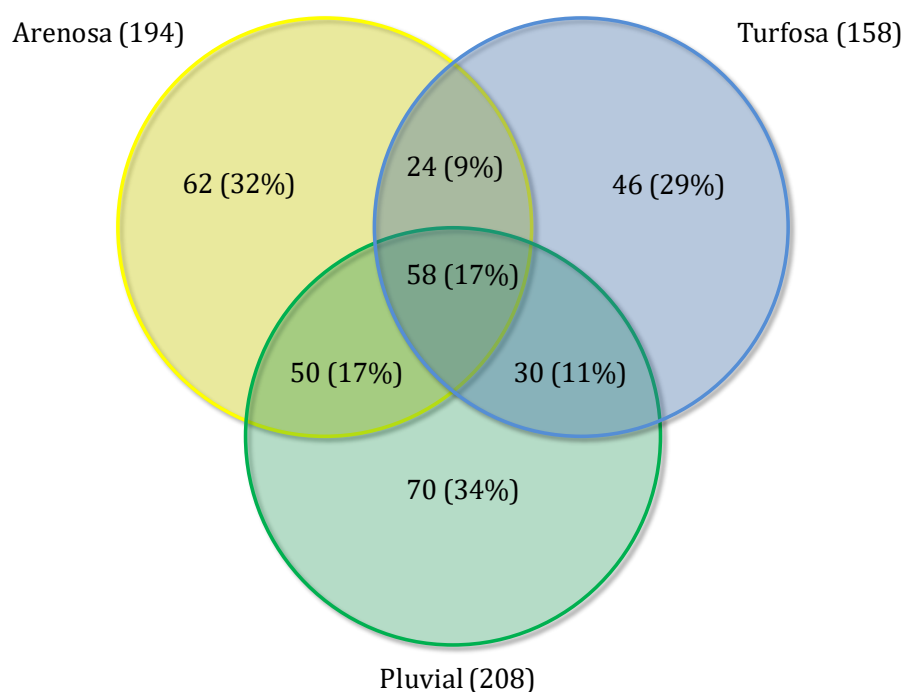
Figura 2. Diagrama de Venn das espécies do estrato herbáceo amostradas em três tipos florestais da planície costeira do sul do Brasil. São dados os valores de riqueza total por cada formação e os valores de riqueza de cada fração (compartilhada e individual) com suas respectivas porcentagens.

Goeppertia monophylla foi a espécie com maior valor de importância quando todas as florestas foram consideradas conjuntamente (Tabela 2). Esta espécie herbácea terrícola foi a que apresentou os maiores valores de cobertura nas florestas pluvial e arenosa. A palmeira *Euterpe edulis* foi a espécie que apresentou os maiores valores de densidade e foi a mais importante na floresta pluvial. As árvores *Guapira opposita* e *Guarea macrophylla* foram as espécies mais frequentes em todo o levantamento, ocorrendo em 20 e 21 das 23 parcelas amostradas, respectivamente. *Guarea macrophylla* foi a espécie mais importante da floresta paludosa, ocorrendo com alta densidade e em todos os fragmentos amostrados deste tipo de floresta.

Tabela 2. Parâmetros fitossociológicos estimados para as espécies do estrato herbáceo (≤ 1 m de altura), amostradas em três tipos florestais ocorrentes na planície costeira do sul do Brasil. São apresentadas somente as espécies com os 10 maiores valores importância (VI), calculado como o somatório dos parâmetros relativos dividido por três. São apresentados também os valores de altura média (ALT) de cada espécie e sua forma de vida. Onde: CA = cobertura absoluta, DA = densidade absoluta, CR = cobertura relativa, DR = densidade relativa, FA = frequência absoluta e FR = frequência relativa.

Todas as florestas (N = 23)	Forma de vida	CA	DA	ALT	CR	DR	FA	FR	VI
Goeppertia monophylla	Herbácea	386	506	69.0	5.8	4.9	60.9	1.1	3.9
Euterpe edulis	Palmeira	271	624	37.8	4.1	6.0	73.9	1.3	3.8
Nidularium innocenti	Herbácea	279	469	49.3	4.2	4.5	52.2	0.9	3.2
Guarea macrophylla	Árvore	181	466	49.4	2.7	4.5	91.3	1.6	2.9
Polybotrya cylindrica	Trepadeira	249	399	37.3	3.8	3.8	65.2	1.1	2.9
Geonoma polyantha	Palmeira	163	212	50.1	2.5	2.0	65.2	1.1	1.9
Psychotria suterella	Árvore	128	241	49.2	1.9	2.3	69.6	1.2	1.8
Mollinedia schottiana	Árvore	143	194	44.8	2.2	1.9	78.3	1.4	1.8
Sorocea bonplandii	Árvore	125	215	50.1	1.9	2.1	69.6	1.2	1.7
Guapira opposita	Árvore	103	203	44.5	1.6	2.0	87.0	1.5	1.7
Total		6612	10394						
Arenosa (N = 5)									
Goeppertia monophylla	Herbácea	107	158	74.7	7.0	6.3	40.0	0.7	4.7
Neomarica candida	Herbácea	46	138	42.5	3.0	5.5	60.0	1.0	3.2
Carex sellowiana	Herbácea	27	151	18.4	1.8	6.0	20.0	0.3	2.7
Psychotria brachyceras	Arbusto	41	77	57.8	2.7	3.1	80.0	1.3	2.4
Guapira opposita	Árvore	33	77	42.4	2.2	3.1	100.0	1.7	2.3
Euterpe edulis	Palmeira	37	85	31.2	2.4	3.4	60.0	1.0	2.3
Mollinedia schottiana	Árvore	36	58	52.7	2.4	2.3	80.0	1.3	2.0
Nidularium innocenti	Herbácea	42	73	52.0	2.8	2.9	20.0	0.3	2.0
Nectandra oppositifolia	Árvore	26	65	29.5	1.7	2.6	80.0	1.3	1.9
Sorocea bonplandii	Árvore	30	58	62.2	2.0	2.3	60.0	1.0	1.8
Total		1525	2519						
Turfosa (N = 8)									
Guarea macrophylla	Árvore	132	405	50.3	6.3	11.6	100.0	2.2	6.7
Nidularium innocenti	Herbácea	193	329	54.8	9.2	9.4	50.0	1.1	6.6
Piper solmsianum	Arbusto	94	253	49.4	4.5	7.2	50.0	1.1	4.3
Polybotrya cylindrica	Trepadeira	121	205	39.6	5.7	5.9	50.0	1.1	4.2
Geonoma schottiana	Palmeira	110	184	48.4	5.2	5.3	87.5	2.0	4.2
Blechnum brasiliense	Herbácea	113	87	71.6	5.4	2.5	87.5	2.0	3.3
Campyloneurum acrocarpon	Herbácea	68	126	32.8	3.2	3.6	87.5	2.0	2.9
Syagrus romanzoffiana	Palmeira	52	101	43.6	2.5	2.9	100.0	2.2	2.5
Asplenium serra	Herbácea	59	97	38.2	2.8	2.8	50.0	1.1	2.2
Psychotria suterella	Árvore	50	91	46.9	2.4	2.6	50.0	1.1	2.0
Total		2108	3490						
Pluvial (N = 10)									
Euterpe edulis	Palmeira	196	482	39.4	6.6	11.0	100.0	1.5	6.4
Goeppertia monophylla	Herbácea	263	327	67.7	8.8	7.5	100.0	1.5	5.9
Geonoma polyantha	Palmeira	133	175	52.0	4.5	4.0	100.0	1.5	3.3
Polybotrya cylindrica	Trepadeira	119	182	35.7	4.0	4.2	90.0	1.4	3.2
Merostachys cf. speciosa	Arbusto	102	200	50.5	3.4	4.6	70.0	1.1	3.0
Sorocea bonplandii	Árvore	88	148	46.3	3.0	3.4	100.0	1.5	2.6
Actinostemon concolor	Árvore	80	115	53.1	2.7	2.6	100.0	1.5	2.3
Mollinedia schottiana	Árvore	76	98	43.5	2.6	2.2	100.0	1.5	2.1
Calyptranthes lucida	Árvores	64	101	53.3	2.1	2.3	90.0	1.4	1.9
Heliconia farinosa	Herbácea	77	84	90.4	2.6	1.9	60.0	0.9	1.8
Total		2979	4385						

Entre as formas de vida (Tabela 2), a única trepadeira que figurou entre as mais importantes foi *Polybotrya cylindrica*, apresentando elevada cobertura nas florestas turfosa e

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pluvial. Já as herbáceas terrícolas foram abundantes nas florestas arenosa e turfosa, com quatro espécies entre as 10 mais importantes em cada tipo florestal. Da mesma forma, as árvores foram igualmente importantes na floresta arenosa e também na floresta pluvial, com quatro espécies entre as 10 mais importantes. As palmeiras, embora com poucas espécies, apresentaram alta densidade e frequência na floresta pluvial e baixa densidade na floresta arenosa. Os arbustos foram pouco representados, sendo que cada tipo florestal apresentou uma espécie exclusiva entre as 10 mais importantes.

Article 1: Diversity and floristic differentiation of South Brazilian coastal plain Atlantic forests based on herb layer life-forms[1]

Abstract

The Brazilian coastal plains comprise very different forest types commonly distinguished by soil conditions. The study of distinct life-forms in the herb layer might contribute to the understanding of forest structure and to the circumscription of forest types. In this paper, we investigated the variation in composition and diversity of the herb layer in three coastal forest types (Dune, Peat and Rain forests) within the Brazilian Atlantic Forest complex and examined if coastal forests' differences, usually characterized by adult trees, are matched by herb layer features. We sampled the herb layer (≤1 m in height) in 23 forest fragments, classifying species in climbers, herbs, palms, shrubs and trees. Peat forest had lower overall diversity relative to Dune and Rain forests. Higher tree species richness and abundance in Rain forest, and higher herbaceous richness and abundance in Peat forest were the major differences between these forest types. Dune forest was similar to Peat forest in relation to herbaceous species and to Rain forest in relation to tree species indicating a transition environment between both forests. Composition between forests is distinguishable for trees and shrubs, but not for climbers and herbaceous species. Thus, the distinctions among these forest types are complex when taking into account the herb layer. Our findings demonstrate the importance of including the herb layer life-forms for a better understanding of the diversity and complexity of tropical and subtropical forests, especially the Atlantic coastal forests, which should be primarily classified as flooded and non-flooded at a regional scale.

Keywords: Dune forest, Ground vegetation, Peat forest, Rain forest, *Restinga*, Subtropical forest

1. INTRODUCTION

The vegetation on the coastal plains in the Brazilian Atlantic Forest Domain (sensu Oliveira-Filho et al., 2015) forms a mosaic that includes forests, shrubby and herbaceous vegetation types, collectively known as Restingas (Marques et al., 2015; Waechter, 1990). The two major forest types of Restingas are the Dune forest, also referred as sandy or psammophilous forests (Dorneles and Waechter 2004a), occurring on well-drained sandy soils, and Peat forests, also referred to as swamp or flooded forests (Menezes and Araujo, 2005; Scarano, 2006; Waechter, 1990), occurring on poorly-drained organic soils. In addition, Atlantic forest sensu stricto (hereafter Rain forest) can also occur in the more continental part of the coastal plains on older soils, richer in nutrients (Marques et al., 2015; Waechter, 1990). This Rain forest is considered to be an extension of the high-diversity slope forests occurring on the mountain chains and extending to the subtropical region along the Brazilian eastern coast (Negrelle, 2002; Scarano, 2002). Structural and diversity differences among these coastal forests have been described (Assis et al., 2011; Eisenlohr et al., 2013; Záchia and Waechter, 2011), and related to some major ecological drivers, such as soil salinity, sandiness, and flooding regimes (Eisenlohr et al., 2013; Marques et al., 2015; Neves et al., 2017). Better soil conditions in the Rain forest, such as higher nutrient availability, sustain taller individuals and tree communities with larger basal area when compared to Restinga forests (Assis et al., 2011; Eisenlohr et al., 2013). On the other hand, sandiness and flooding act as abiotic filters on Restinga forests, limiting the occurrence of species that are able to colonize the inland Rain or Seasonal forests (Oliveira-Filho et al., 2015; Rambo, 1954). Thus the Restinga forests often show less diverse communities and may represent subsets of the more diverse Rain Forest (Oliveira-Filho et al., 2015; Scarano 2002).

Information on ecology and phytogeography of coastal forests is, however, mostly centred on the tree layer. As for other tropical and subtropical forests, much less information on the herb layer is available, despite the ecological importance and the contribution of this component to plant diversity (Both et al., 2011; Gentry and Dodson 1987; Linares-Palomino et al., 2009). The herb layer commonly encompasses distinct plant life-forms, such as obligate terrestrial herbaceous species (Poulsen and Balslev, 1991), also called "resident species" because they remain all their life cycle in the forest understory (i.e. lower forest stratum), and as seedlings and saplings of woody species, also called "transient species" because they grow and complete their life cycle into higher forest strata (Gilliam, 2007). Interactions among these different life-forms (e.g. trees, shrubs, herbs, climbers) significantly contribute to forest dynamics and can indicate distinct environmental conditions (Benitez-Malvido 2006; Gilliam, 2007). Herb layer species respond mostly to soil and light gradients (Both et al., 2011; Denslow and Guzman, 2000) and their responses may differ according to life-forms (Deng et al., 2008; Harms et al., 2004; Murphy

et al., 2016). For example, tree saplings tend to be more abundant in less stressful environments (Harms et al., 2004), whereas herbaceous species may respond differently to environmental gradients depending on their taxonomic group, such as ferns and angiosperms (Costa, 2006; Jones et al., 2014).

Although previous studies have demonstrated clear differences in physiognomy, structure and diversity among coastal forests at local scales, these forests can be floristically less distinguishable at larger scales (Marques et al., 2011). Thus, physical characteristics such as flooded/unflooded may not be sufficient for forest differentiation within the coastal plain at all scales (Marques et al., 2011). Further, these findings are based only on tree species distributions. Studies on herb layer species variation in coastal forests are scarce, but there is some evidence that distribution patterns based on herbaceous species differ from those of the trees in the Atlantic Forest complex (Vieira et al., 2015). These authors suggested differences related to evolutionary strategies associated to growth habits, as well as to a high level of rarity and more restricted geographical distribution. Since life-forms or plant functional groups can tightly respond to environmental conditions (Deng et al., 2008), studies concerning the herb layer species along different forests types, with distinction of different life-forms or species groups, are important for a better understanding of structural and floristic patterns (Harms et al., 2004), and might contribute to a more detailed characterization of forest types, especially in a vegetation complex and increasingly threatened ecosystem as the Brazilian Atlantic coastal forests.

In this paper, we present the first study on a broad geographic scale that explores diversity and floristic differentiation of the herb layer in Brazilian coastal Atlantic Forests. Our objective was to assess the contribution of herb layer life-forms to diversity and floristic variation in the three main coastal forest types: Dune forest, Peat forest and Rain forest. In addition, we investigated if herb layer characteristics match coastal forest distinctions made commonly on the basis of the tree layer. We address the following questions: (i) Do species diversity and the relative contribution of individual life-forms to richness, cover and density of the herb layer differ among forest types? (ii) How much does the floristic variation of the herb layer life-forms contribute to differentiation of a priori defined forest types? Assuming that soil is the major factor driving plant community structure in coastal forests (Marques et al., 2011), we expected to find higher overall species diversity in Rain Forest than in Dune and Peat Forest, because the soils in the former are richer in nutrients and remain mostly unflooded; additionally, they occur in the proximity of the more diverse Atlantic Forest of the mountain slopes. As stressful environments filter out those species without specific adaptations (e.g. herbs with clonal subterraneous organs might be more abundant in sandy soils), we expected that the relative contribution of different life-forms would change among forests. Consequently, we expected that the studied forest types would form distinct floristic groups with distinct diversity patterns in the forest herb layer.

2. MATERIAL AND METHODS

2.1. Study area

The study was conducted in forest fragments located in the coastal plain of northeastern Rio Grande do Sul and southeastern Santa Catarina, the two southernmost states of Brazil (Fig. 1 in general introduction). The coastal plain is geologically recent, formed mostly by sand and lagoonal deposits originated from glacio-eustatic fluctuations of the sea level during the Quaternary (Tomazelli et al., 2000), constituting an extensive flat and low landform (up to 30 m a.s.l) where a great number of coastal lagoons occur. Due to several distinct geological deposits, the region shows a great variety of soil types, as Argisols and Arenosols on sand deposits, and Gleysols and Histosols on lagoonal deposits (IBGE, 1986). The climate of the study area is humid-subtropical, of the Cfa-type according to the Köppen system (Alvares et al., 2013). Annual average temperatures range from 18 to 20°C and annual rainfall is $\cong$ 1600 mm (Alvares et al., 2013).

The South Brazilian coastal plain was originally covered by large continuous forests but is nowadays a severely fragmented forest landscape (Vibrans et al., 2013). The main threats on coastal plain forests, besides the increasing area of cities and beach settlements, are cattle grazing (mostly on areas of Dune forests), agricultural activities, tree monocultures, invasive exotic species, soil drainage (in Peat forests) and selective logging (in Rain forests e.g. the palm heart *Euterpe edulis* Mart.). Many forest fragments are now immersed within an agricultural matrix or to a lesser degree surrounded by forestry with exotic trees, such as *Pinus* and *Eucalyptus* species. Because forest fragments with well-preserved natural conditions are presently scarce in the coastal plain, only relatively few fragments could be effectively sampled, and a balanced sampling design among forest types was not possible in our study.

2.2. Sampling

Field sampling was carried out in forest fragments scattered throughout the southernmost coastal plain related to the Brazilian Atlantic forest. We selected 45 forest fragments by Google Earth and checked their conservation status and general ecological conditions in the field. We classified the forest types as proposed by Waechter (1990), who defined major categories according to physiognomy and environment: i) Dune forest - developing on recent sandy unflooded soils; ii) Peat forest - developing on organic and permanently flooded soils; iii) Rain forest - developing on more inland and more developed unflooded soils. To improve our visual distinction we used digital soil classification maps of the Radam-Brasil project (available in: https://mapas.ibge.gov.br). Criteria for selection of forests for the study were that

they had no evidence of cattle grazing, showed no signs of tree extraction, and were not severely invaded by exotic species (e.g. *Asparagus* sp. and *Hedychium coronarium* J.Koenig). Considering these features, 23 forest sites were chosen for data sampling, including five Dune forests, eight Peat forests and 10 Rain forests. All forest areas had a flat topography, with altitudes up to 30m a.s.l, which corresponds to the height limit of coastal plain as a geomorphologic region in southern Brazil (IBGE, 1986).

In the centre of each forest stand we established three plots of 10 × 4 m, spaced at least 100 m apart from each another. Plots were subdivided into 2 × 2 m subplots for cover estimates and individual counts of each herb layer species. In the case of clonal species, patches located less than 20 cm apart one from another were counted as a single individual (Costa, 2006). Cover was estimated as the percentage of horizontal projection of leaf area of each species, using the logarithmic scale proposed by Causton (1988). We considered each forest stand as a sampling unit for all statistical analyses, thus density was the sum of all individuals and cover was the sum of all values assigned for the species in the forest site.

We defined herb layer vegetation as all vascular plants ≤ 1-m height; a common definition adopted by other authors (Both et al., 2011; Gilliam, 2007; Lu et al., 2010). This definition included herbaceous species (i.e. residents) as well as climbers, shrub and tree saplings (i.e. transients). However, we excluded shrubs and tree seedlings ≤ 10 cm in height and included terrestrial herbaceous species > 1-m height. By this, we excluded newly germinated seedlings and plants that still had their cotyledons, due to the difficulty to identify plants at this stage to the species level (Harms et al., 2004). The height enlargement was adopted to include such important herbaceous families in the Atlantic Forest as the Heliconiaceae and Marantaceae (Santos-Junior et al., 2017). All plants were classified into one of the following life-forms: (1) climbers, (2) herbs (including angiosperms and ferns), (3) palms, (4) shrubs (including spreading-shrubs and sub-shrubs) and (5) trees (including treelets). These life-forms follow general definitions found in several publications, such as Flora de São Paulo, Flora Catarinensis, Flora Arbórea do Rio Grande do Sul, and the Flora do Brasil site. The separation of palms from other life-forms was due to the distinctive architecture, and importance of this plant family in the structure and dynamics of neotropical forests (Harms et al., 2004).

2.3. Data analysis

To compare species richness among forest types we first estimated richness using rarefaction to control for differences in abundance among samples (Gotelli and Colwell, 2011). Rarefaction was conducted based on the forest stand with the smallest abundance of individuals. To assess species diversity we calculated the Shannon (H') and Simpson (1/D) indices for each

plot. Rarefaction and indexes were calculated based on both total cover and density of species. We also evaluated the relative contribution of each life-form to richness, density and cover of the herb layer in each forest type. The relative measures of each life-form were calculated as a percentage of the total within a forest site. Differences in richness, diversity indices and relative measures of life-forms among forest types were tested by One-way Analysis of Variance (ANOVA) with Tukey's Honestly Significant Difference (Tukey's HSD) pair-wise tests. ANOVA assumptions were evaluated before performing the analysis. Some variables showed normal distribution but did not meet the homogeneity of variance assumption. In these cases, we used the Welch test for unequal variance to compare differences between variables means (Lu and Yuan, 2010).

To disentangle how herb layer species contributed to floristic differentiation of forest types, we first explored the floristic variation for each life-form among forest types using Metric Multidimensional Scaling (MDS) based on Euclidean distance. We used Hellinger's transformation on abundance data of species before performing MDS. Statistical differences among forest types were tested by Multivariate Analysis of Variance (MANOVA) and contrast tests. MANOVA was performed with the statistics test Sum of Squares between groups - *Qb* (Pillar and Orloci, 1996), with 10000 permutations, based on a Euclidian distance matrix, which is most appropriate for unbalanced data (Pillar, 2013). For these analyses, palm species were pooled within trees or shrubs because we sampled only five (two trees and three shrubs). However, we also calculated separate MANOVAs for tree and shrub assemblages without palm species to examine the palm abundance effects. In order to see how the abundance of each life-form was contributing to the full herb layer floristic differentiation among forests, we ran a Canonical Analysis of Principal Coordinates (CAP) (Anderson and Willis, 2003) using the abundance of the five life-forms as constraining variables. This analysis was also based on Hellinger's transformation on abundance data and Euclidean distance among forest stands. Unconstrained and constrained ordinations should be done with the same dissimilarities and transformations to their joint information to be interpretable (Anderson and Willis, 2003). Overall test for significance of CAP analysis as well as constraints and axes significances were tested by 9999 permutations with anova.cca function in 'vegan' package (Oksanen et al., 2015). To make comparisons between each life-form possible, frequency was used as the abundance parameter in these analyses, obtained from the sum of species occurrence in each subplot within a forest site.

MANOVA and contrast tests were performed in the software MULTIV (available at http://ecoqua.ecologia.ufrgs.br). Rarefaction (rarefy function), diversity indices (diversity function), MDS and CAP (capscale function) were performed with the package 'vegan' (Oksanen et al., 2015) in the R Statistical Environment (R Core Team, 2015).

3. RESULTS

We recorded 10,394 individual plants belonging to 342 species in the herb layer of the three forest types (Appendix A). Almost 90% of our taxonomic list was identified to the species level (306 species). The remaining 10% of the sampled taxa were identified to the generic level (10 morphospecies), to the family level (two morphospecies), or unidentified (24 morphospecies). Only two species were exotic in the sampled flora, the large herb *Hedychium coronarium* (Zingiberaceae) and the tree *Syzygium jambos* (L.) Alston (Myrtaceae); both species are originally paleotropical (tropical Asia).

Overall, Rain forest exhibited the highest species richness (208), followed by Dune forest (194) and Peat forest (158). Considering the total area sampled in each forest stand (120m2), herb layer richness varied from 55 to 76 in Rain forest, 47 to 74 species in Dune forest, and 33 to 63 species in Peat forest. When the mean rarefied species richness among forests was compared, Rain and Dune forest did not differ and both were richer than Peat forest (Table 1). A similar pattern was observed for Shannon index. Rarefaction and Shannon index had similar results based on cover or density data, and so only the results obtained from cover were reported (Table 1). All three forests did not differ for Simpson index based on species cover data, but for Simpson based on density data, Peat and Rain forests differed significantly, being lower in Peat forest. Dune forest did not differ and showed intermediate Simpson values between both forest types.

Regarding species richness according to life-forms, 146 were trees, 79 were herbaceous, 51 were climbers, 33 were shrubs and five were palms. One species was a saprophyte (*Voyria aphylla* (Jacq.) Pers. – Gentianaceae) and was excluded from the analyses because this species is seasonal in aboveground vegetation and so could not be accurately sampled in all sites. The 24 unidentified species, two species identified to generic level and one to family level could not be assigned to any of the above-defined life-forms, and were also excluded from analyses. Tree species were the most diversified life-form in terms of species richness in all forests, but for cover and density, herb species were likewise or even better represented in both types of Restinga forests (Dune and Peat) (Table 1). Analyzing the relative contribution of each life-form to overall richness, density, and cover showed different patterns between forest types (Table 1). Herbaceous species had higher relative richness, density and cover in Peat forest when compared to Rain forest. In contrast, tree species showed higher relative richness and cover in Rain forest when compared to Peat forest. Dune forests, however, mostly did not differ from the other two forests in terms of relative contribution of herbs and trees to richness, density and cover, except for the higher herb density in relation to Rain Forest and higher tree richness in relation to Peat forest. The relative contribution of palms to total density was equal in Peat and Rain forest, but higher in these forests in relation to Dune forest. There were no differences concerning relative

richness and cover of palms among all forest types. For climbers and shrubs there were no significant differences among all forests for any parameter.

Floristic variation explored by the ordination methods evidenced a great dispersion of sites on the multivariate space especially for Dune and Peat forests, unlike for Rain forest that had the sites more closely grouped, indicating less variation in species composition between Rain forest sites. The MDS and MANOVA showed different patterns of differentiation according to each herb layer life-form (Fig. 2; Table 2). For climbers, species composition was similar among forests, as indicated by the larger overlap of forest types and supported by MANOVA analysis. For herbaceous, species composition in Peat forest significantly differed from the other two types, while Dune and Rain forest did not. Considering shrubs, all forest groups differed significantly, independently of palm shrubs presence (data not shown). For trees, species composition was dissimilar among all forest types, although there was some overlap between Dune and Rain forest in the MDS space. However, when the tree palms were excluded, Dune and Rain forests were not different from each other in terms of species composition (Table 2).

The CAP ordination was significant (F = 1.7495, P = 0.001) and the first two axes explained 62% of the variation in species distribution across forest types, and the first CAP axis was significant (F = 3.6095, P = 0.002) (Fig. 3). The first axis markedly discriminated Peat and Rain forests sites. Herbaceous (F = 3.2250, P = 0.001) and tree (F = 1.8728, P = 0.019) species were the life-forms that significantly contributed to the differentiation of these forests. While herbaceous plants were correlated with Peat forests, abundance of trees was correlated with Rain forests. Dune forests clearly occupied an intermediate position between the other two forests, having sites where trees contributed more with the herb layer abundance and other sites where herbaceous were also prominent. The abundance of climbers (F = 1.3195, P = 0.149), palms (F = 1.1106; P = 0.253) and shrubs (F = 1.2199, P = 0.181) were not significant for the differentiation of forest types.

4. DISCUSSION

Our study framework based on herb layer provided important insights for the understanding of coastal forest diversity and species distribution. First, Rain forest was richer and more diverse than Peat forest, but similar to Dune forest. Second, the higher richness and abundance of herbaceous species in Peat forest and the higher richness and abundance of trees in Rain forest were the major differences between these forests, which also lead to the herb layer floristic distinction. Dune forests were intermediate between Peat and Rain forests, showing some similar features to Peat forest regarding herbaceous life-form and to Rain forest regarding

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trees. Our results suggest that the distinction of these forest types, commonly made on the basis of the tree layer, is more complex when taking into account more life-forms present in the forest herb layer. Species composition is still distinguishable for shrubs and trees when palms are considered, but not for climbers (all types had similar composition) and herbaceous species (Dune and Rain forests were similar). Moreover, diversity and community proportion of life-forms have also shown some similar patterns, indicating that Dune forest seems to be a transition environment between Rain and Peat forests.

Notably, the total richness found in the present study evidenced the high contribution of the herb layer to the total diversity of subtropical coastal forests. Other studies conducted with herb layer, as in a one hectare plot in the Atlantic coastal forest (Negrelle, 2002) and in a chronosequence of subtropical forests in China (Both et al., 2011), found similar values of richness (398 and 240 species, respectively). These studies also found tree species being the most species rich life-form, a pattern observed for all forest types here. Nonetheless, the contribution of non-trees to total richness exceeded more than 50% in some sites (e.g. in Peat forests) highlighting the importance of this ensemble to the total plant diversity in forests, as showed by studies conducted in the tropical region (Gentry and Dodson, 1987; Linares-Palomino et al., 2009). We especially emphasize the contribution of resident herbaceous species – the second most important life-form in terms of richness and often with high cover values. In fact, this group of species may correspond up to 25% of plant species in Rain forests in south Brazil (Sevegnani et al., 2013). Moreover, we showed that Restinga forests might present a high number of species, particularly the Dune forests. Thus, although these forests are recognized as species-poor environments (Eisenlohr et al., 2013; Scarano, 2002; Waechter, 1990), they can substantially contribute to diversity of a specific plant group (e.g. herbaceous species in Peat forests) or even contribute to the regional diversity, as demonstrated by Draper et al. (2018) for Amazonian Peat forests where this forest type enhances the beta diversity.

Diversity and abundance of life-forms varied between forests, which can be associated to distinct environmental conditions of each forest type (Deng et al., 2008). A higher diversity of trees on well-drained soils has been shown (Deng et al., 2008), as flooding can constrain the recruitment of many species of this life-form (Stevenson, 2007). The Peat forests of our study showed lower richness and abundance of trees in comparison to the other two forests, which may be related to such constraints. On the other hand, coverage, density and even richness of herbaceous species were higher in Peat forest, especially when compared to Rain forest. We know that herbaceous species are sensitive to environmental changes (Murphy et al., 2016), and some forest disturbances, such as flooding, might favour the establishment of species with clonal growth (Schleuning et al., 2008). Thus, particular community patterns of distinct life-forms in the

forest herb layer may be important for a better characterization of the forest structure and its environment.

Dune and Rain forest were quite similar in terms of diversity and proportion of each life-form in the forest herb layer. The higher diversity of the Rain forest has been shown by previous works focused on the tree layer (Marques et al., 2011, Oliveira-Filho et al., 2015). The coastal-plain Rain forests are an extension of the more diverse Atlantic rain forests occurring on the mountain slopes, and they also have more fertile and developed soils when compared to Dune forests (Marques et al., 2015). These, in contrast, occur on recent and stressful soils, where sandiness and salinity are major constraints for the establishment of many species occurring in Rain forests (Oliveira-Filho et al., 2015). Although soil conditions of these forest types differ for nutrients (Marques et al., 2011), they are similar in terms of being unflooded. Unflooded conditions are more suitable for the establishment of trees (Deng et al., 2008), a life-form better represented in Dune and Rain forests (in terms of richness and abundance) than in Peat forests. Peat forests are stressful habitats mostly due to often long-lasting flooding, which limit the establishment of Rain forest tree species (Scarano, 2006). Accordingly, Peat forests are often described as species-poor and structurally less complex, showing a monodominant or oligarchic pattern in terms of tree species abundance (Dorneles and Waechter, 2004b; Kurtz et al., 2013; Mancino et al., 2015).

Dune and Rain forest were also similar for the species composition of herbaceous and climber life-forms. At the same time, the higher palm density in Rain forests was a noticeable distinction between them, as shown for species composition of trees (palm trees were pooled together). This difference was influenced by the high abundance of *Euterpe edulis*, a very common species sampled in studies performed with tree layer of Atlantic Rain forests (Mancino et al., 2015; Orihuela et al., 2015). Drier environments such as those found in coastal Dune forests are less suitable for palms (Dorneles and Waechter, 2004a). Likewise, these environments might favor the establishment of xerophytic species, such as grasses, bromeliads, and eventually thorny low trees (Záchia and Waechter, 2011).

5. CONCLUSIONS

Our findings evidenced the importance to disentangle the herb layer life-forms for a better understanding of the diversity and complexity of subtropical Atlantic coastal forest. We found that the major life-forms that occurred in the herb layer (i.e. trees and herbaceous plants) varied among forests in terms of composition, diversity and abundance, and may contribute to floristic and structural differentiation of coastal forests. We also found that Dune forest, one of the

Restinga forest types occurs presently with very few remnants in the study region, and that these forests show a relatively high species richness and were more similar to Rain forests than to Peat forests in terms of composition, diversity and relative contribution of distinct life-forms to the herb layer. Thus, our results indicate that at least for the regional scale we worked on the forests within coastal plains should be primarily divided into unflooded (Dune and Rain forests) and flooded (Peat forest). In addition, the few forest remnants in the South Brazilian coastal plain hold high plant species diversity in the herb layer that greatly contribute to the whole forest structure and characterization. Therefore we suggest that conservation initiatives should be developed based on the community as a whole, and not only on the most commonly focused adult trees.

6. TABLES AND FIGURES

Table 1. Diversity parameters and the relative contribution of different life-forms to cover, density and richness of the herb layer in three forest types of South Brazilian coastal plain Atlantic forest. Numbers are mean ± standard deviation. Differences among forests were assessed by ANOVA and Tukey's HSD pairwise tests. Different letters in the same row indicate significant differences.

Forest types	Dune (n=5)	Peat (n=8)	Rain (n=10)	ANOVA	
Diversity				*F*	*P*
Rarefied richness	48 ± 6.3[a]	38 ± 7.6[b]	52 ± 3.8[a]	13.26	**0.0002**
Shannon (H')	3.48 ± 0.2[a]	3.15 ± 0.3[b]	3.60 ± 0.1[a]	9.143	**0.001**
Simpson (1/D) cover	20.78 ± 7.1	16.36 ± 6.4	17.99 ± 4.6	2.764	0.08
Simpson (1/D) density	14.41 ± 3.5[a, b]	11.24 ± 5.1[b]	17.99 ± 3.2[a]	6.432	**0.006**
Life-forms					
Climber					
Cover	8.82 ± 3.59	12.84 ± 7.86	13.79 ± 5.82	1.077	0.36
Density	7.34 ± 3.89	11.22 ± 7.27	14.83 ± 6.70	2.319	0.124
Richness	10.59 ± 3.56	16.10 ± 8.15	16.31 ± 4.16	1.849	0.183
Herb					
Cover	34.38 ± 5.83 [a, b]	37.58 ± 11.51 [a]	23.09 ± 7.55 [b]	6.512	**0.006**
Density	36.92 ± 6.29 [a]	35.56 ± 15.44 [a]	20.94 ± 7.07 [b]	5.717	**0.01**
Richness	19.86 ± 6.13 [a, b]	26.37 ± 9.59 [a]	15.36 ± 3.60 [b]	5.921	**0.009**
Palm					
Cover	6.45 ± 4.55	10.39 ± 4.27	11.50 ± 3.33	2.798	0.085
Density	7.05 ± 5.29 [a]	10.23 ± 4.66 [a, b]	14.70 ± 5.11 [b]	4.3	**0.028**
Richness	3.36 ± 2.42	8.19 ± 4.44	4.17 ± 1.26	3.232*	0.092
Shrub					
Cover	13.70 ± 2.40	9.48 ± 7.15	10.87 ± 5.65	0.826	0.452
Density	15.58 ± 3.19	11.98 ± 10.86	12.15 ± 6.94	1.013*	0.39
Richness	12.50 ± 2.52	8.52 ± 3.24	10.14 ± 2.69	2.98	0.073
Tree					
Cover	36.65 ± 4.56 [a, b]	29.72 ± 10.27 [a]	40.75 ± 5.91 [b]	4.783	**0.02**
Density	33.12 ± 2.11	31.00 ± 14.74	37.39 ± 6.94	1.642*	0.234
Richness	53.68 ± 4.93 [a]	40.81 ± 8.52 [b]	54.01 ± 5.09 [a]	10.65	**0.0007**

*Welch test for unequal variances.

Table 2. Multivariate analyses of variance performed with the statistics test Sum of Squares between groups - *Qb* (Pillar & Orloci 1996), based on a Euclidean dissimilarities of herb layer life-forms sampled in 23 sites of three coastal Atlantic forest types: Dune, Peat and Rain forest. P-value was obtained by 10.000 permutations.

Source of variation	Climbers		Herbaceous		Shrubs		Trees		Trees without palms	
	SS	*P*	*SS*	*P*	*SS*	*P*	*SS*	*P*	*SS*	*P*
Between groups	637.95	0.1081	2777.4	**0.0004**	2045.5	**0.0002**	3718.4	**0.0002**	2726.9	**0.0002**
Contrasts										
Dune *vs* Peat	300.9	0.2309	1539.4	**0.0039**	782.38	**0.0088**	1248.2	**0.014**	1147.5	**0.0088**
Dune *vs* Rain	373.47	**0.0391**	802.5	0.0658	730.93	**0.0049**	1111.3	**0.0204**	756.8	0.0562
Peat *vs* Rain	286.62	0.1838	1768.3	**0.0003**	1439.6	**0.0001**	2923.8	**0.0001**	2024.9	**0.0001**
Within groups	4042.1		10681		5004.8		11064		9466.4	
Total	4680		13458		7050.3		14782		12193	

Fig. 2. Metric multidimensional scaling (MDS) ordinations yielded from herb layer composition in the 23 forest fragments representing three forest types (Dune, Peat and Rain forests) in the coastal plain of the South Brazilian Atlantic forest.
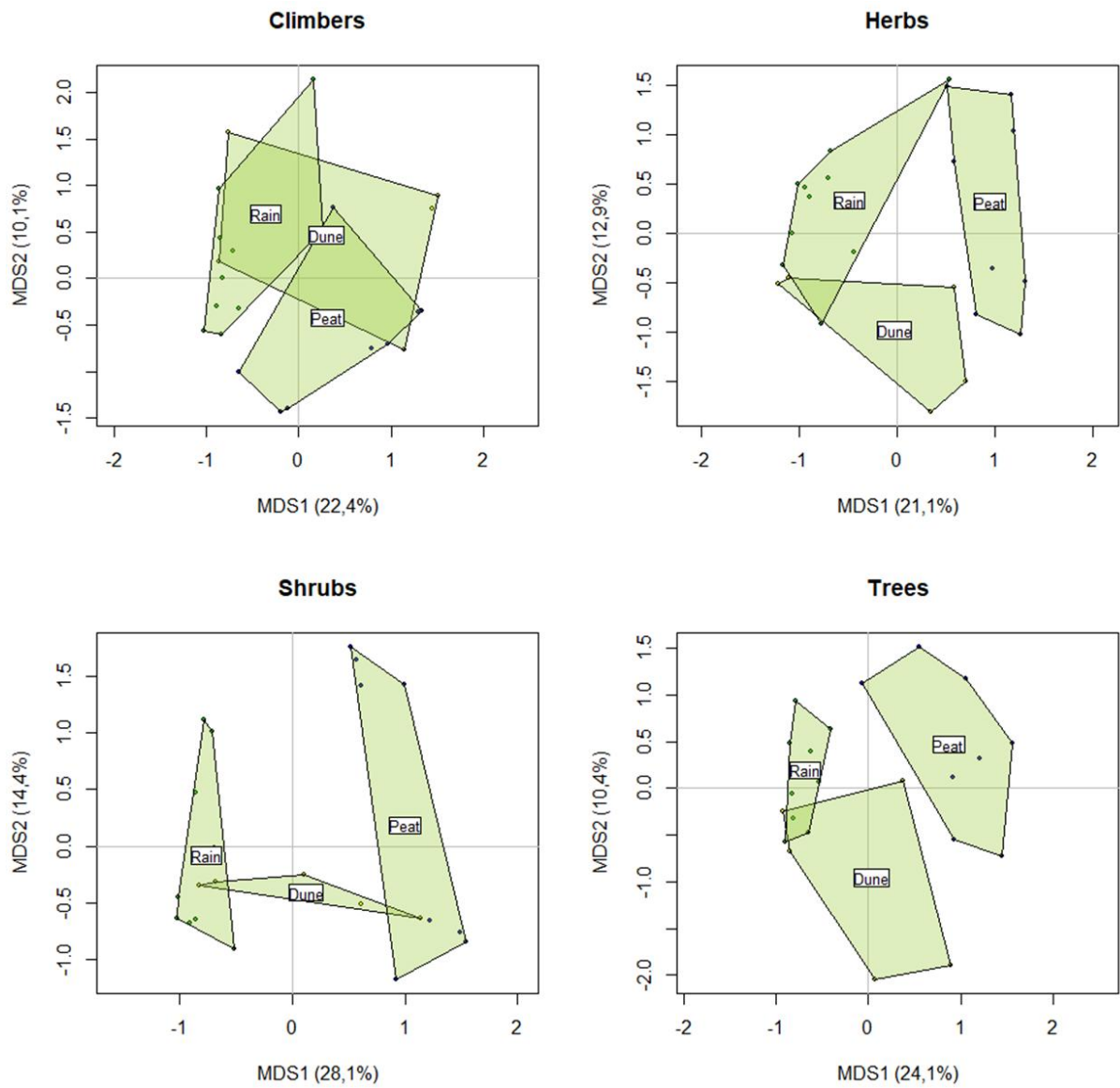
Fig. 3. Canonical analysis of principal coordinates (CAP) for the composition of all herb layer of three forest types (Dune, Peat and Rain forests) in the coastal plain of the South Brazilian Atlantic forest using life-form abundances as the constraining variable.
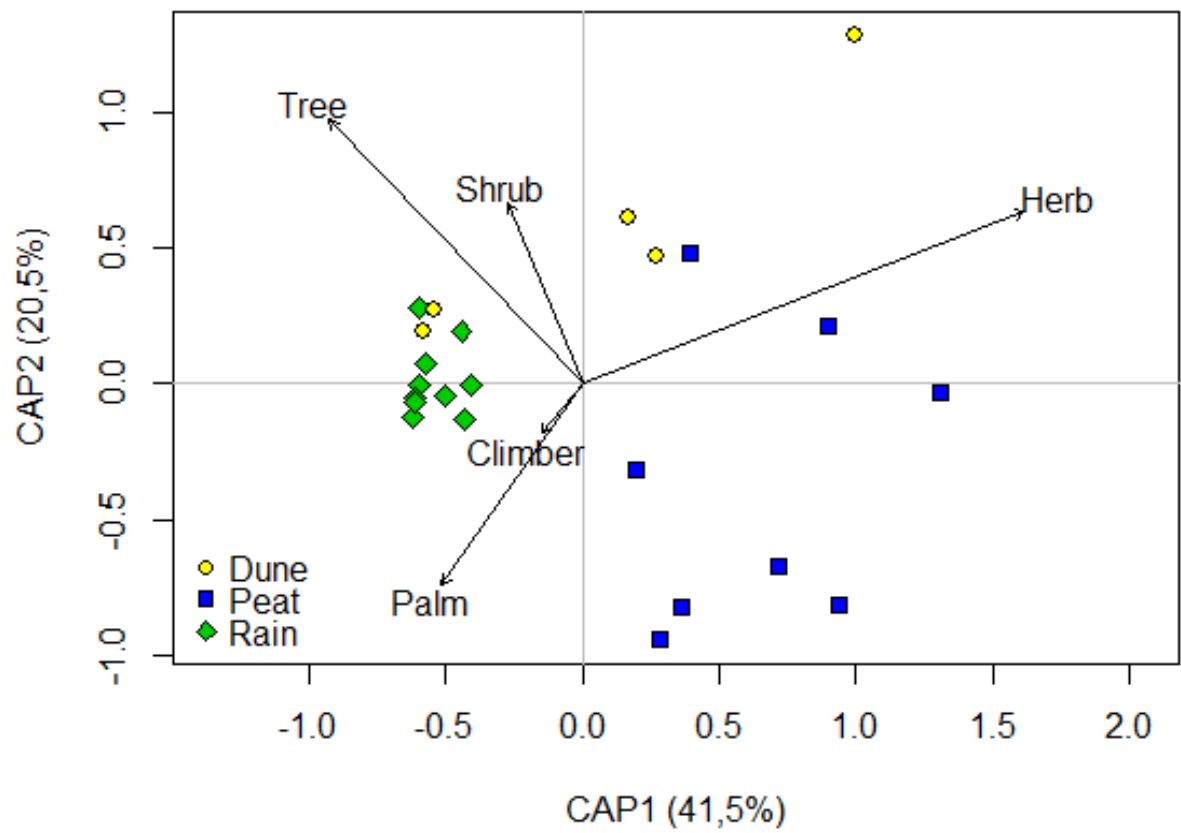
Article 2: Ecological drivers of alpha and beta diversity in the herb layer of South Brazilian Atlantic Forest fragments

Short running title: Alpha and beta diversity in the herb layer of Atlantic Forest

Abstract

Forest fragmentation can affect distinct plant groups, such as trees, shrubs, climbers and herbaceous plants, which may respond differently to abiotic changes. Different soil conditions and climate variables are considered to be the major drivers structuring herb layer communities. In the Brazilian Atlantic Forest, the coastal plain formations occur on striking different soil types and the landscape is highly fragmented, providing an interesting scenario for the study of fragmentation effects and ecological drivers on plant communities. Here, we investigated the ecological factors driving alpha and beta diversity of the herb layer in forest fragments scattered across the coastal plain of Atlantic Forest in southern Brazil. We sampled the herb layer (≤1 m in height) in 23 forest fragments, distinguishing species into five life-forms: herbs, shrubs, palms, trees, and climbers. Variation partitioning and regression analyses indicated that soil type is the major driver of alpha and beta diversity of the herb layer when all life-forms were considered together. Others factors were similarly important for beta diversity, as space for climbers and shared environmental effects (i.e. climate and soils) and space for trees. Soil type affected alpha diversity for trees and climbers. We could not detect strong fragmentation effects on alpha and beta diversities on each herb layer life-form, but for herbaceous plants we found a positive relationship between fragment area and species richness. We showed that herb layer life-forms are shaped by deterministic processes mostly related to soil conditions, but other ecological drivers may be important when disentangling the herb layer life-forms. Although habitat fragmentation can impose drastic changes on diversity and composition of herb layer assemblages, soil conditions and climate variables still contribute to explaining diversity variation in a steep environmental gradient, despite fragmentation effects.

1. INTRODUCTION

Habitat fragmentation and their consequences on patch and landscape configurations has been widely recognized to cause biodiversity loss and alter structure and species distribution in forest ecosystems (Fischer and Lindenmayer 2007). Habitat loss and edge effects as sub-components of fragmentation can drastically affect important ecological processes as biotic interaction, dispersion and succession (Harper et al. 2005). Forest habitats that are affected by these factors show an increase of invasion of disturbance-adapted plants (Costa and Magnusson 2002, Laurance et al. 2006) and an impoverishment of late-successional species, leading to promote biotic homogenization (Lobô et al. 2011) and consequently changes in functional and species compositions of communities (Laurance et al. 2006, Girão et al. 2007). Additionally, habitat fragmentation imposes new abiotic experiences, as an increase in wind turbulence and light availability, as well as changes in soil conditions in the patch edges (Laurance et al. 2002, Fischer and Lindenmayer 2007). These effects are believed to affect distinct plant groups, including trees, shrubs, lianas and herbaceous plants, which may respond differently to these abiotic changes (Benítez-Malvido and Martínez-Ramos 2003, Laurance et al. 2014, Pasion et al. 2018). In this sense, studies that address comparisons across multiple plant life-forms provide a better understanding of the fragmentation effects and habitat loss on plant communities as a whole (Pasion et al. 2018), and are important for identifying common factors structuring forest plant communities (Jones et al. 2013). However, relatively few studies have looked simultaneously at patterns of species richness and composition of more than one group in fragmented ecosystems (Yu et al. 2015), especially for life-forms inhabiting the forest herb layer (Benítez-Malvido and Martínez-Ramos 2003, Paison et al. 2018).

The herb layer is an important component occurring inside tropical and subtropical forests, comprising an ecologically and taxonomically diverse layer (Gentry and Dodson 1987, Both et al. 2011), which commonly encompasses distinct plant life-forms, such as obligate terrestrial herbaceous species (Poulsen and Balslev 1991), palms, climbers, and seedlings and saplings of woody species (Harms et al. 2004, Both et al. 2011). Early studies have demonstrated that herb layer species (i.e. herbaceous *vs*. woody species) compete directly and indirectly for space and environmental resources, and that these interactions contribute to forest dynamics (Benitez-Malvido 2006, Griffiths et al. 2007). At a local scale, the major mechanisms governing herb layer communities are topographic variations and the associated soil conditions, as well as light gradients in the understory (Costa 2006, Jones et al. 2006). Herb layer variations are also affected by tree structure and composition, since canopy trees may change the luminosity reaching the forest floor, litter accumulation and soil properties (Barbier et al. 2008, Albrecht and McCarthy 2009, Both et al. 2011). At large spatial scales, herb layer is mostly shaped by climate

and soils conditions (Jones et al. 2013, Murphy et al. 2016). In addition, many species present high dispersal limitation, which also affects diversity and structure of plant communities (Both et al. 2011). Thus, because fragmentation generates changes in environmental resources, mostly in forest edges (Laurance et al. 2002, Fischer and Lindenmayer 2007), herb layer life-forms are expected to be affected by these environmental changes induced by fragmentation (Lima et al. 2015, Paison et al. 2018). For instance, composition and diversity of trees, herbs and climbers change in response to fragment area and edge effects, and in this way light-demanding species are favoured at the expense of shade-tolerant species, because of higher light availability in the forest edges (Costa and Magnusson et al. 2002, Paciencia and Prado 2005; Laurance et al. 2006, Laurance et al. 2014, Normann et al. 2016).

One of the most important questions in ecology is to understand the forces driving community assembly in highly complex ecosystems, as the tropical rainforest. Ecological studies have focused on the relative importance of stochastic and deterministic processes structuring plant communities at multiple scales (Jones et al. 2008), as predicted in neutral and niche theories, respectively. In general, the studies addressing environmental filtering on herb layer community assembly of tropical forests have accounted climate and soils parameters (Jones et al. 2013), but fragmentation (i.e. path and landscape metrics) are rarely considered. In this context, a scenario with fragmented forests and harsh environmental gradients as those prevailing in present coastal plains of the Brazilian Atlantic Forest Domain (sensu Oliveira-Filho et al. 2015) may be interesting for measuring the relative importance of fragmentation and environmental resources on herb layer community assembly. Particularly because coastal forests occur on a variety of soil-types, as well-drained sandy soils, poor-drained organic soils, and deeper and older soils, richer in nutrients and usually located in more inland parts of the Brazilian coastal plains (Scarano 2002, Santos Junior et al. 2018). Soil proprieties as salinity, sandiness, and flooding regimes are the major factors responsible for structural and diversity differences among coastal forests, mostly regarding tree communities at a local scale (Eisenlohr et al. 2013, Marques et al. 2015, Neves et al. 2017), but these differences are less evident at large spatial scales (Marques et al. 2011), where climate is an important factor in structuring plant communities.

In this study we investigated the ecological factors driving alpha and beta diversity (as *variation*, following Anderson et al. 2011) of the herb layer in forest fragments scattered across coastal plains in the subtropical zone of the Brazilian Atlantic Forest. We defined the herb layer to include herbaceous species, climbers, palms, shrubs, and tree seedlings and saplings (Both et al. 2011). Given that, in our study area soil conditions and climate are considered as the major drivers structuring plant communities at local to regional scale (Marques et al. 2011, Neves et al. 2017), and that fragmentation can differently affect the diversity of herb layer life-forms (Pasion et al. 2018). We specifically asked the following questions: How is the herb layer modulated by

soil and climate gradients and spatial distance in face of the presently existing habitat fragmentation? Are fragmentation effects significant in explaining the alpha and beta diversity in a steep environmental gradient as in coastal plain? And, how different are the responses of each herb layer life-form to the ecological drivers? Due to the strong environmental gradient of our study, mostly by incorporating from stressful to high-nutrient soils, we expected that inter-site soil differences to be the major driver of herb layer beta diversity, independently from other mechanisms related to climate, space, or fragmentation (Murphy et al. 2016, Draper et al. 2018). At the site scale, we expected an influence of both environmental set of conditions (soil and climate) and fragmentation on species richness, where smaller and isolated fragments with higher edge effects and on stressful soils should present an overall lower richness. However, since distinct herb layer life-forms may vary their responses to environmental and fragmentation conditions due, for instance, to differences in life-history, dispersal ability and flooding tolerance (Jones et al. 2013, Murphy et al. 2016), we expected differences in the strength and direction of alpha and beta diversity among the distinct groups of life-forms.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in forest fragments scattered throughout the southernmost coastal plain in the Brazilian Atlantic forest (Figure 1 in general introduction). The upper deposits of the coastal plain is geologically recent, formed during the Quaternary (Tomazelli et al. 2000), and constitutes an extensive flat and low landform (up to 30 m a.s.l.), including a great number of coastal lagoons. The regional climate is humid-subtropical, corresponding to the Cfa-type according to the Köppen system (Alvares et al. 2013). Mean annual temperature ranges from 18 to 20°C and mean annual rainfall is ≅ 1600 mm (Alvares et al. 2013). Due to several distinct geological deposits, the region shows a great variety of soil types, such as Acrisols and Arenosols on sand deposits, and Gleysols and Histosols on lagoonal deposits (IBGE 1986, FAO 2015).

The Atlantic coastal plain forests can be defined according to their physiognomy and main environmental conditions (Waechter 1990, Scarano 2006, Marques et al. 2015). Three major types are often recognized: i) Dune forest - developing on recent sandy unflooded soils; ii) Peat forest - developing on organic and permanently flooded soils; iii) Rain forest (Atlantic forest stricto sensu – Oliveira Filho and Fontes 2000) - developing on more inland and more developed unflooded soils. The more favourable soil conditions of the Rain forest sustain taller and larger trees compared to tree communities of the other two forests (Assis et al. 2011, Eisenlohr et al.

2013). Soil constraints act as abiotic filters on Dune and Peat forests, limiting the occurrence of many species from the inland Rain or Seasonal forests (Rambo 1954, Oliveira-Filho et al. 2015). Thus, Dune and Peat forests often show less diverse tree communities and may represent subsets of the more diverse Rain Forest (Scarano 2002, Oliveira-Filho et al. 2015). Taking into account the herb layer, composition between forests is distinguishable for trees and shrubs, but not for climbers and slightly for herbaceous species. In addition, overall herb layer alpha diversity is higher in Rain and Dune forests when compared to Peat forest (Santos-Junior et al. 2018).

2.2. Sampling

We sampled the herb layer in 23 forest fragments (Appendix B) selected using Google Earth images and checked their conservation status and general ecological conditions in the field. Only fragments without evidences of cattle grazing, evident signs of tree extraction, and not severely invaded by exotic species (e.g. *Asparagus* and *Hedychium*) were sampled. In the centre of each forest patch we established three plots of 10 x 4 m, spaced at least 100 m apart from each another. Each plot was subdivided into ten 2 x 2 m subplots for frequency estimates that were used as the abundance parameter in the analyses. Frequency was obtained from the sum of species occurrences in each subplot within a forest site. We considered each forest patch as a sampling unit for all statistical analyses.

We defined herb layer vegetation as all vascular plants ≤ 1-m height; a common definition adopted in other studies (Both et al. 2011, Gilliam 2007, Lu et al. 2010, Santos-Junior et al. 2018). This definition included herbaceous species (i.e. residents) as well as climbers, shrubs, and tree saplings (i.e. transients). However, we excluded shrubs and tree seedlings with less than 10 cm in height and included terrestrial herbaceous species with more than 1 m height. We thus excluded newly germinated seedlings that are very difficult to identify down to the species level (Harms et al. 2004). The height enlargement for herbaceous species was adopted to include important families in the Atlantic Forest, as the commonly large-sized Heliconiaceae and Marantaceae (Santos-Junior et al. 2017). All plants were classified into one of the following life-forms: (1) climbers, (2) herbaceous (including angiosperms and ferns), (3) palms (4) shrubs (including spreading-shrubs and sub-shrubs) and (5) trees (including treelets). These life-forms follow general definitions found in several publications, as Flora de São Paulo, Flora Catarinensis, Flora Arbórea do Rio Grande do Sul, and the on-line database Flora do Brasil.

2.3. Explanatory variables

We used four sets of explanatory variables: soil, climate, fragmentation context, and space. Soil variables corresponded to the main soil type of each forest patch – Acrisols, Cambisols, Gleysols or Arenosols – compiled from digital soil classification maps of the Radam-Brasil project (available in: https://mapas.ibge.gov.br). Although soil chemistry should be more appropriated to capture habitat specificity, soil types have been effective in predicting floristic variation on tropical herb layer communities (Jones et al. 2006, Murphy et al. 2016). The 19 variables available in the WorldClim 2.0 database (http://www.worldclim.org) were initially included in the climatic set (Fick et al. 2017). These variables were extracted with 30 arc-s of resolution ($\cong$ 1 km^2 spatial resolution) for each site, using the package raster in the R Statistical Environment.

We measured four metrics to indicate fragmentation and derived processes as habitat loss, disruption of biological connectivity and edge-effects: fragment area in hectares (A), shape index (SI), edge-affected habitat (EH) and isolation (I) (Appendix B). SI was calculated as SI = P/200·[(π·A)$^{0.5}$] (Laurance and Yensen 1991), where P is the perimeter in meters and A is the area in hectares. Higher values of SI indicate more irregular and complex shapes. EH was calculated as the percentage of edge-habitat, using a 50 m internal buffer into each forest patch area (Pinto et al. 2010). We used 50 m distance because most edge-effects important to the herb layer occur within this distance, such as increase of temperature and luminosity and invasion of disturbance-adapted plants (Laurance et al. 2002). Isolation was quantified as the percentage of forest within a 1-km external buffer set from the perimeter of each fragment (Santos et al. 2008). Path isolation is a measure of habitat amount in the landscape surrounding the patch (Fahring 2003). Fragmentation metrics were quantified using QGIS version 2.16.1 on the basis of Google Earth images.

To account for the space influence on community patterns, we obtained spatial variables using a Principal Coordinates of Neighbour Matrices (PCNM) as described by Borcard and Legendre (2002), and used them as an additional set of predictor variables.

2.4. Data analyses

To assess the relative importance of soil types, climate, fragmentation metrics and spatial variables on beta diversity, we used variation partitioning with distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999). We used Hellinger's transformation and Euclidean distance on abundance data of species as a measure of beta diversity, i.e. a measure of species composition variation between forest sites. Before analyses, we used the forward selection procedure in order to select those explanatory variables with a significant contribution

to explaining variation in species composition. This procedure was done separately for each set of explanatory variables (except for soil that was a set of categorical variables) and response matrices (i.e. distinct life-form groups), using double-stopping criteria for variables selection (Blanchet et al. 2008). Variables were selected with alpha= 0.05 and when the adjusted R^2 of the global model was exceeded. Forward selection reduces the number of explanatory variables that explain a similar amount of variance and, consequently, the overestimation of explained variance, and type I errors (Blanchet et al. 2008). In addition, in order to eliminate collinearity among variables, we calculated variance inflation factors (VIF) and selected only variables with VIF < 10 as suggested by Neter et al. (1996). We tested the fractions of variation independently explained by each dataset using R^2 adjusted values and statistical significance determined by 9999 permutations (Peres-Neto et al. 2006). Next, we ran Canonical Analysis of Principal Coordinates (CAP) (Anderson and Willis, 2003) to illustrate the influence of climatic, soil, and fragmentation metrics in driving beta diversity, using explanatory variables selected in forward selection. Overall test for significance of CAP analysis as well as constraints and axes significances were tested by 9999 permutations with anova.cca function in 'vegan' package (Oksanen et al., 2015). Variation partitioning, forward selection and CAP were performed with the 'vegan' package in R environment with *varpart*, *ordir2step* and *capscale* functions, respectively.

To examine the effect of the explanatory variables on herb layer richness, we performed Generalized Linear Models (GLM) using Poisson error distribution which is most appropriated for count data. Total richness per forest patch represented the alpha diversity and was used as a response variable for analyses with the whole herb layer and for each life-form. Before running GLM, we also performed a forward selection with the same procedure used in db-RDA analyses, in order to select only explanatory variables which showed a strong relationship with the dependent variable. The regression assumptions were tested after modelling, using Shapiro-Wilk Normality Test for residuals normality and Durbin-Watson Test for residuals autocorrelation. The normal distributions were met and residuals were not autocorrelated (P>0.05). Regression models were computed using function *glm* and forward selection using *forward.sel* function in 'packfor' package in R.

3. RESULTS

We recorded 342 species assigned to 89 families (73 angiosperms and 16 ferns) in the herb layer of the three major types of Atlantic coastal forests (Appendix A). Herb layer richness varied from 33 to 76 species with a mean and standard deviation of 55.5 ± 12.9, when considering the total area sampled in each forest patch (120 m^2). Regarding the identified species, 146 were

trees, 79 were herbaceous, 51 were climbers, 33 were shrubs, and five were palms. In face of the low number of palm species, we pooled them within trees or shrubs (two trees and three shrubs) for the run of all further analyses. Tree richness varied from 15 to 43 species, with a mean and standard deviation of 29.2 ± 9.2 per 120 m^2, herbaceous plants varied from 5 to 20 species with a mean of 10.8 ± 4, climber richness varied from 0 to 16 species with a mean of 8.4 ± 3.7, and shrub species richness varied from 4 to 11 species with a mean of 7 ± 2.1.

3.1. Drivers of beta diversity

Forward selection retained a total of 12 variables, including all models of species variation, both for the whole herb layer and for each life-form separately (Table 1). The selected climate variables were those that were associated with extreme climatic conditions. There were no fragmentation and spatial variables selected for the shrub model, and thus for this life-form partitioning was performed only with the soil and climate variable sets (Figure 2).

The total amount of explained variation was between R^2adj = 19-29% (P = 0.001), being the higher explication found for trees (Figure 2). Soil was the major component explaining variation for almost all models: whole herb layer life-forms (R^2adj = 8%, P = 0.01), herbaceous plants (R^2adj = 8%, P= 0.001) and shrubs (R^2adj = 10%, P = 0.002) (Figure 2). For climbers, climate (R^2adj = 3%, P = 0.052) and fragmentation (R^2adj = 3%, P = 0.059) only marginally explained variation, and space had the highest independent contribution (R^2adj = 10%, P = 0.005). Beta diversity of trees was most explained by the joint effect of soil, climate and space (R^2adj = 8%), and the contribution of each set alone decreased from soil to climate to space (5%, 4%, and 3%), being no one significant. The joint effect of soil and climate was also high for shrubs (R^2adj = 12%), but soil was much more important than climate (10% vs. 3%). There was no statistically significant contribution of fragmentation and no of climate to explain variation in herb layer life-forms composition, when they were measured independent from other factors.

Ordinations clearly segregated forest patches on gleysols from forests on acrisols and cambisols, but it was less evident for forests on arenosols, which were mostly scattered among other soil types (Figure 3). For all life-forms, soil types contributed largely for variation in species composition, but these effects were not significant for climbers (F = 1.34, P = 0.06). Although life-forms were affected by slightly different individual variables of each set (Table 1), a common pattern is observed: axis 1 clustered forest patches on gleysols associated with patch area under general warmer conditions, and clustered forest patches on acrisols and cambisols associated with edge-affected habitat. Only for trees, the climatic variable mean temperature of wettest quarter was significant in explaining variation (F = 1.98, P = 0.017).

3.2. Drivers of alpha diversity

Overall the effects of soil types and temperature seasonality were the most significant explanatory variables driving the changes in species richness when all herb layer life-forms were considered (Table 2). A significant negative effect of gleysols on richness was observed when comparing to the other soil types. Likewise, temperature seasonality had a negative effect on richness. When each life-form was analyzed separately, these results were similar to trees, with gleysols and temperature seasonality having negative effects on richness. Climber richness was significantly higher in cambisols forests, and herbaceous plants richness was the only life-form affected by fragmentation metrics, being positively correlated to patch area. For shrubs, there was no significant effect explaining richness patterns.

4. DISCUSSION

Overall, our results indicate that soil type is the major driver of alpha and beta diversity of the forest herb layer when all life-forms were considered together. However, when each life-form is considered separately, other factors were similarly important for beta diversity, as space for climbers and shared environmental (i.e. climate and soils) and space effects for trees. For richness patterns of each life-form, soil type affected trees and climbers only. We were not able to detect strong fragmentation effects on alpha and beta diversities of the herb layer as whole, but for herbaceous plants richness we found a positive association to fragment area. Our findings highlight the importance to disentangle plant groups that share the same habitat resources in the forest understory, but differ in life-history and responses to ecological drivers, and so demonstrating the range of ecological processes structuring plant communities (Costa et al. 2005, Nervo et al. 2019).

4.1. Drivers of beta diversity

Soil conditions have been shown to be one of the main factors driving the understory plant communities from small to large scales (Costa et al. 2005, Jones et al. 2013). In addition, studies considering peat or swamp habitats evidenced high contribution to beta diversity, despite the lower species richness in these environments (Murphy et al. 2016, Draper et al. 2018). The edaphic conditions represent extremes of low soil fertility in coastal plains of the Atlantic Forest Domain (Neves et al. 2017), and thus have an important role in driving floristic variation of the adult tree component of forests (Eisenlohr et al. 2013, Mancino et al. 2015). This is in accordance

with our study where soil type was the major driver of beta diversity. Variation on soil conditions certainly contribute for the floristic differentiation among coastal forest types (Santos-Junior et al. 2018).

Despite most composition differences, soil types were not sufficient to explain variation in climber composition. Previous studies already reported relatively weak habitat associations for adult and seedling climbers in tropical forests (Dalling et al. 2012, Murphy et al. 2016). This could be due to the fact that climber seedlings (and tree saplings and seedlings) have not yet experienced a long enough time interval for environmental filtering effects to become evident (Murphy et al. 2016). However, the amount of variation of climbers was mostly explained by space, which can be attributed either to stochastic processes (e.g. dispersal limitation), or by additional spatially structured environmental variables that were not measured in this study (Anderson et al. 2011), including light or soil chemical variables (Dalling et al. 2012, Jones et al. 2013). The same is true for tree beta diversity in the forest herb layer, which was less explained by space but was largely explained by the joint effects of environment and space in our study.

Although the variance partitioning model for beta diversity of trees showed that environment alone did not independently explained variation in tree composition, the ordination method evidenced that soil type and mean temperature of the wettest quarter were significant in explaining variance. We previously showed (Santos-Junior et al. 2018) that higher tree species abundance in Rain forest (established in Acrisols and cambisols) and higher herbaceous abundance in Peat forest (established in Gleysols) were the major differences between these forest types. Organic soils in coastal plains are subjected to water accumulation caused by high precipitation in the rainy season (Kurtz et al. 2013). On the other hand, soil dryness can be caused by low precipitation and/or fast water drainage, as observed in sandy soils (Marques et al. 2011). These features can limit plant growth, as trees in swamp or flooding habitats (Murphy et al. 2016, Stevenson et al. 2007) where only physiologically adapted species are able to survive (Scarano et al. 2001). The association of mean temperature of the wettest quarter with the variation pattern of tree species indicates differences only when related to the high or poor-drainage soils, where sites under high atmospheric temperatures and gleysols conditions have distinct occurrence or abundance of trees adapted for such stressful habitats.

4.2. Drivers of alpha diversity

Our results evidenced that the increase in temperature seasonality decreases richness of the herb layer as a whole. This is in accordance with other studies that also demonstrated that higher temperature seasonally contributes for lower richness and species variation in a latitudinal gradient of subtropical region of the Atlantic Forest (Oliveira-Filho et al. 2015, Neves et

al. 2017). These results also suggest a north to south decrease in herb layer richness, since temperature seasonality increases moderately towards southernmost coastal plain forests (R = - 0.43, P = 0.03). The above mentioned studies were conducted in a geographical scale where climate variation is more evident, differing from our study that covered a lower latitudinal range, but where interestingly climate also affected species richness variation. In addition, this pattern found for herb layer as whole seems to be conditioned by the variation of tree species richness, since the trees contribute substantially to the herb layer total richness, presenting the same pattern when compared to the herb layer as a whole.

We also found that soil types contributed for alpha diversity when all life-forms were considered together, and this is probably related to the soil effects on tree species richness patterns. In fact, flooding can constrain the recruitment of many species of trees in the coastal plains (Marques et al. 2015). Although we have earlier demonstrated differences between the relative contribution of herbaceous plants to total richness in Rain and Peat forests (Santos-Junior et al. 2018), soil types per se did not contribute for herbaceous species richness variation. On the other hand, we observed a positive effect of patch area on herbaceous species richness, that is, the higher the forest fragment is, higher is the amount of herbaceous species in the forest understory. Studies comparing fragments versus continuous forests showed that herbaceous richness and recruitment tend to decline in forest fragments (Benítez-Malvido and Martínez-Ramos 2003, Lima et al. 2015), but herbaceous richness may be negatively related with patch area (Lima et al. 2015), and so contrasting our results. The authors suggested that in small forest fragment there is an increment of light-demanding species, increasing the total number of species and balancing the extirpation of shade-tolerant species and habitat specialists (Lima et al. 2015). This effect was also observed in another study concerning herbaceous communities in Atlantic secondary moist forests (Santos-Junior et al. 2017). So, the absence of relationships among fragmentation metrics and the other studied life-forms may follow this rationale (McCune and Vellend 2015). On the other hand, the reduction of fern richness in forest edges (Paciencia and Prado 2005) and its proliferation in large old-growth forest patches (Lima et al. 2011, Santos-Junior et al. 2017) can be explaining the positive relationship between herbaceous species richness and patch area here observed, since almost half of the sampled herbaceous species were ferns. In addition, most forest patches in our study system were edge-dominated (EI was correlated negatively with patch area, R= - 0.62, P < 0.01), and so many plant groups may be excluded as shade-tolerant ferns (Lima et al. 2015).

It is noteworthy that some plant groups may proliferate in edges (Gonzalez et al. 2010). Climbers for instance, may be highly affected by forest edge or patch area (Benítez-Malvido and Martínez 2003, Schnitzer and Carson 2010), but this did not happen in our study. Otherwise, climber richness was affected by soil conditions. Thus, although the characteristic as the fragment

size and edge-habitats of forest patches in our study are suitable for the increase and proliferation of many species groups, and consequently cause changes in species composition, this was not sufficient to affect all plants groups. Also, ecological factors as soil conditions are still important in explaining richness variance, even in a scenario with high forest fragmentation.

5. CONCLUSIONS

In conclusion, we showed that herb layer life-forms are driven by deterministic processes mostly related to soil conditions, but others ecological drivers associated to climate and space may be important when disentangling the herb layer into distinct life-forms. Similar results were found in tropical and subtropical forests where herb layer life-forms responded differently to distinct drivers (Both et al. 2011, Murphy et al. 2016, Pasion et al. 2018). Our study also suggests that even on a regional scale where the effect of climate can be less evident, some climatic variation especially when associated to soil conditions and space might contribute to changes in species diversity among plant communities. Moreover, although habitat fragmentation can impose changes on forest herb layer assemblages, especially herbaceous species, soil and climate conditions overwhelm the contribution in explain alpha and beta diversity along a short but steep environmental gradient, as the one here analysed in coastal plain Atlantic forests.

6. TABLES AND FIGURES

Table 1. Environmental and spatial variables selected by a forward selection for distance-based redundancy analysis (dbRDA), used as predictors of the herb layer composition of Brazilian Atlantic coastal forests. Forward selection procedures were done for each set of explanatory variables (i.e. climate, fragmentation metrics and spatial distances), including all herb layer species and separately for each life-form. The selection criteria were assessed by adjusted coefficients of determination (Adj.R^2) and F-values with significance level of alpha = 0.05.

	All herb layer		Climbers		Herbaceous		Shrubs		Trees	
	Adj.R^2	F	Adj.R^2	F	Adj.R^2	F	Adj.R^2	F	Adj.R^2	F
Climate										
MaxTempWarmM	0.11	1.54			-	-	-	-	-	-
PreciColdQ	-	-			-	-	-	-	-	-
PreciWettM	-	-			-	-	-	-	0.15	2.38
TempDrieQ	0.05	2.31			0.04	2.1	0.1	3.55	-	-
TempWarmQ	0.09	1.82	0.05	2.22	-	-	0.1	2.26	0.10	1.64
TempWettQ	-	-			-	-	-	-	0.07	2.75
Fragmentation metrics										
Fragment Area	0.04	2.07	0.03	1.85	-	-	-	-	-	-
Edge-affected habitat	-	-			0.04	2.15	-	-	0.05	2.27
Space										
PCNM1	0.07	1.79	0.08	1.76	-	-	-	-	0.03	1.78
PCNM2	0.03	1.84	-	-	0.03	1.90	-	-	0.07	1.84
PCNM4	0.09	1.55	0.05	2.28	-	-	-	-	0.11	1.88
PCNM9	-	-	0.11	1.63	-	-	-	-	0.14	1.60

MaxTempWarmM = Max Temperature of Warmest Month; *PreciColdQ* = Precipitation of Coldest Quarter; *PreciWettM* = Precipitation of Wettest Month; *TempDrieQ* = Mean Temperature of Driest Quarter, *TempWarmQ* = Mean Temperature of Warmest Quarter; TempWettQ = Mean Temperature of Wettest Quarter.

Table 2. Results of the generalized linear models, analyzing the relationships of herb layer species richness and predictor variables for whole herb layer and for each life-form separately. Significant *P* values (<0.05) are in bold.

Variables	Estimate	Std. Error	*z* value	*P*
All herb layer				
Intercept	8.203	1.691	4.85	
Arenosols	-0.048	0.082	-0.58	0.560
Cambisols	0.058	0.080	0.72	0.469
Gleysols	-0.334	0.079	-4.24	**0.000**
Temperature Seasonality	-0.012	0.005	-2.42	**0.016**
Climbers				
Intercept	2.104	0.156	13.47	
Arenosols	-0.217	0.234	-0.93	0.353
Cambisols	0.461	0.199	2.31	**0.021**
Gleysols	-0.158	0.206	-0.77	0.441
Herbaceous				
Intercept	2.173	0.146	14.88	
Arenosols	0.044	0.196	0.23	0.821
Cambisols	-0.038	0.201	-0.19	0.852
Gleysols	-0.054	0.188	-0.29	0.773
Area	0.007	0.002	3.65	**0.000**
Shrubs				
Intercept	-1.692	2.228	-0.76	
Arenosols	0.125	0.226	0.55	0.448
Cambisols	0.072	0.234	0.31	0.758
Gleysols	-0.233	0.232	-1.00	0.315
Precipitation of Warmest Quarter	0.009	0.005	1.68	0.096
Trees				
Intercept	9.052	2.301	3.93	
Arenosols	-0.110	0.118	-0.93	0.353
Cambisols	-0.019	0.109	-0.17	0.862
Gleysols	-0.620	0.137	-4.52	**0.000**
Mean Temperature of Driest Quarter	0.002	0.024	0.09	0.924
Temperature Seasonality	-0.017	0.007	-2.41	**0.016**

Figure 2. Variation partitioning models based on distance based redundancy analysis (db-RDA) relating herb layer composition of 23 forest fragments in the Brazilian Atlantic coastal plain to soil type, climate, fragmentation and space. Floristic dissimilarity was based on Hellinger distance. Space was represented by PCNMs. Individual factors compounding each variable set were previously selected by forward selection (Table 1). For shrubs, fragmentation metrics and spatial descriptors were not selected and thus we reported the model based in the other two set of variables. The numbers are adjusted R^2 for independent and shared fractions. Significance of individual fractions was tested by 999 permutations.
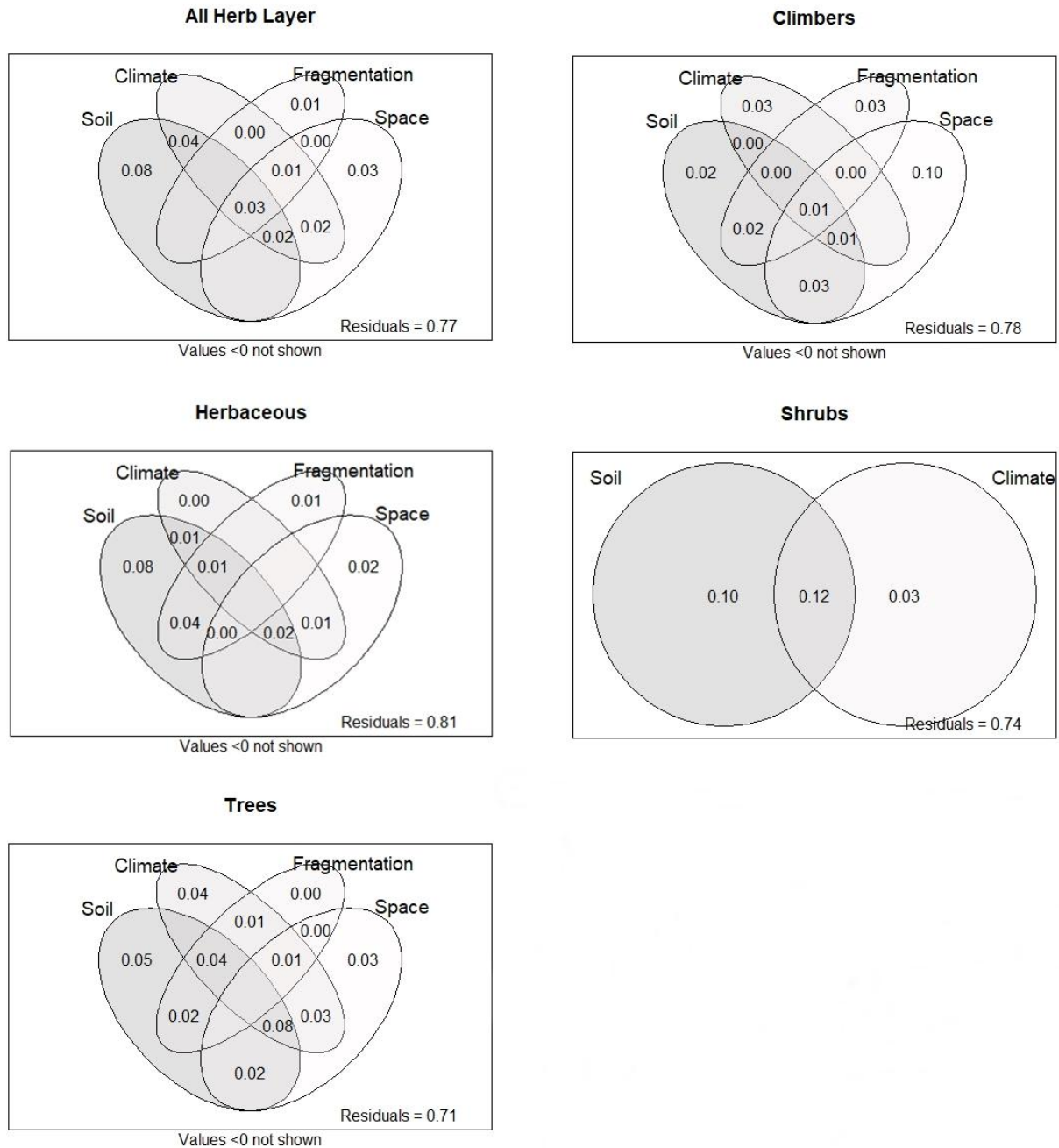
Figure 3. Canonical analysis of principal coordinates (CAP) with the herb layer composition of 23 forest fragments in the coastal plain of southern Brazil, showing the relationships with soil type, climate and fragmentation variables. Individual variables were previously selected by forward selection (Table 1). MaxTempWarmM = Max Temperature of Warmest Month; PreciColdQ = Precipitation of Coldest Quarter; PreciWettM = Precipitation of Wettest Month; TempDrieQ = Mean Temperature of Driest Quarter, TempWarmQ = Mean Temperature of Warmest Quarter; TempWettQ = Mean Temperature of Wettest Quarter.
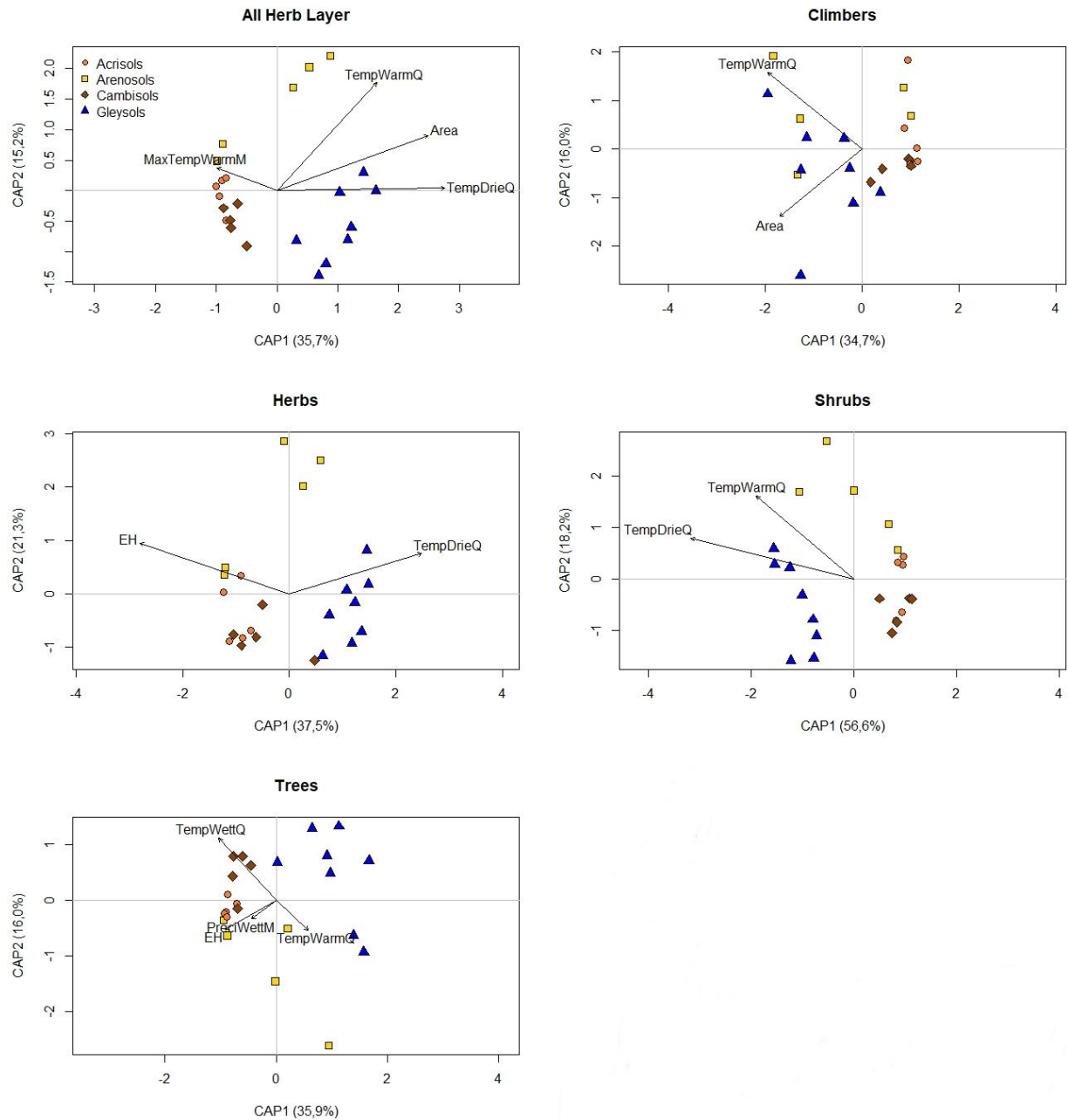
CONSIDERAÇÕES FINAIS

Este estudo traz novas contribuições para o entendimento da ecologia das formações florestais da planície costeira atlântica. Primeiro, o estrato herbáceo contribui de maneira substancial para a diversidade alfa, haja vista a comparação com estudos realizados com o componente arbóreo adulto nestas florestas no sul do Brasil (ver Dorneles & Waechter 2004ab). Segundo, como já amplamente discutido na literatura (Marques et al. 2015), a variação florística e estrutural destas florestas é governada sobretudo pelas características edáficas nas quais os tipos florestais se desenvolvem. Entretanto, pelo menos na escala espacial utilizado no estudo, o clima e as configurações do habitat florestal também podem influenciar a riqueza e variação florística do estrato herbáceo destas florestas. Terceiro, as espécies mais importantes ecologicamente bem como gêneros e famílias mais ricas são similares entre os tipos florestais da planície, embora haja uma grande quantidade de espécies não compartilhadas. Além disso, a diferenciação florística entre os tipos florestais definidos *a priori* não é tão evidente quando levado em conta algumas formas de vida do estrato herbáceo e por isso, no mínimo, observam-se pelo menos dois tipos florestais distintos: Floresta não-inundada (Pluvial e Arenosa) e Floresta inundada (Turfosa) (Artigo 1). Desta forma, sugere-se que a vegetação florestal ocorrente na planície costeira deva ser tratada como um ecossistema único, como já sugeridos por outros autores (Marques et al. 2011), considerando as diferenças florísticas e de diversidade entre pelo menos dos tipos principais florestais, estruturados mais em função das variações ambientais do que da localização espacial dentro da planície costeira (Artigo 2).

Cabe aqui ressaltar o estado de conservação destas florestas. Pode-se perceber durante os trabalhos de campo que os fragmentos florestais que ainda restam na planície costeira estão fortemente ameaçados. Muitos fragmentos estão imersos em matrizes agriculturais, as quais acabam muitas vezes, pela necessidade de cultivo, drenando ambientes florestais naturais ou ainda tomando o espaço das florestas aos poucos, através de cortes ilegais. Também é possível observar grande abundância de espécies exóticas invasoras como *Asparagus* sp. e *Hedychium coronarium* no interior de alguns fragmentos florestais. Certamente, isto acarreta mudanças na estrutura das comunidades vegetais nativas, e que precisam ser melhor estudadas. Outro fator de degradação nas florestas costeiras é a entrada do gado, sobretudo no interior das florestas arenosas. Nestas florestas, que em geral possuem vegetação campestre adjacente, o gado penetra no interior da floresta em busca de abrigo e acaba pisoteando o solo e degradando a vegetação regenerante. Muitas florestas arenosas são verdadeiras "cascas de ovos", não possuindo sub-bosque florestal. Sem regeneração, o futuro destas florestas é uma incógnita.

APÊNDICES

Appendix A. Families and species of the herb layer life-forms sampled in three types of Brazilian Atlantic coastal forests: Dune forest (D), Peat forests (P) and Rain forest (R).

Family	Species	Life-form	D	P	R
Acanthaceae	*Justicia carnea* Lindl.	Shrub	x	x	x
	Mendoncia sp.	Climber	x		x
	Mendoncia puberula Mart.	Climber	x		
	Ruellia cf. *brevifolia* (Pohl) C.Ezcurra	Shrub	x		
	Stenandrium tenellum Nees	Herb			x
Amaranthaceae	*Gomphrena vaga* Mart.	Shrub	x		x
Anemiaceae	*Anemia phyllitidis* (L.) Sw.	Herb		x	x
Annonaceae	*Annona maritima* (Záchia) H.Rainer	Tree	x		
	Annona neosericea H.Rainer	Tree	x		
	Duguetia lanceolata A.St.-Hil.	Tree	x		x
	Guatteria australis A.St.-Hil.	Tree			x
	Xylopia brasiliensis Spreng.	Tree	x		x
Apiaceae	*Centella asiatica* (L.) Urb.	Herb	x		
Apocynaceae	Apocynaceae sp.	-		x	
	Aspidosperma olivaceum Müll.Arg.	Tree	x		x
	Fischeria cf. *stellata* (Vell.) E.Fourn.	Climber		x	
	Forsteronia glabrescens Müll.Arg.	Climber	x		x
	Forsteronia thyrsoidea (Vell.) Müll.Arg.	Climber	x		x
	Gonolobus cf. *rostratus* (Vahl) Schult.	Climber		x	
	Marsdenia montana Malme	Climber		x	x
	Orthosia cf. *urceolata* E. Fourn.	Climber		x	x
	Tabernaemontana catharinensis A.DC.	Tree	x		
Aquifoliaceae	*Ilex brevicuspis* Reissek	Tree		x	x
Araceae	*Anthurium gaudichaudianum* Kunth	Herb	x		
	Philodendron appendiculatum Nadruz & Mayo	Climber	x	x	
	Philodendron missionum (Hauman) Hauman	Climber	x	x	x
Araliaceae	*Dendropanax australis* Fiaschi & Jung-Mend.	Shrub		x	x
	Dendropanax cuneatus (DC.) Decne. & Planch.	Tree			x
Arecaceae	*Bactris setosa* Mart.	Palm		x	x
	Euterpe edulis Mart.	Palm	x	x	x
	Geonoma pohliana Mart.	Palm	x	x	x
	Geonoma schottiana Mart.	Palm	x	x	x
	Syagrus romanzoffiana (Cham.) Glassman	Palm	x	x	x
Aspleniaceae	*Adiantum pentadactylon* Langsd. & Fisch.	Herb			x
	Asplenium serra Langsd. & Fisch.	Herb		x	
	Asplenium kunzeanum Klotzsch ex Rosenst.	Herb			x
Asteraceae	*Chaptalia nutans* (L.) Pol.	Herb	x		
	Mikania sp.	Climber		x	x
	Mikania ternata (Vell.) B.L.Rob.	Climber	x	x	x
	Mikania campanulata Gardner	Climber	x	x	
	Mikania glomerata Spreng.	Climber		x	x
	Mikania involucrata Hook. & Arn.	Climber	x	x	
	Mikania lundiana DC.	Climber	x	x	x
	Piptocarpha sellowii (Sch.Bip.) Baker	Shrub		x	
Athyriaceae	*Diplazium cristatum* (Desr.) Alston	Herb			x
	Diplazium plantaginifolium (L.) Urb.	Herb			x
Bignoniaceae	*Adenocalymma dusenii* Kraenzl.	Climber	x		x
	Amphilophium crucigerum (L.) L.G.Lohmann	Climber	x	x	x
	Amphilophium dusenianum (Kraenzl.) L.G.Lohmann	Climber	x		x
	Dolichandra cynanchoides Cham.	Climber	x		
	Dolichandra quadrivalvis (Jacq.) L.G.Lohmann	Climber			x
	Fridericia chica (Bonpl.) L.G.Lohmann	Climber			x

Family	Species	Habit			
	Handroanthus umbellatus (Sond.) Mattos	Tree	x	x	x
	Mansoa difficilis (Cham.) Bureau & K.Schum.	Climber		x	x
	Tanaecium pyramidatum (Rich.) L.G.Lohmann	Climber	x	x	x
	Tynanthus cognatus (Cham.) Miers	Climber			x
Blechnaceae	*Austroblechnum lehmannii* (Hieron.) Gasper & V.A.O. Dittrich	Herb			x
	Blechnum australe L.	Herb		x	
	Lomaridium binervatum (Poir.) Gasper & V.A.O.Dittrich	Climber		x	x
	Neoblechnum brasiliense (Desv.) Gasper & V.A.O. Dittrich	Herb		x	x
	Parablechnum cordatum (Desv.) Gasper & Salino	Herb		x	
Bromeliaceae	*Bromelia antiacantha* Bertol.	Herb	x		
	Nidularium innocentii Lem	Herb	x	x	x
	Nidularium procerum Lindm.	Herb	x	x	
Burseraceae	*Protium kleinii* Cuatrec.	Tree	x		x
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.	Shrub	x		
Cardiopteridaceae	*Citronella paniculata* (Mart.) R.A.Howard	Tree	x		x
Celastraceae	*Maytenus cassineformis* Reissek	Tree	x		
	Pristimera celastroides (Kunth) A.C.Sm.	Climber	x		x
Chrysobalanaceae	*Hirtella hebeclada* Moric. ex DC.	Tree	x		x
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi	Tree	x	x	x
Commelinaceae	*Commelina obliqua* Vahl	Herb	x		
	Tradescantia fluminensis Vell.	Herb	x		
Cucurbitaceae	Cucurbitaceae 01	Climber		x	
Cyatheaceae	*Alsophila setosa* Kaulf.	Tree		x	x
	Cyathea atrovirens (Langsd. & Fisch.) Domin	Tree		x	
Cyperaceae	*Carex sellowiana* Schltdl.	Herb	x		
	Pleurostachys gaudichaudii Brongn.	Herb			x
	Pleurostachys stricta Kunth	Herb		x	
	Scleria latifolia Sw.	Herb	x	x	x
Didymochlaenaceae	*Didymochlaena truncatula* (Sw.) J.Sm.	Herb	x		x
Dilleniaceae	*Doliocarpus glomeratus* Eichler	Climber		x	x
	Tetracera sellowiana Schltdl.	Climber	x		x
Dioscoreaceae	*Dioscorea laxiflora* Mart. ex Griseb.	Climber			x
Dryopteridaceae	*Ctenitis submarginalis* (Langsd. & Fisch.) Ching	Herb			x
	Elaphoglossum luridum (Fée) Christ	Herb		x	
	Lastreopsis amplissima (C.Presl) Tindale	Herb			x
	Megalastrum connexum (Kaulf.) A.R.Sm. & R.C.Moran	Herb	x		x
	Megalastrum oreocharis (Sehnem) Salino & Ponce	Herb			x
	Mickelia scandens R.C.Moran, Labiak & Sundue	Climber	x		x
	Polybotrya cylindrica Kaulf.	Climber	x	x	x
	Rumohra adiantiformis (G.Forst.) Ching	Herb	x		
Ebenaceae	*Diospyros inconstans* Jacq.	Tree		x	
Elaeocarpaceae	*Sloanea guianensis* (Aubl.) Benth.	Tree	x		x
	Sloanea monosperma Vell.	Tree		x	
Erythroxylaceae	*Erythroxylum argentinum* O.E.Schulz	Tree	x	x	
	Erythroxylum cuspidifolium Mart.	Tree	x		x
	Erythroxylum vacciniifolium Mart.	Tree	x	x	
Euphorbiaceae	*Actinostemon concolor* (Spreng.) Müll.Arg.	Tree	x		x
	Alchornea triplinervia (Spreng.) Müll.Arg.	Tree		x	
	Pachystroma longifolium (Nees) I.M.Johnst.	Tree			x
	Sebastiania argutidens Pax & K.Hoffm.	Tree			x
	Sebastiania serrata (Baill. ex Müll.Arg.) Müll.Arg.	Tree	x	x	
Fabaceae	*Abarema langsdorffii* (Benth.) Barneby & J.W.Grimes	Tree	x		
	Dahlstedtia pentaphylla (Taub.) Burkart	Tree			x
	Dahlstedtia pinnata (Benth.) Malme	Tree			x
	Dioclea violacea Benth.	Climber	x		
	Inga marginata Willd.	Tree		x	x
	Inga sessilis (Vell.) Mart.	Tree	x	x	x
	Machaerium hirtum (Vell.) Stellfeld	Tree			x

Family	Species	Habit			
	Phanera angulosa (Vogel) Vaz	Climber			x
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	Tree			x
	Schnella microstachya Raddi	Climber			x
Gentianaceae	*Voyria aphylla* (Jacq.) Pers.	Saprophyte	x	x	
Heliconiaceae	*Heliconia farinosa* Raddi	Herb	x	x	x
Hymenophyllaceae	*Trichomanes cristatum* Kaulf.	Herb		x	
	Vandenboschia rupestris (Raddi) Ebihara & K. Iwats.	Climber			x
Iridaceae	*Neomarica candida* (Hassl.) Sprague	Herb	x		
Lauraceae	*Aiouea saligna* Meisn.	Tree	x	x	x
	Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.	Tree			x
	Endlicheria paniculata (Spreng.) J.F.Macbr.	Tree	x	x	x
	Nectandra oppositifolia Nees & Mart.	Tree	x	x	x
	Ocotea mandioccana A.Quinet	Tree	x		
	Ocotea elegans Mez	Tree	x		x
	Ocotea lanata (Nees & Mart.) Mez	Tree	x		
	Ocotea odorifera (Vell.) Rohwer	Tree			x
	Ocotea puberula (Rich.) Nees	Tree	x		
	Ocotea pulchella (Nees & Mart.) Mez	Tree	x	x	
	Ocotea silvestris Vattimo	Tree	x		x
	Ocotea teleiandra (Meisn.) Mez	Tree	x		x
Lindsaeaceae	*Lindsaea lancea* (L.) Bedd.	Herb			x
	Lindsaea quadrangularis Raddi	Herb		x	
Loganiaceae	*Strychnos brasiliensis* Mart.	Shrub	x		x
Lomariopsidaceae	*Lomariopsis marginata* (Schrad.) Kuhn	Climber	x		x
Lygodiaceae	*Lygodium volubile* Sw.	Climber			x
Magnoliaceae	*Magnolia ovata* (A.St.-Hil.) Spreng.	Tree		x	x
Malpighiaceae	*Heteropterys* sp.	Climber	x	x	
	Heteropterys aenea Griseb.	Climber	x	x	
Malvaceae	*Byttneria australis* A.St.-Hil.	Shrub			x
	Triumfetta semitriloba Jacq.	Shrub	x		
Marantaceae	*Ctenanthe muelleri* Petersen	Herb	x		
	Goeppertia monophylla (Vell.) Borchs. & S.Suárez	Herb	x	x	x
	Maranta arundinacea L.	Herb			x
Marcgraviaceae	*Marcgravia polyantha* Delpino	Climber	x	x	x
Melastomataceae	*Leandra australis* (Cham.) Cogn.	Shrub		x	
	Leandra sp.	-		x	x
	Leandra variabilis Raddi	Tree			x
	Miconia sp.	-		x	
	Miconia cubatanensis Hoehne	Tree	x	x	
	Miconia hyemalis A. St.-Hil. & Naudin	Tree	x	x	
	Miconia latecrenata (DC.) Naudin	Tree		x	x
	Miconia pusilliflora (DC.) Naudin	Tree	x	x	x
	Miconia sellowiana Naudin	Tree	x		
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	Tree	x	x	x
	Guarea macrophylla Vahl	Tree	x	x	x
	Trichilia elegans A.Juss.	Tree	x		
	Trichilia lepidota Mart.	Tree	x		x
	Trichilia pallens C.DC.	Tree		x	x
Monimiaceae	*Hennecartia omphalandra* J. Poiss.	Tree			x
	Mollinedia schottiana (Spreng.) Perkins	Tree	x	x	x
Moraceae	*Brosimum glaziovii* Taub.	Tree	x		x
	Ficus adhatodifolia Schott	Tree			x
	Ficus cestrifolia Schott	Tree		x	
	Sorocea bonplandii (Baill.) W.C.Burger, Lanj. & de Boer	Tree	x	x	x
Myristicaceae	*Virola bicuhyba* (Schott) Warb.	Tree	x		x
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O.Berg	Tree	x		
	Calyptranthes grandifolia O.Berg	Tree	x		x

	Calyptranthes lucida Mart. ex DC.	Tree	x	x	x
	Campomanesia sp.	Tree			x
	Campomanesia rhombea O.Berg	Tree			x
	Campomanesia xanthocarpa (Mart.) O.Berg	Tree	x		
	Eugenia bacopari D.Legrand	Tree	x		x
	Eugenia brevistyla D.Legrand	Tree		x	x
	Eugenia handroana D.Legrand	Tree		x	
	Eugenia hiemalis Cambess.	Tree	x		
	Eugenia multicostata D.Legrand	Tree	x		
	Eugenia ramboi D.Legrand	Tree			x
	Eugenia stigmatosa DC.	Tree	x		
	Eugenia supraaxillaris Spreng.	Tree			x
	Eugenia ternatifolia Cambess.	Tree	x		x
	Eugenia uniflora L.	Tree	x		
	Eugenia verticillata (Vell.) Angely	Tree	x	x	x
	Marlierea eugeniopsoides (D.Legrand & Kausel) D.Legrand	Tree		x	x
	Marlierea excoriata Mart.	Tree		x	
	Myrceugenia campestris (DC.) D.Legrand & Kausel	Tree	x	x	
	Myrceugenia myrcioides (Cambess.) O.Berg	Tree		x	x
	Myrcia aethusa (O.Berg) N.Silveira	Tree	x		x
	Myrcia costeira M.F.Santos	Tree		x	
	Myrcia anacardiifolia Gardner	Tree			x
	Myrcia brasiliensis Kiaersk.	Tree	x	x	x
	Myrcia glabra (O.Berg) D.Legrand	Tree	x	x	x
	Myrcia multiflora (Lam.) DC.	Tree		x	x
	Myrcia palustris DC.	Tree	x		
	Myrcia pubipetala Miq.	Tree	x	x	x
	Myrcia spectabilis DC.	Tree	x		
	Myrcia splendens (Sw.) DC.	Tree	x		x
	Myrcia tijucensis Kiaersk.	Tree	x	x	x
	Myrciaria floribunda (H.West ex Willd.) O.Berg	Tree	x		x
	Myrciaria plinioides D.Legrand	Tree	x		x
	Myrrhinium atropurpureum Schott	Tree		x	
	Neomitranthes cordifolia (D.Legrand) D.Legrand	Tree		x	
	Psidium cattleianum Afzel. ex Sabine	Tree	x	x	
	Syzygium jambos (L.) Alston	Tree	x		x
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	Tree	x	x	x
	Neea pendulina Heimerl	Shrub	x	x	x
Ochnaceae	*Ouratea parviflora* (A.DC.) Baill	Tree	x	x	x
Oleaceae	*Chionanthus filiformis* (Vell.) P.S.Green	Tree			x
Orchidaceae	*Aspidogyne decora* (Rchb.f.) Garay & G.A.Romero	Herb	x		x
	Corymborkis flava (Sw.) Kuntze	Herb			x
	Liparis nervosa (Thumb.) Lindl.	Herb	x		
	Malaxis excavata (Lindl.) Kuntze	Herb	x	x	x
	Malaxis parthonii C.Morren	Herb	x		
	Mesadenella cuspidata (Lindl.) Garay	Herb	x	x	
	Oeceoclades maculata (Lindl.) Lindl.	Herb	x		
	Prescottia stachyodes (Sw.) Lindl.	Herb	x	x	x
	Psilochilus modestus Barb.Rodr.	Herb		x	x
	Sauroglossum elatum Lindl.	Herb	x	x	x
	Stigmatosema polyaden (Vell.) Garay	Herb	x		x
Peraceae	*Pera glabrata* (Schott) Poepp. ex Baill.	Tree		x	
Phytolaccaceae	*Petiveria alliacea* L.	Shrub	x		
Piperaceae	*Manekia obtusa* (Miq.) T.Arias, Callejas & Bornst.	Climber			x
	Peperomia corcovadensis Gardner	Herb		x	
	Peperomia glabella (Sw.) A.Dietr.	Herb	x	x	
	Peperomia pereskiaefolia (Jacq.) Kunth	Herb	x	x	
	Peperomia urocarpa Fisch. & C.A.Mey.	Herb		x	
	Piper amalago L.	Tree			x

Family	Species	Habit	1	2	3
	Piper arboreum Aubl.	Tree	x	x	
	Piper dilatatum Rich.	Shrub		x	x
	Piper gaudichaudianum Kunth	Shrub	x	x	x
	Piper miquelianum C.DC.	Shrub	x	x	x
	Piper solmsianum C.DC.	Shrub		x	x
	Piper xylosteoides (Kunth) Steud.	Shrub	x		
Poaceae	*Chusquea* sp.	Shrub	x		
	Ichnanthus pallens (Sw.) Munro ex Benth.	Herb	x	x	x
	Merostachys sp.	Shrub	x		
	Merostachys cf. *speciosa* Spreng.	Shrub	x	x	x
	Olyra humilis Nees	Herb	x		x
	Olyra latifolia L.	Herb			x
	Oplismenus hirtellus (L.) P.Beauv.	Herb	x		
	Paspalum inaequivalve Raddi	Herb		x	
	Paspalum mandiocanum Trin.	Herb	x		
	Pharus lappulaceus Aubl.	Herb	x		
	Streptochaeta spicata Schrad. ex Nees	Herb			x
Polygalaceae	*Securidaca lanceolata* A.St.-Hil.	Shrub	x		x
Polygonaceae	*Coccoloba arborescens* (Vell.) R.A.Howard	Climber			x
Polypodiaceae	*Campyloneurum acrocarpon* Fée	Herb	x	x	x
	Pecluma chnoophora (Kunze) Salino & Costa Assis	Herb			x
	Pecluma pectinatiformis (Lindm.) M.G.Price	Herb	x	x	
	Pecluma robusta (Fée) M.Kessler & A.R.Sm.	Herb		x	
	Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	Herb	x	x	x
	Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	Herb		x	
Primulaceae	*Ardisia guianensis* (Aubl.) Mez	Tree	x		x
	Myrsine guianensis (Aubl.) Kuntze	Tree	x	x	x
	Myrsine hermogenesii (Jung-Mend. & Bernacci) M.F.Freitas & Kin.-Gouv.	Tree	x	x	x
	Myrsine umbellata Mart.	Tree		x	
Proteaceae	*Roupala montana* Aubl.	Tree	x		x
Pteridaceae	*Doryopteris pentagona* Pic.Serm.	Herb		x	
	Pteris brasiliensis Raddi	Herb		x	x
	Pteris decurrens C.Presl	Herb		x	
Ranunculaceae	*Clematis* sp.	Climber			x
Rosaceae	*Prunus myrtifolia* (L.) Urb.	Tree	x		x
Rubiaceae	*Amaioua intermedia* Mart. ex Schult. & Schult.f.	Tree	x		
	Bathysa australis (A.St.-Hil.) K.Schum.	Tree			x
	Borreria cf. *palustris* (Cham. & Schltdl.) Bacigalupo & E.L.Cabral	Herb		x	
	Chiococca alba (L.) Hitchc.	Shrub	x		
	Coccocypselum capitatum (Graham) C.B.Costa & Mamede	Herb	x	x	x
	Coccocypselum condalia Pers.	Herb		x	
	Coccocypselum geophiloides Wawra	Herb		x	x
	Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	Herb	x		
	Coutarea hexandra (Jacq.) K.Schum.	Tree	x		
	Faramea montevidensis (Cham. & Schltdl.) DC.	Tree	x	x	x
	Margaritopsis cymuligera (Müll.Arg.) C.M.Taylor	Shrub			x
	Palicourea mamillaris (Müll.Arg.) C.M.Taylor	Shrub			x
	Posoqueria latifolia (Rudge) Schult.	Tree	x	x	x
	Psychotria brachyceras Müll.Arg.	Shrub	x	x	x
	Psychotria brachypoda (Müll.Arg.) Britton	Shrub	x		x
	Psychotria carthagenensis Jacq.	Shrub	x	x	
	Psychotria laciniata Vell.	Shrub	x		
	Psychotria leiocarpa Cham. & Schltdl.	Shrub	x	x	x
	Psychotria suterella Müll.Arg.	Tree	x	x	x
	Psychotria tenerior (Cham.) Müll.Arg.	Shrub		x	x
	Rudgea parquioides (Cham.) Müll.Arg.	Shrub	x		
	Rudgea jasminoides (Cham.) Müll.Arg.	Tree	x		x
Rutaceae	*Esenbeckia grandiflora* Mart.	Tree	x	x	x

Family	Species	Habit			
	Zanthoxylum rhoifolium Lam.	Tree	x		
Sabiaceae	*Meliosma sellowii* Urb.	Tree	x		x
Salicaceae	*Banara parviflora* (A.Gray) Benth.	Tree	x		
	Casearia decandra Jacq.	Tree	x	x	x
	Casearia obliqua Spreng.	Tree			x
	Casearia sylvestris Sw.	Tree	x	x	
Sapindaceae	*Allophylus edulis* (A.St.-Hil., A.Juss. & Cambess.) Radlk.	Tree	x	x	
	Cupania vernalis Cambess.	Tree	x		x
	Matayba elaeagnoides Radlk.	Tree		x	
	Matayba intermedia Radlk.	Tree	x	x	x
	Paullinia cf. *trigonia* Vell.	Climber	x	x	x
	Urvillea sp.	Climber	x		
Sapotaceae	*Chrysophyllum inornatum* Mart.	Tree	x		x
	Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Tree	x		x
	Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	Tree	x		
Smilacaceae	*Smilax quinquenervia* Vell.	Climber		x	x
	Smilax cognata Kunth	Climber	x		
Solanaceae	*Cestrum intermedium* Sendtn.	Tree			x
Styracaceae	*Styrax acuminatus* Pohl	Tree			x
	Styrax leprosus Hook. & Arn.	Tree	x		
Tectariaceae	*Tectaria incisa* Cav.	Herb		x	
Theaceae	*Laplacea acutifolia* (Wawra) Kobuski	Tree			x
	Laplacea fruticosa (Schrad.) Kobuski	Tree		x	
Thelypteridaceae	*Amauropelta amambayensis* (Ponce) Salino & T.E.Almeida	Herb			x
	Goniopteris riograndensis (Lindm.) Ching	Herb		x	
Thymelaeaceae	*Daphnopsis racemosa* Griseb	Shrub	x	x	
	Daphnopsis fasciculata (Meisn.) Nevling	Tree	x	x	x
Urticaceae	*Coussapoa microcarpa* (Schott) Rizzini	Tree			x
	Urera nitida (Vell.) P.Brack	Shrub			x
Verbenaceae	*Citharexylum myrianthum* Cham.	Tree	x		
	Recordia reitzii (Moldenke) Thode & O'Leary	Tree	x		
Violaceae	*Anchietea pyrifolia* (Mart.) G.Don	Climber		x	
Vitaceae	*Cissus verticillata* (L.) Nicolson & C.E.Jarvis	Climber		x	
Zingiberaceae	*Hedychium coronarium* J.Koenig	Herb		x	
Non-identified	*Non-identified.01*	-	x		
	Non-identified.02	-	x		
	Non-identified.03	-	x		
	Non-identified.04	-			x
	Non-identified.05	-		x	
	Non-identified.06	-	x		x
	Non-identified.07	-			x
	Non-identified.08	-			x
	Non-identified.09	-		x	x
	Non-identified.10	-			x
	Non-identified.11	-			x
	Non-identified.12	-			x
	Non-identified.13	-			x
	Non-identified.14	-			x
	Non-identified.15	-			x
	Non-identified.16	-			x
	Non-identified.17	-		x	
	Non-identified.18	-	x		
	Non-identified.19	-			x
	Non-identified.20	-		x	
	Non-identified.21	-		x	
	Non-identified.22	-			x
	Non-identified.23	-		x	
	Non-identified.24	-		x	

Appendix B. The geographical localization, soil type and four fragmentation metrics of the 23 forest fragments used for sampling of herb layer in Brazilian Atlantic coastal forests. Soil types were compiled from digital soil classification maps of the Radam-Brasil project. A = fragment area in hectares; SI = shape index; EH = edge-affected habitat; I = isolation. SI was calculated as SI = P/200•[(π•A)0.5] (Laurance and Yensen 1991), where P is the perimeter in meters and A is the area in hectares. Higher values of SI indicate more irregular and complex shapes. EH was calculated as the percentage of edge-habitat, using a 50 m internal buffer into each forest patch area (Pinto et al. 2010). Isolation was quantified as the percentage of forest within a 1-km external buffer set from the perimeter of each fragment (Santos et al. 2008). Path isolation is a measure of habitat amount in the landscape surrounding the patch (Fahring 2003). Fragmentation metrics were quantified using QGIS version 2.16.1 on the basis of Google Earth images.

Code name	Latitude	Longitude	Soil type	A	SI	EH	I
Terra	-29.56311	-50.04384	Arenosols	5.27	1.63	99.22	7.84
Saibreira	-29.63305	-50.07066	Gleysols	41.94	1.59	37.35	14.02
Prof. Batista	-29.38295	-49.83830	Acrisols	10.48	1.93	74.32	13.20
Cornélios	-29.63389	-50.05831	Gleysols	136.25	2.53	33.49	4.90
Mambituba	-29.22758	-49.91336	Acrisols	35.74	2.10	51.49	5.07
Pixirica	-29.31887	-49.92424	Cambisols	31.12	2.35	62.04	11.56
Pixirica2	-29.29033	-49.91576	Cambisols	11.18	1.56	60.19	6.96
Dom	-29.39439	-49.86497	Gleysols	20.10	1.67	51.47	8.75
Osório	-29.84802	-50.23642	Gleysols	15.35	1.69	56.04	8.57
São João	-29.25276	-49.83357	Cambisols	29.61	1.75	46.97	8.37
Praia Grande	-29.17003	-49.90457	Cambisols	24.96	1.36	40.12	7.84
Tramandaí	-29.97252	-50.20566	Arenosols	58.76	2.52	51.82	1.88
Paraíso	-29.42080	-49.82681	Gleysols	7.12	1.59	69.78	6.48
Sombrio	-29.04026	-49.65808	Acrisols	21.73	1.21	40.58	11.93
Araranguá	-28.86121	-49.37083	Acrisols	18.30	2.13	68.27	23.84
Assis	-29.03544	-49.61473	Arenosols	9.65	1.56	79.18	5.77
Torres	-29.34265	-49.78393	Arenosols	3.30	1.78	95.29	7.06
Lajeadinho	-29.41674	-49.91379	Cambisols	6.02	1.35	78.05	9.94
Azaléia	-30.08752	-50.23601	Gleysols	32.73	2.16	50.36	7.70
Içarinha	-28.76587	-49.31621	Acrisols	4.02	1.63	96.38	2.15
Seu César	-29.07030	-49.60431	Gleysols	31.67	1.66	46.15	2.94
Guglielme	-28.73083	-49.22535	Gleysols	36.19	1.23	33.25	28.55
Jaguaruna	-28.70076	-49.04962	Arenosols	73.51	2.79	50.40	9.44

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