


Composition and diversity patterns of terrestrial herb communities in old-growth and secondary South Brazilian Atlantic Forest

Ronaldo dos Santos-Junior¹  · Vanilde Citadini-Zanette² · Robson dos Santos² · Peterson Teodoro Padilha² · San Zatta Custódio² · Lislaine Cardoso de Oliveira² · Jorge Luiz Waechter³

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Abstract The conversion of old-growth into secondary forest changes profoundly the community structure of most plant life-forms, including the communities of terrestrial herbs. Here, we verify how herb communities are affected by environmental variables of old-growth and secondary stands of South Brazilian Atlantic Forest. We identified all herbaceous species and estimated their frequency and cover in 16 plots of 6 × 6 m in each forest type. We used the structural characteristics of the tree component (i.e., basal area, density, average height and canopy openness) and soil parameters as environmental variables of each forest. Results showed that old-growth and secondary forests have distinct herb composition, with the later showing higher plant cover and species diversity. Canopy openness and soil parameters explained part of the variation in herb composition between forests. Herb cover and richness responded positively to soil fertility in both forests, and in secondary forest these two descriptors were also positively correlated with canopy openness. The abiotic differences between forests allowed the establishment of herbaceous species with different ecological requirements, especially in the secondary forest, marked by input of species typically found in disturbed environments. These species contribute to the higher cover values and species richness in secondary forest. Our findings suggest that changes in

environmental conditions in a forest substantially change the herb community. Because of their importance as environmental indicators, herb communities can contribute to a better understanding of successional patterns in the Atlantic Forest.

Keywords Anthropic impact · Forest succession · Ground herbs · Subtropical moist forest

1 Introduction

Tropical and subtropical moist forests are composed by a wide range of plant life-forms, spatially distributed in different forest layers. The terrestrial herbaceous plants, growing in the understory of these forests, contribute significantly both to life-form diversity and to species diversity (Gentry and Dodson 1987; Sevegnani et al. 2013a; Vieira et al. 2015). Furthermore, herb plants play an important role in interactive processes that occur in forest succession (Benítez-Malvido 2006; Cheung et al. 2009). In these processes, herbaceous species compete for below-ground and aboveground abiotic resources with seedlings and saplings of tree species (Gilliam 2007; Griffiths et al. 2007). These interactions might increase in disturbed habitats and so contribute in defining the forest structure and composition, which will be established in the future (Gilliam 2007).

Physical characteristics in secondary forests are quite different from those inside old-growth forests (Werner 1984; Denslow and Guzman 2000), resulting mostly from a modified structure of the tree component, which affects especially light incidence and soil properties (Guariguata and Ostertag 2001). Generally, changes in physical characteristics affect the composition and abundance of many

✉ Ronaldo dos Santos-Junior
rsjecoveg@gmail.com

¹ Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

² Herbário Pe. Dr. Raulino Reitz, Universidade do Extremo Sul Catarinense, Criciúma, SC, Brazil

³ Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

plant life-forms during forest succession, such as tree seedlings and lianas (Laska 1997; Van Andel 2001; DeWalt et al. 2003; Capers et al. 2005; Moora et al. 2007; Jules et al. 2008). In herb communities, the abundance and diversity of the species found in secondary forests are relatively high and decrease toward old-growth forests (Behera and Misra 2006; Cheung et al. 2009; Both et al. 2011). Disturbed habitats, as secondary forests, usually favor the establishment of light-demanding herb species, which are more common in open environments (Costa and Magnusson 2002; Maraschin-Silva et al. 2009) and thus modify the composition of herb communities (Paciencia and Prado 2005). This is due to that secondary forests may show more open canopies, allowing higher light availability in understory compared to old-growth forests (Laska 1997; Jules et al. 2008). Secondary forests may also show poorer soils that favor the establishment of pioneer or generalist species (Maraschin-Silva et al. 2009). In addition, the structural characteristics of the tree layer, especially cover and height of upper trees, may suppress the abundance of herb species in the course of forest succession (Both et al. 2011).

The loss of primary forests and their conversion into secondary forests is nowadays a widespread reality in tropical and subtropical ecosystems. In South Brazil, most of the original Atlantic Forest is presently defined as secondary forest (Sevegnani et al. 2013b). In the same way as old-growth forests, secondary forests may also maintain high species diversity and hold important ecosystem processes and services (DeWalt et al. 2003). Given this scenario, it becomes necessary to understand the structure and function of these environments and to assess how the impact of forest modification affects species diversity and ecosystem processes, especially in complex and disturbed environments like the Brazilian Atlantic Forest (Oliveira-Filho and Fontes 2000; Ribeiro et al. 2009). There are many studies dealing the dynamics of secondary forests, providing a well-established knowledge about of this forest type, especially from a tree component perspective (Guariguata and Ostertag 2001). However, the knowledge of the relations between terrestrial herb communities and forest successional stages is still very scarce in tropical and subtropical moist forests (Turner et al. 1996; Paciencia and Prado 2005; Maraschin-Silva et al. 2009; Both et al. 2011).

In this study, we evaluated the composition and diversity patterns of terrestrial herb communities in old-growth and secondary stands of subtropical Brazilian Atlantic Forest. Firstly, our interest was to analyze how differences in structural characteristics of the tree component and soil parameters between old-growth and secondary forest affect herbaceous composition. We hypothesized that differences in canopy openness and soil fertility gradients between old-

growth and secondary forests drive the establishment of herbaceous species with different abiotic requirements. Secondly, we analyzed whether herb cover and richness differ between forests and how these community descriptors are associated with environmental variables within each forest type. As secondary forests can provide higher light availability near the ground and less fertile soils than old-growth forests, we expected to find higher herbaceous cover and richness in secondary forests, as a result of an exceeding invasion of generalist species in relation to the local extinction of old-growth selective species.

2 Materials and methods

Study area – This study was conducted in protected forests of the Serra Furada State Park (SFSP) and in non-protected surrounding areas, located in southern Santa Catarina State, Brazil (28°11'30.52"S and 49°23'33.18"W at the Park headquarters). The climate of this region is humid subtropical (Cfa) according to the Köppen system (Nimer 1979). Mean annual temperature is 18.7 °C, and mean annual precipitation is 1700 mm (FATMA 2010). Topography varies from a rounded hilly relief at lower elevations (up to 650 m) to very steep slopes at higher elevations (up to 1.480 m). The typical soil types occurring on these landforms are Cambisols and Neosols, respectively (EMBRAPA 2009; FATMA 2010). The original vegetation can be classified as subtropical moist forest according to Holdridge system (Holdridge et al. 1971) or as Montane Dense Ombrophilous Forest following the Brazilian Vegetation System (IBGE 2012).

The study area can be described as a fragmented landscape composed by forests of different successional stages intermixed with pastures, agricultural lands and exotic tree plantations (e.g., *Eucalyptus* spp. and *Pinus* spp.). The SFSP presently shows a relatively large and well-preserved old-growth forest with large trees and many characteristic species of the original climax forests (Veloso and Klein 1957), some of them rare and endangered (e.g., *Ocotea catharinensis* Mez). Tree extraction probably occurred to some extent before the establishment of the Park in the 1980s. The forest vegetation around the SFSP comprises mostly secondary forest patches with different sizes and distinct successional stages. These secondary forests originated from the complete suppression of forested land for timber harvesting, and the subsequent establishment of pastures or crop plantations (e.g., tobacco). Secondary forests have additionally suffered significant changes along time due to exploitation of natural resources, mostly selective extraction of timber and palm heart from one of

the most common palm species (*Euterpe edulis* Mart.) in the region (FATMA 2010).

Sample design and vegetation sampling – We distinguished old-growth and secondary forest according to Clark (1996) and Guariguata and Ostertag (2001). These authors defined secondary forest as a regenerating forest after complete clear-cutting and old-growth forest as having structural parameters of the original tree community (e.g., higher stand basal area, larger variance in the distribution of stem diameters, presence of very large individuals, etc.). The selection of sampling sites in old-growth and secondary forest was based in recent satellite images (Google Earth Pro©) and aerial photographs taken by the Brazilian Army in the years 1956 and 1978. The old-growth forest sampling sites were scattered into the SFSP where the forest was mostly preserved and without evidences of clear-cutting according to historic images. The secondary forest sampling sites were located in surrounding areas of SFSP. Based on aerial historical photographs, we estimated that secondary forest patches had an age of ± 50 years at the time of data collection (2013). The exact age of the forests was difficult to estimate because of the low quality of images and the time lapse between the take of pictures.

We established 16 random plots with 6×6 m in each forest type to sample the herb communities. We avoided sites near streams and clearings. Plots were placed on flat relief in order to standardize old-growth and secondary sampling sites. All sampling sites were distributed at elevations between 430 and 650 m above sea level. Inside the plots, each herbaceous species was identified and quantified according to cover, using the logarithmic scale proposed by Causton (1988). We divided each plot in nine 2×2 m quadrates to improve cover estimation in smaller areas. Only obligate herbaceous species were sampled (Poulsen and Balslev 1991), i.e., species spending their entire life cycle on the forest floor. Saprophytes, hemiepiphytes and fallen epiphytes were left out in the sampling.

All species were identified with the aid of taxonomic monographs and later often confirmed by experts in systematic botany and/or comparisons with herbarium specimens. The circumscription of ferns families follows Smith et al. (2008), and those of angiosperms APG IV (2016). Authors of plant names follow the Flora do Brazil website (<http://floradobrasil.jbrj.gov.br>). Vouchers of sampled herb species were deposited in ICN (UFRGS, Porto Alegre) and CRI (UNESC, Criciúma).

Environmental factors – We used stand basal area, tree density, tree average height and canopy openness as structural variables of the tree component of both old-growth and secondary forest. These parameters vary

through forest succession (Denslow and Guzman 2000) and can affect understory species diversity and abundance (Both et al. 2011). Measurements were taken in 10×10 m plots centered on the herbaceous plots, including all tree species with $DBH \geq 5$ cm. In the center of each plot, we also took hemispherical photographs to quantify canopy openness, using a Canon EOS Rebel XT camera equipped with a fisheye lens directed upright to the sky and positioned at 1 m above the ground on a tripod. Photographs were taken in the early morning and late afternoon. We estimated percentage of canopy openness as an indirect measure of light availability using Gap Light Analyzer software version 2.0 (Frazer et al. 1999).

The soil parameters considered were pH, total phosphorus (P), amount of organic matter (OM), the sum of exchangeable bases (SB) and cation exchange capacity (CEC). These parameters are affected in the course of forest succession and can be used as soil fertility indicators (Guariguata and Ostertag 2001; Ronquim 2010). Four topsoil (0–20) samples were taken in each 6×6 m plot and mixed to produce a composite sample. The soil chemical analyses were carried out at the Soil Analysis Laboratory of the Federal University of Rio Grande do Sul (UFRGS).

Data analysis – We estimated absolute and relative cover and frequency for each herb species, and importance values (IV) as the average relative parameters of these two estimates (Mueller-Dombois and Ellenberg 1974). Differences in total herb cover and environmental factors between old-growth and secondary forest were tested by analysis of variance (ANOVA). The variables without a normal distribution were log-transformed to improve homoscedasticity.

Differences in floristic composition between forest habitats were evaluated by non-metric multidimensional scaling (NMDS) and a permutation multivariate analysis of variance (PerMANOVA) (Anderson 2001), both using Bray–Curtis as dissimilarity measure. PerMANOVA was performed with 999 permutations for pseudo- F ratio significance. This analysis require homogeneous multivariate dispersion, which was found through a distance-based test for homogeneity of multivariate dispersion (PERMDISP2: $F = 0.50$, $P = 0.468$). Additionally, we performed an indicator species analysis to detect the most characteristic species of each forest habitat, using indicator value (IndVal) as an association index (De Cáceres and Legendre 2009). The significance association index was tested by 999 permutations with a significance level $P < 0.05$.

Species diversity was evaluated by species richness and Rényi diversity profiles (Tóthmérész 1995). Rényi diversity profiles give more weight to rare or abundant species as the scale parameter α changes, that is, when α value is

equal to 0 it corresponds to species richness (more weight to rare species), when $\alpha = 1$ it corresponds to the Shannon index (more weight to intermediate species) and when $\alpha = 2$ it corresponds to the Simpson ($1/C$) index (more weight to common species). Individual-based rarefaction was performed to identify the effect of total cover per sample in species richness (Gotelli and Colwell 2001). For both analyses, we used the total absolute cover of each herb species and a confidence interval of 95%.

In order to assess the influence of environmental variables on the variation of herb communities composition, we used the log-transformed predictor variables as covariates in PerMANOVA analysis (Oksanen et al. 2013). This analysis is analogous to the MANCOVA and a powerful method for ecological data because multivariate normal distribution is not required and because it is possible to perform the analysis with more variables than sampling units (MacArdle and Anderson 2001). Additionally, we performed Spearman's rank correlations to determine how the herbaceous cover and richness were associated with site parameters of each forest habitat. Before this analysis, we calculated correlations between all possible pairs of environmental variables and excluded one of each pair that showed a rank correlation >0.7 . The variables excluded were SB which was positively correlated with basal area and pH in old-growth forest, and total P and CEC which was negatively correlated with pH, and SB which was positively correlated with pH in secondary forest.

ANOVA, NMDS, Rényi diversity profiles, individual-based and Spearman's correlations were performed in the software PAST (Hammer et al. 2001). PerMANOVA, PERMDISP2 and IndVal were performed in the R environment (R Core Team 2015). PerMANOVA was performed with 'adonis' function and PERMDISP2 with 'betadisper' function in the 'vegan' package (Oksanen et al. 2013). IndVal was performed with 'multipatt' function in the 'indicspecies' package (De Cáceres and Jansen 2013).

3 Results

We sampled a total of 38 terrestrial herb species belonging to 17 families (Table 1). Angiosperms accounted for 24 species in nine families, whereas ferns 14 species in eight families. The families with highest species richness were Orchidaceae (6), Poaceae (5), Rubiaceae (4) and Aspleniaceae (4). These four families totaled 50% of all sampled species. The more diversified genera were *Coccolopogon* P. Browne and *Asplenium* L., each with three species. In old-growth forest, we sampled 18 species and in secondary forest 26 species. Only six species were common to the

both forest habitats: *Goepertia monophylla* (Vell.) Borchs. & S. Suárez, *Heliconia farinosa* Raddi, *Nidularium innocentii* Lem., *Pleurostachys urvillei* Brongn., *Pteris decurrens* C. Presl and *Sauroglossum elatum* Lindl.

The herb cover was significantly higher in secondary forest than in old-growth forest ($F = 5.31$, $P = 0.028$), with mean cover \pm standard deviation of 31.62 ± 16.98 and 19.06 ± 13.64 in each forest, respectively. Angiosperms had higher cover than ferns in both forest habitats, but mainly in secondary forest. This result is due to the very high covers of the large-leaved *Goepertia monophylla* and *Heliconia farinosa* in both forests. *Goepertia monophylla* was the most important species in both forest habitats, followed by *Didymochlaena truncatula* (Sw.) J.Sm. and *Blechnum brasiliense* Desv., the first in old-growth and the second in secondary forest. *Heliconia farinosa* also showed a high cover and frequency, being the third most important species in both forest habitats (Table 1). These four species were the most frequent and accounted for more than 60% of total cover in each forest habitat and 53 and 46% of VI in old-growth and secondary forest, respectively. The fern *Lastreopsis amplissima* (C. Presl) Tindale was the fourth most important species in old-growth forest. The grasses *Panicum laxum* Sw. and *Hiladaea pallens* (Sw.) C. Silva & R. P. Oliveira were the fourth and fifth most important species in secondary forest. Similarly, these species were exclusive of each forest habitat, and they showed relatively high cover, but low frequency when compared with the most important species.

We found clear differences in species composition between old-growth and secondary forest. The NMDS ordination showed an evident difference in herb composition, evidenced by the formation of two groups of sample units along axis I (Fig. 1). PerMANOVA analysis with species cover data also showed that the forest type and associated covariables contributed to variation in herbaceous composition (Table 4). The indicator species analysis (Table 2) evidenced three species for old-growth forest (all large ferns of the family Dryopteridaceae) and four species for secondary forest (with a single large fern of the family Blechnaceae, plus two grasses and one orchid).

The Rényi diversity profiles (Fig. 2) showed that diversity in secondary forest was higher than in old-growth forest for all alpha parameters. However, the alpha parameter corresponding to the Simpson index ($1/C$) was not different between the two forest habitats in a 95% confidence interval. Rarefaction analysis (Fig. 3) showed that with the same sampled cover in both forest types the secondary forest still had a higher richness than the old-growth forest.

Most structural variables of the tree component were significantly different between the two forest types, but most soil variables did not differ (Table 3). In general, old-

Table 1 Families and species of terrestrial herbs sampled in old-growth and secondary subtropical moist forests in Serra Furada State Park, southern Brazil

Family/species	Old-growth		Secondary	
	Σ_{freq}	Σ_{cov}	Σ_{freq}	Σ_{cov}
Anemiaceae				
<i>Anemia phyllitidis</i> (L.) Sw.			8	8
Aspleniaceae				
<i>Asplenium brasiliense</i> Sw.	2	3		
<i>Asplenium kunzeanum</i> Klotzsch ex Rosenst.	2	3		
<i>Asplenium uniseriale</i> Raddi	2	2		
<i>Hymenasplenium triquetrum</i> (N. Murak. & R. C. Moran) L. Regaldo & Prada	1	1		
Asteraceae				
<i>Chaptalia nutans</i> (L.) Pol.			5	5
<i>Elephantopus mollis</i> Kunth			1	1
<i>Podocoma notobellidiastrum</i> (Griseb.) G. L. Nesom			6	6
Athyriaceae				
<i>Diplazium cristatum</i> (Desr.) Alston			3	3
Blechnaceae				
<i>Blechnum brasiliense</i> Desv.			37	79
Bromeliaceae				
<i>Nidularium innocentii</i> Lem.	16	19	3	4
Cyperaceae				
<i>Pleurostachys gaudichaudii</i> Brongn.	3	4		
<i>Pleurostachys urvillei</i> Brongn.	7	10	14	22
Dennstaedtiaceae				
<i>Dennstaedtia globulifera</i> (Poir.) Hieron.	2	4		
Dryopteridaceae				
<i>Didymochlaena truncatula</i> (Sw.) J.Sm.	29	73		
<i>Lastreopsis amplissima</i> (C. Presl) Tindale	15	28		
<i>Megalastrum connexum</i> (Kaulf.) A.R.Sm. & R. C. Moran	9	18		
Heliconiaceae				
<i>Heliconia farinosa</i> Raddi	14	31	32	80
Marantaceae				
<i>Goepertia monophylla</i> (Vell.) Borchs. & S. Suárez	46	97	58	145
Melastomataceae				
<i>Bertolonia mosenii</i> Cogn.	3	3		
Orchidaceae				
<i>Aspidogyne fimbriaris</i> (B. S. Williams) Garay	4	4		
<i>Liparis nervosa</i> (Thunb.) Lindl.			13	14
<i>Malaxis excavata</i> (Lindl.) Kuntze			2	2
<i>Prescottia stachyodes</i> (Sw.) Lindl.	1	1		
<i>Psilochilus modestus</i> Barb.Rodr.			1	1
<i>Sauroglossum elatum</i> Lindl.	1	1	8	8
Poaceae				
<i>Dichantherium surrectum</i> (Chase ex Zuloaga & Morrone) Zuloaga			9	9
<i>Hildaea pallens</i> (Sw.) C. Silva & R. P. Oliveira			25	31
<i>Homolepis glutinosa</i> (Sw.) Zuloaga & Soderstr.			2	4
<i>Panicum laxum</i> Sw.			32	45
<i>Paspalum corcovadense</i> Raddi			1	1
Pteridaceae				

Table 1 continued

Family/species	Old-growth		Secondary	
	Σ_{freq}	Σ_{cov}	Σ_{freq}	Σ_{cov}
<i>Pteris decurrens</i> C. Presl	2	2	3	5
<i>Pteris denticulata</i> Sw.			1	1
Rubiaceae				
<i>Borreria palustris</i> (Cham. & Schldl.) Bacigalupo & E. L. Cabral			4	4
<i>Coccocypselum geophiloides</i> Wawra			15	18
<i>Coccocypselum hasslerianum</i> Chodat			1	1
<i>Coccocypselum lanceolatum</i> (Ruiz & Pav.) Pers.			6	6
Thelypteridaceae				
<i>Thelypteris rivularioides</i> (Fée) Abbiatti			2	2
Sum of values	159	304	292	505

Σ_{freq} = sum of all frequency estimates, i.e., the total number of subplots in which the species occurred ($n = 144$); Σ_{cov} = sum of all cover estimates, i.e., the total absolute cover in the sample

Fig. 1 Non-metric multidimensional scaling (NMDS) of 32 plots obtained from herb communities in old-growth (*black squares*) and secondary (*open diamonds*) stands of South Brazilian Atlantic Forest. Stress = 0.2299

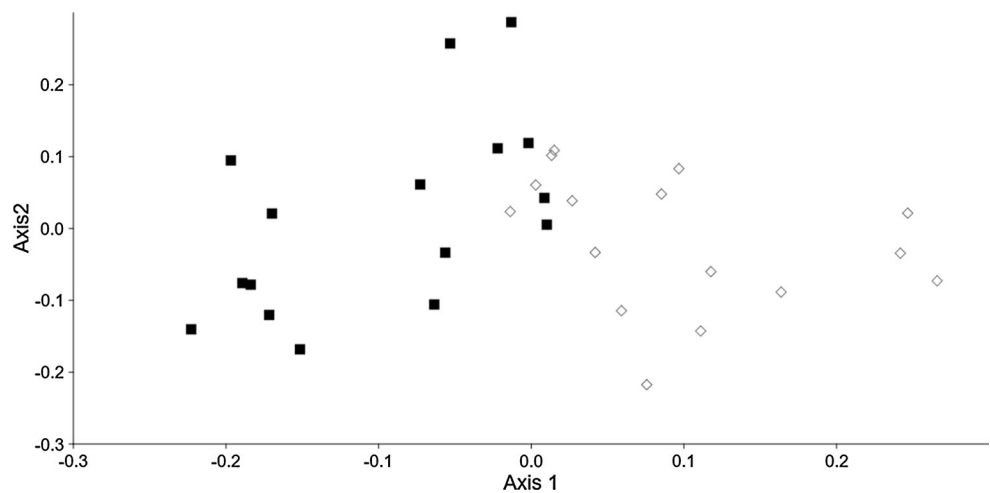


Table 2 Herbaceous species with significant indicator values (IndVal) for old-growth and secondary subtropical moist forests in Serra Furada State Park, southern Brazil

Forest type	Indicator species	IndVal	P
Old-growth	<i>Didymochlaena truncatula</i> (Sw.) J.Sm.	0.71	0.004
	<i>Lastreopsis amplissima</i> (C.Presl) Tindale	0.61	0.014
	<i>Megalastrum connexum</i> (Kaulf.) A.R.Sm. & R. C. Moran	0.56	0.045
Secondary	<i>Blechnum brasiliense</i> Desv.	0.87	0.001
	<i>Panicum laxum</i> Sw.	0.66	0.010
	<i>Hiladaea pallens</i> (Sw.) C. Silva & R. P. Oliveira	0.61	0.021
	<i>Liparis nervosa</i> (Thunb.) Lindl.	0.56	0.049

growth forest showed a more developed structure, manifested by higher basal area, higher average height, smaller tree density, and lower canopy openness in comparison with secondary forest. The soil fertility differences were less evident between forests, but the higher total P and

smaller CEC in old-growth forest (CEC showed a high percent of aluminum content in both forests, which contributed to a lower soil pH—data not shown) evidenced better soil conditions in this forest type. The PerMANOVA results (Table 4) showed that the variables canopy

Fig. 2 Rényi diversity profiles of herb communities of secondary (*lines above*) and old-growth (*lines below*) subtropical moist forests in Serra Furada State Park, southern Brazil. *Solid lines* are alpha parameters and *dotted lines* are 95% confidence intervals

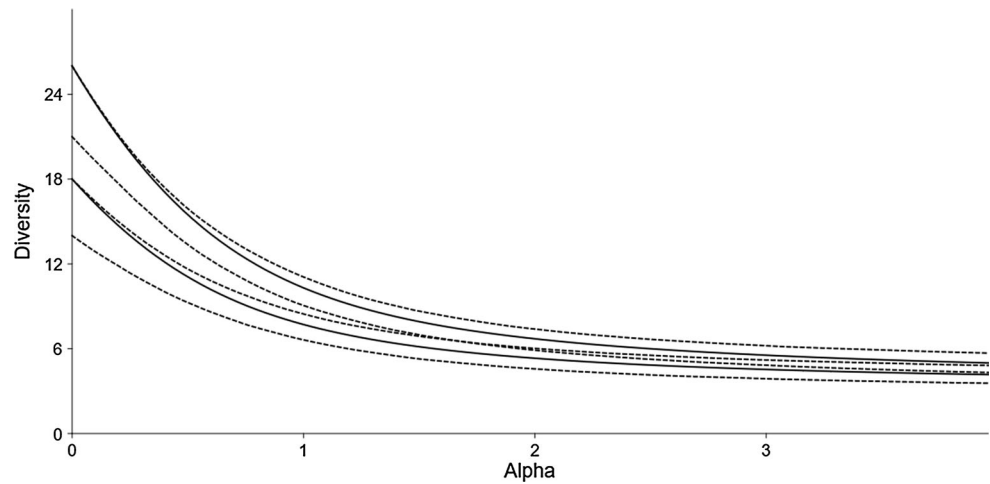


Fig. 3 Individual-based species rarefaction of herbaceous communities in old-growth and secondary stands of South Brazilian Atlantic Forest, based on cover values. External lines are 95% confidence intervals

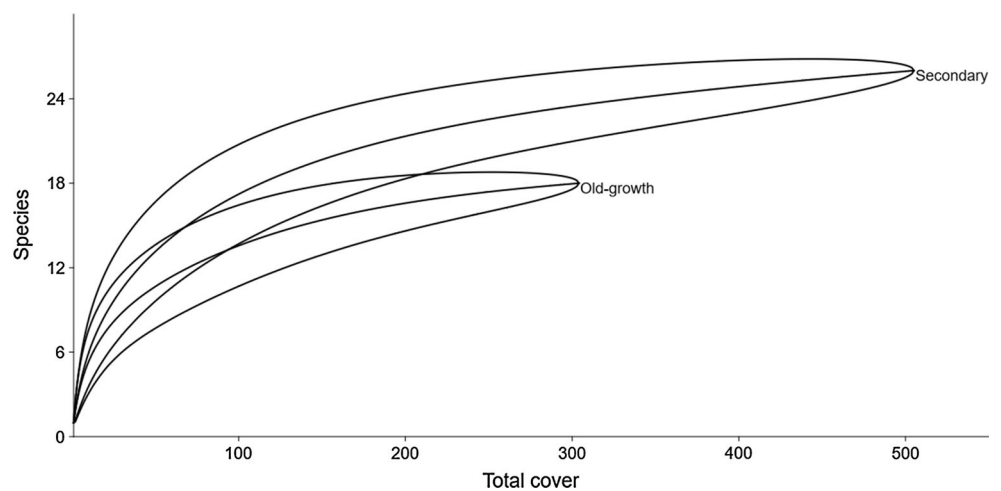


Table 3 Differences of tree and soil variables between old-growth and secondary moist subtropical forests in Serra Furada State Park, southern Brazil, based on analysis of variance

Habitat factors	Parameters	Old-growth	Secondary	F
Tree variables	Basal area (m ²)	0.725 ± 0.44	0.357 ± 0.13	15.63 ^{***}
	Density (nr. individuals)	20.87 ± 4.52	27.43 ± 8.08	8.50 ^{**}
	Average height (m)	8.81 ± 0.93	8.31 ± 1.12	1.93 ^{ns}
	Canopy openness (%)	16.54 ± 2.17	21.79 ± 4.16	21.26 ^{***}
Soil variables	pH (H ₂ O)	4.29 ± 0.24	4.30 ± 0.25	0.01 ^{ns}
	Organic matter (%)	3.21 ± 0.92	3.05 ± 1.03	0.23 ^{ns}
	Sum of bases (cmol dm ⁻³)	0.86 ± 0.50	1.06 ± 0.89	0.17 ^{ns}
	CEC (cmol dm ⁻³)	18.57 ± 7.67	28.26 ± 10.96	8.37 ^{**}
	Total phosphorus (mg dm ⁻³)	3.96 ± 3.74	1.86 ± 0.46	6.77 [*]

The values shown are the mean ± standard deviation obtained from 16 plots of 10 × 10 m in each forest habitat

ns no significant

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

openness (pseudo- $F = 2.10$, $P = 0.042$), pH (pseudo- $F = 4.02$, $P = 0.001$), organic matter (pseudo- $F = 3.14$, $P = 0.004$) and total P (pseudo- $F = 2.11$, $P = 0.039$) significantly explained a proportion of the herb

composition variability between forests. The full model (including the factor 'forest type' and the environmental variables) explained 54% of the composition variability in herb communities.

Table 4 Differences in herb composition between old-growth and secondary subtropical moist forests in Serra Furada State Park, southern Brazil, based on permutation multivariate analysis of variance (PerMANOVA) on Bray–Curtis distances; biotic and abiotic factors were used as covariables in the analysis

Variables	DF	SS	F	R ²	P
Forest type ^a	1	1.60	6.46	0.14	0.001***
Basal area	1	0.26	1.05	0.02	0.412
Tree density	1	0.34	1.38	0.03	0.190
Tree average height	1	0.41	1.65	0.04	0.08
Canopy openness	1	0.52	2.10	0.05	0.042*
pH	1	1.00	4.03	0.09	0.001***
Organic matter amount	1	0.77	3.14	0.07	0.004**
Sum of bases	1	0.27	1.11	0.02	0.321
CEC	1	0.28	1.15	0.02	0.342
Total P	1	0.52	2.11	0.05	0.039*
Residuals	21	5.21	–	0.46	–
Total	31	11.22	–	1	–

DF degrees of freedom, SS sum of squares, F pseudo-F statistic, P P value

Significance (999 permutations): * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

^a Old-growth and secondary forest

In old-growth forest, Spearman's correlations showed that total herb richness and cover were positively correlated with total P ($r = 0.54$, $P = 0.03$; 0.64 , $P < 0.001$, respectively). The total cover was also negatively correlated with CEC ($r = -0.70$, $P < 0.001$). In secondary forest, total herb richness and cover were positively correlated with canopy openness ($r = 0.49$, $P = 0.05$; $r = 0.60$, $P = 0.01$, respectively). In addition, total herb cover was positively correlated with pH ($r = 0.51$, $P = 0.04$). Others site parameters in both old-growth and secondary forest had no significant correlation with cover and richness of herbaceous species. Thus, in both forest habitats herb cover and richness were positively correlated with more favorable soil conditions, and in secondary forest these community descriptors were also positively correlated with canopy openness.

4 Discussion

Our findings showed that old-growth and secondary forests have distinct herb composition, with the later showing higher cover and diversity. In both forests, a few species were dominant, two large-leaved monocots being common to the two forest habitats and two equally large-leaved ferns being highly selective to one or another forest type. The canopy openness and soil parameters (i.e., pH, OM

and total P) contributed significantly in explaining part of the variation in herb composition between forests. Herb cover and richness responded positively to soil fertility in both forests, and in secondary forest these two descriptors were also positively correlated with canopy openness. As expected, the abiotic differences found between forests allowed the establishment of herbaceous species with different ecological requirements, especially in secondary forest, distinguished by the input of several generalist species, which are typical of disturbed environments. This input probably contributed to higher cover and richness values in secondary forest than in well-preserved old-growth forest.

The herb composition of old-growth and secondary forest was quite different in terms of major taxonomic groups, with both ferns and angiosperms species differing markedly when comparing the two forest habitats. Among angiosperms, several species are typical of disturbed environments, as for instance, all the species belonging to the large and widespread families Poaceae and Asteraceae, which occurred exclusively in the secondary forest of our study. These families have many common species in disturbed environments in the South Brazilian Atlantic Forest, including *Chaptalia nutans* (L.) Pol. and *Hildeaea pallens*, which are often found in more exposed sites, as forest edges and clearings (Citadini-Zanette 1984; Cestaro et al. 1986; Liebsch and Acra 2004). These species are also able to tolerate nutrient-poor aluminum-rich soils (Maraschin-Silva et al. 2009), reinforcing their presence of species in secondary forest. Among ferns, disturbed environments can be both restrictive to shade-adapted species (Paciencia and Prado 2005) and on the other hand be favorable to more light-tolerating species, as in the case of *Blechnum brasiliense* (Maraschin-Silva et al. 2009; Kozera et al. 2009). Species of *Blechnum* are generally invasive and thus frequently found with high relative abundance in young secondary forest (Paciencia and Prado 2005). Therefore, as herbaceous ferns and angiosperms respond differently to environmental gradients (Costa et al. 2005; Jones et al. 2014), the abiotic changes in a forest can exclude species typical of preserved forest or favor generalist species, contributing consequently to differentiate secondary forest from old-growth forest composition.

Canopy openness in our study contributed to differentiate herb composition and was correlated with herb cover and richness in secondary forest. Although soil conditions have contributed to differentiate composition too, the relations between soil variables and herb cover and richness are the same in both forests. The differences in species composition, cover and richness between old-growth and secondary forest found in this study agree with other studies that contrasted herbaceous communities in old-growth and secondary forest or otherwise analyzed

herbaceous communities in different successional stages, both in tropical and subtropical forests (Maraschin-Silva et al. 2009; Both et al. 2011) as well as in temperate and boreal forests (Moora et al. 2007; Jules et al. 2008). This tendency was also observed for other understory components, such as shrub and tree regeneration (Laska 1997; Denslow and Guzman 2000; Capers et al. 2005). In general, these studies indicate that more light availability in secondary forests, caused by higher canopy openness, allows the input of many light-demanding and generalist species into the forest, such as grasses with a strong colonization power (Manninen et al. 2009). In South Atlantic Forests, as suggested by Müller and Waechter (2001), terrestrial herb diversity is higher in dry and in secondary forests than in moist and well-preserved rainforests, probably due to higher light incidence, resulting from a relatively lower canopy or from habitat disturbance. Thus, our study seems to confirm this idea that more favorable light conditions in secondary forests represent one major differentiating factor for terrestrial herb communities.

The diversity profiles showed that secondary forest holds more species diversity (alpha parameters 0 and 1) than old-growth forest, but the alpha parameters that correspond to Simpson's Index did not differ. So, in terms of dominant species, both forests showed similar results (each one with three dominant species in terms of cover). The most important species among the dominant ones was *Goepertia monophylla*, presenting a high frequency and cover both in old-growth and secondary forest. *Goepertia monophylla* is additionally common and widespread in different successional stages of South Atlantic Forest understories (Klein 1980). In face of this great abundance and wide distribution, this species can possibly play an important role on tree regeneration, as also demonstrated for other large understory plants such as palms (Harms et al. 2004) or by plants able to form dense monospecific stands (Griffiths et al. 2007).

Our results indicate that changes in the environmental conditions in a forest cause start a strong shift in the composition and structure of the herb community in stands of South Brazilian Atlantic Forest. These changes may exclude those herbaceous species that are more sensible to stressful environments, as found in disturbed environments. This exclusion may also cause changes in functional traits and consequently impacts on ecosystem processes (Díaz et al. 2004). Although our work focused a relatively small forest chronosequence, the study showed that herb communities at one particular stage of secondary forest (± 50 years) are quite different in relation to old-growth forest, thus highlighting the quality of herbaceous species as environmental indicators. In this context, the structure of herb communities represents an important knowledge to improve the Brazilian laws regarding classification of

forest successional stages. Because herbaceous species may interact with regenerating trees, and consequently affect forest succession (Benítez-Malvido 2006), we suggest that more studies should be carried out with herb communities along forest chronosequences, in order to better understand the successional patterns in moist Atlantic Forests.

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