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Small scale structure of forest stands in the Atlantic Rainforest – Notes on understorey light fluctuation

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Abstract: The effect of small scale structural dynamics of forest stands and their canopies on spatiotemporal heterogeneity of the understorey light regime was assessed in this study. Forest structure and woody species composition in combination with canopy structure parameters and photosynthetic photon flux density (PPFD) were measured in three investigation plots. Sampling took place during two periods in 2004 and 2005 to check on inter-annual differences of canopy conditions and light availability. All plots differed considerably in species composition and high α-diversity was recorded. Forest structure and canopy openness differed between plots. No differences in leaf area estimations and photon flux density were found during the same sampling period. Inter-annual differences were identified for leaf area index and canopy openness, but not in conjunction. On the other hand, inter-annual differences in photon flux density were only identified in combination with significant canopy openness changes. Our study confirmed hemispherical photography and quantum sensor based PPFD measurement as a valid tool for rapid assessment approaches regarding canopy structure and their spatiotemporal heterogeneity and the effect on understorey PPFD fluctuations. The variability and heterogeneity of canopy structure may help to explain the impact on stand dynamics and the reduced importance of classic gaps in communities identified for some rainforests.

Resumen: Este estudio evaluó el efecto de la dinámica estructural de pequeña escala de rodales de bosque y sus doseles sobre la heterogeneidad espacio-temporal del régimen lumínico del sotobosque. En tres parcelas de investigación se midieron la estructura del bosque y la composición de especies leñosas, junto con parámetros de la estructura del dosel y la densidad de flujo de fotones fotosintéticos (DFFF). El muestreo se llevó a cabo durante dos periodos en 2004 y 2005 para examinar diferencias interanuales en las condiciones del dosel y de disponibilidad de luz. Todas las parcelas difirieron considerablemente en su composición de especies y se registró una diversidad α alta. La estructura del bosque y el grado de apertura del dosel difirieron entre parcelas. No hubo diferencias en las estimaciones de área foliar y del flujo de fotones fotosintéticos durante el mismo periodo de muestreo. Se identificaron diferencias interanuales para el índice de área foliar y la apertura del dosel, pero no de forma conjunta. Por otra parte, sólo se identificaron diferencias interanuales en la DFFF en combinación con cambios significativos en la apertura del dosel. Nuestro estudio confirmó que la fotografía hemisférica y el sensor de quantum basado en la medida de la DFFF son herramientas válidas para enfoques de evaluación rápida relacionados con la estructura del dosel y su heterogeneidad espacio-temporal, y el efecto de las fluctuaciones de la DFFF en el sotobosque. La variabilidad y la heterogeneidad de la estructura del dosel pueden ayudar a explicar el impacto sobre la dinámica del rodal y la importancia reducida de la clásicos claros del dosel en comunidades identificadas para algunos bosque lluviosos.

Resumo: Este estudo avalia o efeito das dinâmicas na pequena escala da estrutura das

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parcelas florestais e nos seus copados na heterogeneidade espacial-temporal dos regimes de luz no sub-coberto. A estrutura da floresta e a composição das espécies lenhosas, em conjugação com os parâmetros da copa e a densidade do fluxo dos fotões fotossintéticos (PPFD), foram medidos em três parcelas de investigação. A amostragem realizou-se durante dois períodos em 2004 e 2005 para avaliar as diferenças inter-anuais das condições do copado e a disponibilidade de luz. Todas as parcelas diferiram consideravelmente quanto à composição das espécies tendo também sido registada uma elevada diversidade α. A estrutura do copado da floresta e a abertura do copado diferiram entre parcelas. Não se verificaram, contudo, durante o mesmo período de amostragem, diferenças nas estimações da área folhear e na densidade do fluxo de fotões. Foram identificadas diferenças inter-anuais para o índice de área folhear e a abertura dos copados mas estas não se verificaram em conjugação. Por outro lado, as diferenças inter-anuais na densidade do fluxo de fotões só foram encontradas em conjugação com mudanças significativas nas aberturas do copado. O nosso estudo confirmou que a fotografia hemisférica e a medida com base no sensor quântico PPFD é um instrumento válido para uma abordagem rápida da estrutura do copado e da sua heterogeneidade espaço-temporal e do efeito no sub-coberto das flutuações do PPFD. A variabilidade e heterogeneidade da estrutura do copado pode ajudar a explicar o impacte nas dinâmicas das parcelas e para ajudar a reduzir a importância das clareiras clássicas identificados para algumas florestas de chuvas.

Key words: Canopy structure, forest structure, hemispherical photography, Photosynthetic Photon Flux Density (PPFD).

Introduction

Forest structure parameters and canopy geometry, in particular, are known to have direct effects on the light regime in the understorey (Liebermann *et al.* 1989; Montgomery & Chazdon 2001; Rich *et al.* 1993). There are many non-linear responses of plant ecophysiological processes to the dynamics of availability and quality of solar radiation flux in the understorey (Baldocchi & Collineau 1994; Denslow 1987; Vierling & Wessman 2000). Photosynthetic photon flux density (PPFD) within forest stands is characterized by high heterogeneity. Especially wet tropical forests are systems with strong dynamics and are highly diverse in their structure. Therefore, detailed information of these processes is essential for assessing questions in vegetation regeneration and succession.

The majority of studies on tropical understorey light environment focused on consequences of canopy gaps at different scales (Ferreira de Lima & Cunha de Moura 2006; Martinez-Ramos *et al.* 1989; Rijkers *et al.* 2000; Romell *et al.* 2009; Smith *et al.* 1992). But, a distinct categorisation into gap and canopy-shade leaves the complex architecture beneath the canopy and their dynamics aside (Grubb 1996; Popma *et al.* 1988). Stand structure and species composition can have obvious effects on light transmittance without big canopy gaps (Kabakoff & Chazdon 1996; Sattler & Lindner 2009).

There are different approaches of studies dealing with understorey light conditions in assessing quantum sensor based PPFD data. A large part of those studies are providing valuable information about the light regime in addition to supplementary data of forest composition and structure over a comparable large area, but only as a snapshot without taking temporal dynamics into account (e.g. Ferreira de Lima & Cunha de Moura 2006; Montgomery & Chazdon 2001; Pearcy 1983). On the other hand, some studies provide data of long term PPFD monitoring in tropical forests, but they are limited to few sampling points. Furthermore, supplementary data of forest structure is often neglected in favour of high resolution temporal variability of understorey radiation (e.g. Dou *et al.* 2005; Raich 1989; Rich *et al.* 1993). The results of studies with such limitations in sampling areas can become questionable within a forest with a high spatial heterogeneity like the Atlantic Rainforest in south-eastern Brazil (Morellato & Haddad 2000; Pardini *et al.* 2005), where this study was carried out.

The results of Romell *et al.* (2009) demonstrated the influence of artificial gap creation on forest floor light conditions in Borneo and provided results in structural as well as temporal scales. In spite of quantifying the effects of an artificial treatment, this study focused on the consequences of forest structure and natural dynamics on understorey light fluctuations in a small scale approach. The following objects were addressed :

1. The investigation of spatio-temporal changes in canopy structure on understorey light conditions.
2. The evaluation of hemispherical photography in combination with measurements of photosynthetic photon flux density (PPFD) as a tool to estimate small scale changes in forest structure.

Materials and methods

Study site

The study was conducted in the Atlantic Rainforest (Mata Atlântica) at the national park "Serra dos Orgãos" in Teresópolis, state of Rio de Janeiro in south-eastern Brazil (22° 27' 24" S, 42° 59' 48" W). The recently enlarged reserve was founded in 1939 and incorporates an area of about 20.024 ha covering an altitudinal gradient from 80 - 2263 m asl. Because of the differences in elevation and a mosaic of steep slopes and hillsides, the relief is characterized by a high level of heterogeneity. The general climate conditions of the area are tropical montane humid with a pronounced wet season from November to February. Long-term mean annual rainfall is 2821 mm in combination with high relative humidity and a mean temperature of 17.8 °C (Guimarães & Arlé 1984; Rizzini 1954).

Vegetation can be classified as dense ombrophilous forest (Veloso *et al.* 1991) up to an elevation of 2000 m asl. This forest formation can be subdivided into four zones: (1) lowland (< 50 m asl), (2) submontane (50 - 500 m asl), (3) montane (500 - 1500 m asl), (4) high-montane (1500 - 2000 m asl) (Rambaldi *et al.* 2003). The research area is situated within the montane forest formation.

Plot design

Three research plots were established to examine vegetation, stand structure and light conditions. The plots were set up with a size of 60 x 60 m and subdivided into 10 x 10 m subplots. Two plots were located at an elevation of 1196 m asl with a distance of 100 m between each other. Another plot was established at a distance of 600 m from this area located at 1265 m asl. PPFD measurements and hemispherical photographs were taken in September 2004 and September 2005 in the centre of each subplot. Hemispherical photography was limited to the inner 16 subplots with a complete size of 40 x 40 m. This resulted in 16 photos and 36 PPFD measurements in each plot per series. A sampling grid like this provides high resolution data to avoid problems because of high spatial variability (Baldocchi & Collineau 1994). Vegetation was sampled in the 20 x 20 m core area of the plots (Fig. 1).

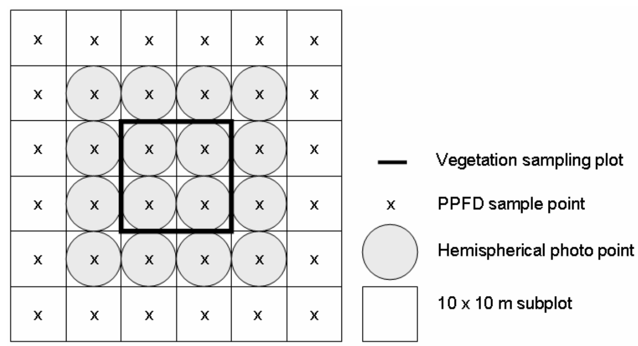

Fig. 1. Plot setup and sampling design: each plot (60 x 60 m in total) comprised 36 subplots (10 x 10 m each). Repeated PPFD measurements were made within every subplot, whereas hemispherical photography was limited to 16 centre subplots and vegetation was sampled in the 4 inner subplots (20 x 20 m).

Measurements

In this 400 m² core area of each plot, the woody plant community was evaluated using the main principles of Condit (1998). All woody plants with diameter at breast height (DBH) ≥ 5 cm were marked and sampled. The specimens were identified to species. If exact determination was not possible, species were distinguished on the basis of morphology (morphospecies). DBH was measured by using a calliper at 1.30 m above ground on the uphill side of the tree. A measuring tape was used when the diameter exceeded 50 cm. The height of each individual was visually estimated using five height classes: (1) < 10 m; (2) 10 - 15 m; (3) 15 - 20 m; (4) 20 -25 m; (5) > 25 m.

PPFD measurements were taken at breast height (1.30 m) at every sample point (Fig. 1) during both research periods in 2004 and 2005. A

LI-250A LightMeter in combination with a LI-190SA Quantum sensor (electromagnetic spectrum 400 - 700 nm, maximum deviation of 1 % up to 10,000 µmol $s^{-1}m^{-1}$) was used (LI-COR Environmental, NE, USA). Measurements were only taken on overcast days between 12:00 and 13:00 pm to assure that they are not confounded by sunflecks or other changing conditions. The average mode of the LightMeter was used to measure PPFD at each sample point. Information about absolute PPFD (above canopy PPFD) was gathered by reference measurements on a clearance near the sample sites right before the PPFD recordings in the research plots (Montgomery & Chazdon 2001). Five light measurement series per plot were made in each research period.

Hemispherical photography is a useful tool for the assessment of forest structure parameters such as canopy openness and leaf area index (Fassnacht *et al.* 1994; Jonckheere *et al.* 2004; Trichon *et al.* 1998). To take the hemispherical photographs, a Nikon™ Coolpix 4500 digital camera with a Nikon™ FC-E8 fisheye-lens was used. Resolution was set to 2272 x 1704 pixels. The camera was fixed on a tripod 1.30 m above the ground, leveled and looking upwards to the sky. Pictures were only taken under overcast conditions to avoid over-exposed regions around the sun and to reduce reflections on leaves which could be construed as openings. One photo series in every plot in both research periods, i.e. 2004 and 2005, was taken to capture the effects of inter-annual variability of leaf and tree crown development.

Statistical analyses

To assess the composition of the woody plant community, the family importance values (FIV) as introduced by Mori *et al.* (1983) were calculated for each plant family in all plots.

The basal area (*ba*) of each tree was calculated ($ba = \pi (DBH/2)^2$). A One-Way Analysis of Variance (ANOVA), including the Student-Newman-Keuls multiple comparison procedure, was used to check for significant differences in basal area and tree height classes between the plots (normal data distribution checked).

The WinScanopy 2005ab software (Regent Instruments Inc., 2005) was used to analyze the hemispherical photographs and to derive data about canopy openness (CO) and leaf area index (LAI). Canopy openness is defined as proportion of open sky area in a 180° hemisphere monitored from a centre point. Pixels of digital images are to be classified as either "canopy" or "sky" based on the grayscale value (pictures are automatically transformed to grayscale from color photographs by the software). Leaf area index (LAI) is the total one-sided area of leaf tissue per ground unit. The LI-COR LAI2000 modified algorithm (assuming random leaf distribution, transmittance is equivalent to gap fraction, modeled by the Poisson model) was used to calculate LAI values (Welles & Norman 1991). A One-Way ANOVA, including the Student-Newman-Keuls multiple comparison procedure, was used to check for significant differences in canopy openness and LAI among the plots (normal data distribution checked). To compare the inter-annual difference of those canopy structure parameters a One-Way repeated-measures ANOVA was performed.

Based on the series of average measurements on each sample point, the median and mean values of the total photon flux density ($PPFD_t$) were calculated for each plot. The coefficient of variation (*cv*, ratio of standard deviation to the mean) was calculated for $PPFD_t$ to assess the heterogeneity within this data set. Because of the reduction of diffuse assimilation by tree crowns and stand density (Rich *et al.* 1993; Romell *et al.* 2009), all measurements resulting in a $PPFD_r$ value > 0.8 were considered out of range and discarded. $PPFD_r$ is the quotient of the measurements inside the forest plots and the recordings in the clearance (above canopy PPFD). The data of the PPFD measurements failed to provide a normal distribution. Therefore, a non-parametric Kruskall-Wallis One-Way ANOVA on ranks was used to check for significant differences between the plots. To get information about the inter-annual variance in understorey radiation regimes, the total and relative photon flux density ($PPFD_t$, $PPFD_r$) was compared in each plot regarding the two sampling periods in 2004 and 2005. The comparison was made using a non-parametric Friedman repeated-measures-ANOVA on ranks.

Because of the hierarchical sample design (nested data set) and expected structural heterogeneity between the three research plots, a mixed effects modelling approach (plot as random factor) was used to determine the coherency between inter-annual $PPFD_r$ difference (dependent variable) and canopy structure parameters (canopy openness and LAI – independent variables). Additionally, linear regression was used to analyze this interrelation for each plot separately, whereas possible co-interactions were excluded using a stepwise forward procedure.

Table 1. Family importance values (FIV) of the most important families in the investigation plots, based on ten families holding the highest FIV scores in each plot (400 m^2). Only three families out of the resulting pool of 17 families are occurring in all plots.

	Plot 1	Plot 2	Plot 3
Arecaceae (*Euterpe edulis*)	130.05	33.04	17.44
Lauraceae	17.31	53.69	31.45
Myrtaceae	34.92	39.80	41.95
Σ	182.28	126.52	90.84
Cecropiaceae	26.36	-	-
Chrysobalanaceae	11.15	-	10.99
Cyatheaceae	-	-	13.67
Flacourtiaceae	9.79	-	-
Hippocrateaceae	8.74	-	-
Melastomataceae	-	-	11.14
Meliaceae	27.70	-	-
Monimiaceae	-	14.97	-
Moraceae	11.15	-	12.29
Nyctaginaceae	-	21.64	12.86
Rubiaceae	-	26.59	59.91
Sapindaceae	-	5.19	27.34
Sapotaceae	8.77	39.60	-
Vochysiaceae	-	19.16	-
Σ	103.66	127.15	148.19
Σ others	14.06	46.32	60.97

Statistical analyses were performed using the SigmaStat Software Package (version 3.0.1, SPSS Inc., 2003) and SyStat (version 13, SyStat Software, 2009). The Shannon-index of diversity (H') and the corresponding evenness index (J') were determined according to Krebs (1998).

Results

Floristic and stand structure

Altogether, 67 species representing 32 families were identified in all the plots, with five families accounting for 57 % of all species (Myrtaceae: 15 spp., Lauraceae: 9 spp., Rubiaceae: 7 spp., Monimiaceae: 4 spp., Melastomataceae: 3 spp.). Other families were represented by only one or seldom by two species. Floristic composition differed considerably between plots (Table 1). Plot 1 was strongly dominated by *Euterpe edulis* Mart. (Arecaceae), whereas in plot 2 a more heterogeneous composition characterized by Lauraceae, Myrtaceae and Sapotaceae was found, even though it was situated nearby (only 100 m). In plot 3, which was located at about 70 m higher elevation and within a distance of 600 m, a heterogeneous composition of tree species was found as well. Rubiaceae and Myrtaceae were the most dominant families in this area. Shannon diversity (H') and evenness (J') indices were low in plot 1 (H' = 1.17, J' = 0.30) in comparison to plot 2 (H' = 4.26, J' = 0.81) and plot 3 (H' = 3.62, J'= 0.75). An α-diversity of H' = 3.87 (J' = 0.63) can be stated when assuming all plots as interrelated areas.

When only the ten families with the highest family importance value (FIV) for each plot (17 families in total) were considered, only three families (Arecaceae, Lauraceae and Myrtaceae) occurred in all the three plots, representing 30.3 (plot 3) to 60.8 % (plot 1) of the FIV of the whole community (Table 1).

Stem density ranged from 96 to 126 per 400 m^2 vegetation sampling area (2,400 to 3,150 per ha). Basal area was significantly higher in plot 2 than in the other plots, and tree heights were significantly lower in plot 3 than in the other plots (Table 2).

Canopy structure and light conditions

Canopy openness was significantly lower in plot 3 in both sampling periods (2004 and 2005). There was no such difference in the mean leaf area index (LAI) among the plots in the same sampling period (Table 2). Mean relative photosynthetic photon flux density ($PPFD_r$) was at the same level as well and ranged from 4.7 (plot 3) to 5.0 % (plot 2) in 2004 and from 3.5 (plot 3) to 4.6 % (plot 1) in 2005. Due to data distribution median, $PPFD_r$ values were clearly lower and were covering a range as low as 0.5 (plot 1) to 0.9 % (plot 2) in 2004 and 0.3 % in all plots in 2005. Equally, no significant differences were found in mean total photosynthetic photon flux densities ($PPFD_t$), although above canopy PPFD was higher in plot 3 in both sampling periods due to higher elevation of this plot (Table 2). $PPFD_t$ showed a high level of heterogeneity in all plots during all sampling series (*cv*: 0.34 - 0.56).

Table 2. Comparison of main floristics, forest structure, canopy structure (canopy openness = CO, leaf area index = LAI), PPFD conditions and inter-annual differences of canopy and light aspects among all plots [data of main floristic and forest structure in the 4 inner subplots (20 x 20 m)]. Small letters (*a, b* and *c*) indicate the horizontal grouping within the table resulting from ANOVA testing.

	Plot 1	Plot 2	Plot 3	*<P*
Elevation (m asl)	1196	1196	1265	
Species richness	17	37	30	
Family richness	12	19	21	
Shannon-Diversity H’	1.17	4.26	3.62	
Evenness J’	0.3	0.81	0.75	
Forest structure				
Number of stems	126 (3150 ha^{-1})	100 (2500 ha^{-1})	96 (2400 ha^{-1})	
(1) Basal area (m^2)	1.7 (42.5 ha^{-1})*a*	2.65 (66.2 ha^{-1})*b*	1.36 (34.0 ha^{-1})*a*	*0.025*
(1) Tree height (classes)^	2.68 ± 0.06 *a*	2.65 ± 0.10 *a*	1.98 ± 0.11 *b*	*0.001*
Canopy structure & light				
yr 2004				
(1) CO (%)	7.27 ± 0.24 *a*	7.27 ± 0.20 *a*	6.17 ± 0.26 *b*	*0.002*
1) LAI	3.6 ± 0.08	3.73 ± 0.13	3.59 ± 0.13	*0.644*
(2) $PPFD_t$	86.4 ± 32.9 (*cv* = 0.38)	89.7 ± 50.3 (*cv* = 0.56)	156.4 ± 79.5 (*cv* = 0.51)	*0.631*
(2) $PPFD_r$ (%)	4.81 ± 10.99	5.01 ± 16.78	4.68 ± 17.18	*0.845*
median $PPFD_r$ (%)	0.51	0.92	0.63	
yr 2005				
(1) CO (%)	7.15 ± 0.20 *a*	6.89 ± 0.18 *a*	5.88 ± 0.20 *b*	*0.001*
(1) LAI	4.09 ± 0.16	4.03 ± 0.14	4.12 ± 0.23	*0.935*
(2) $PPFD_t$	90.3 ± 43.0 (*cv* = 0.48)	74.6 ± 27.6 (*cv* = 0.37)	73.0 ± 24.7 (*cv* = 0.34)	*0.082*
(2) $PPFD_r$ (%)	4.56 ± 13.03	3.77 ± 8.36	3.48 ± 7.05	*0.161*
median $PPFD_r$ (%)	0.33	0.34	0.31	
Inter-annual difference				
(3) CO	*P = 0.641*	*P = 0.035*	*P = 0.058*	
(3) LAI	*P = 0.022*	*P = 0.112*	*P = 0.025*	
(4) $PPFD_r$	*P = 0.317*	*P = 0.046*	*P = 0.505*	

^ tree height classes:
(1) <10 m
(2) 10-14.9 m
(3) 15-19.9 m
(4) 20-24.9 m
(5) >25 m

$PPFD_t$ readings in µmol $\cdot m^{-2} \cdot s^{-1}$
cv Coefficient of variation
(1) One-Way-ANOVA (Student-Newman-Keuls multiple comparison procedure)
(2) Kruskall-Wallis-One-Way-ANOVA on Ranks
(3) One-Way-RM-ANOVA
(4) Friedman-RM-ANOVA on Ranks

Table 3. Comparison with other phytosociological studies in the Atlantic forest (all DBH ≥ 5 cm) in terms of sample method, sampling effort, species richness, basal area (ba) per hectare and α-diversity (Shannon H', Evenness J').

Reference	Method[1]	Total site size	Number of species	Ba (m^2ha^{-1})	H'	J'
This study	plot	0.12 ha	67	47.58[2]	3.87	0.63
Kurtz & Araújo (2000)	pcq	150 points	138	-	4.20	0.85
Guedes-Bruni *et al.* (2006)	plot	1.0 ha	97	23.77	3.98	0.87
Vilela *et al.* (2000)	plot	1.6 ha	116	53.13	3.79	0.45
Ruschel *et al.* (2005)[3]	pcq	468 points	51	36.5	3.73	0.86
Jarenkow & Waechter (2001)	plot	1.0 ha	55	41.66	2.24	0.56

[1] plot - plot based sampling
pcq - point center quarter
[2] extrapolation from mean value of 0,04 ha vegetation sampling plots
[3] total of samplings made in 12 forest fragments

Inter-annual differences

LAI increased significantly in plot 1 and plot 3, but was not accompanied by significant decrease in canopy openness. Such fluctuation was only observed in plot 2, where canopy openness decreased significantly and $PPFD_r$ changed alike (Table 2).

Mixed models analyses, including all three plots, showed a distinct signal for the inter-annual change in canopy openness as predictor for differences in $PPFD_r$. No significant effect was identified for the inter-annual change in LAI in predicting $PPFD_r$ differences (Fig. 2). Additionally, this significant coherence between the inter-annual change of canopy openness and $PPFD_r$ was identified in all plots separately (stepwise forward regression - plot 1: $F = 18.85$; $P < 0.001$, plot 2: $F = 11.91$; $P = 0.004$ and plot 3: $F = 10.98$; $P = 0.006$). Overall, no interrelation between the inter-annual change of LAI and $PPFD_r$ was found (stepwise forward regression - plot 1: $F = 2.39$; $P = 0.15$, plot 2: $F = 0.29$ and $P = 0.60$ and plot 3: $F = 0.14$; $P = 0.71$).

Thus, for all plots, a significant relation between inter-annual differences in canopy openness and $PPFD_r$ was identified, whereas no such relation was found between inter-annual differences in LAI and $PPFD_r$ (Fig. 3).

Discussion

Even in such a small scale approach, the high diversity and heterogeneity of the Atlantic Rainforest in south-eastern Brazil is confirmed. The outcome in terms of α-diversity and basal area of the woody plant community are comparable to other more extensive studies in this region (Table 3).

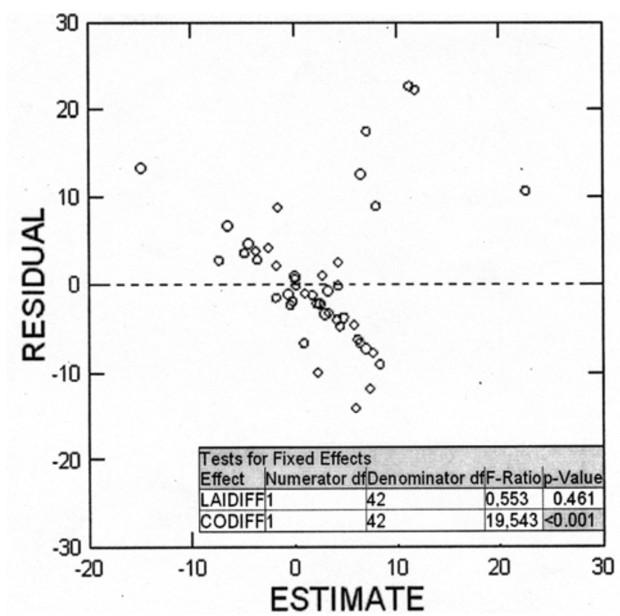

Fig. 2. Residuals vs. predicted values in mixed models analysis (nested data set; dependent variable: interannual difference of $PPFD_r$; fixed covariates: LAIDIFF interannual difference of LAI, CODIFF interannual difference of canopy openness; random factor: plot).

Spatial and temporal heterogeneity

The Atlantic Rainforest of south-eastern Brazil features a high level of endemism and is among the biodiversity hotspots of the world (Myers *et al.* 2000). Such diversity is due to a high level of habitat heterogeneity. The research plots differ considerably in floristic composition and exemplify the mosaic of different microhabitats within the same geographic level. The dominance of *Euterpe edulis* in plot 1 is as typical (Silva Matos & Alves 2008) as tree community composition with Myrtaceae and Lauracae as important components and its variance in plot 2 and 3 (Kurtz & Araújo 2000; Mori *et al.* 1983; Peixoto *et al.* 2004). Not only floristic composition but also stand structure was variable, although investigation areas were in close proximity to each other.

The significant differences in tree height and canopy openness in plot 3 (smaller trees and more closed canopy) compared to the other two plots might be due to its higher elevation. Despite those differences in species composition and structure parameters, LAI values did not differ among plots. Therefore, LAI cannot be easily related directly to structural aspects, especially when data is obtained by hemispherical photography (Anderson 1981; Sattler & Lindner 2009).

Only in plot 1 and plot 3 a significant increase in LAI was observed, whereas in plot 2 this is only true for the decrease in canopy openness. Solely, this inter-annual change in canopy openness is conjoined with altered radiation in the understorey, whereas LAI differences did not affect the light regime.

Determining factors of PPFD fluctuations

Generally, understorey light conditions were comparable to other studies under closed canopy conditions (Motzer 2005; Rich *et al.* 1993), and results of PPFD measurements showed a distinct variation (Dou *et al.* 2005; Montgomery & Chazdon

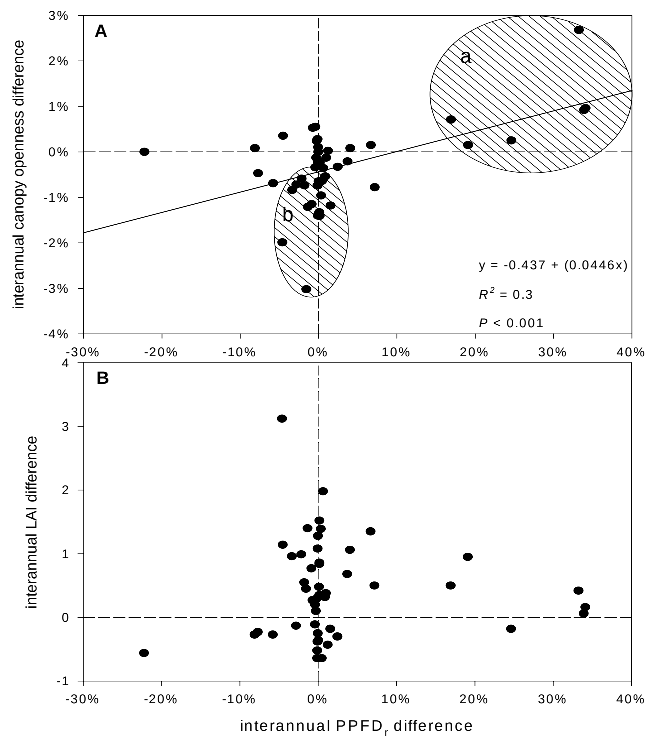

Fig. 3. Relation between inter-annual canopy structure changes (A: canopy openness, B: LAI) and differences in relative photosynthetic photon flux density difference ($PPFD_r$) within all investigation plots. Increasing canopy openness is attended by increasing $PPFD_r$ (a), whereas no distinct effect on $PPFD_r$ was recorded when canopy openness was decreasing (b). No relation at all between inter-annual changes of LAI and $PPFD_r$ was detected.

2001; Rich *et al.* 1993). But overall no significant difference was found among plots at the same measuring period. Consequently, there were comparable PPFD conditions in the understorey, although a high level of structural and species diversity was recorded. This is in accordance to the results of other studies in tropical forest systems (Denslow & Guzman 2000; Montgomery & Chazdon 2001).

As aforementioned, a significant inter-annual difference in the understorey light regime was only detected in one plot. Within the same area, a significant inter-annual change was also detected in canopy openness. But, it is critical to rely on consolidated data (mean values), especially, if significant differences are accompanied by high heterogeneity within data series (Table 2).

The relation between inter-annual differences in canopy openness and $PPFD_r$ was statistically significant for all plots (Fig. 3A), which is quite contrary to the relation between LAI and $PPFD_r$ (Fig. 3.B). Despite the lack of a synchronistic significant change in canopy openness and $PPFD_r$ there was a distinct coherence between both parameters. Thus, this leads to the assumption that those maximum differences in canopy openness will be of high interest instead of mean values for a given area. Therefore, small scale canopy dynamics and micro-gaps are the determining factors of PPFD fluctuations. Especially, the increase in canopy openness had a positive effect on PPFD, whereas the decrease in canopy openness barely caused any change in PPFD. A possible explanation could be: when starting at a certain threshold value, more open canopy conditions permit a bigger share of direct radiation to reach the understorey (Fig. 3A.a). Because of the nearly complete absorption rate of photosynthetically active radiation in the upper canopy layer level (Leigh 1975; Leopoldo *et al.* 1993; Parker 1995), a further decrease of canopy openness has little effect on PFFD at understorey level (Fig. 3A.b).

Canopy openness is known as a good indicator of basic geometry of the canopy and the potential penetration of solar radiation (Walter & Torquebiau 1997) and it is highly correlated to the microclimatic conditions of a forest stand (Pohlman *et al.* 2007; Whitmore *et al.* 1993). Montgomery & Chazdon (2001) concluded that forest structure might be a suitable predictor for light availability at large studies, but more subtle factors like tree architecture, species composition and vertical distribution of foliage are the better ones at small scale. The results of this study confirm this statement when canopy openness is related to factors such as tree architecture and leaf distribution. In contrast to the study of Montgomery & Chazdon (2001), fluctuation of light transmittance does not immediately accord to structural patterns or species composition. Instead, canopy openness and its dynamics were isolated as critical factors for PPFD fluctuations at a small scale.

In general, canopy openness is a more sensitive parameter in expressing the spatio-temporal heterogeneity of small scale forest structure (Trichon *et al.* 1998). The dynamics of this variable can be used as tool for understanding related parameters like understorey light availability.

A constitutive approach on that subject might be the implementation of plant functional traits, because an emphasis on functional relationships between variables (e.g. canopy structure dynamics and light regime) feeds rapidly into the identification of general patterns and, hence, the possibility of prediction (McGill *et al.* 2006).

Methodological review and summary

In this study, repeated series of PPFD measurements were used. This method is a trade-off between permanent and short-term monitoring and one-time measurements. Due to practicability and economic feasibility, long-term studies are limited in sampling area (e.g. Dou *et al.* 2005; Raich 1989; Rich *et al.* 1993). In contrast, short-term or one-time measurements might cover a larger area, but would lack explanatory power about temporal dynamics (e.g. Ferreira de Lima & Cunha de Moura 2006; Montgomery & Chazdon 2001; Pearcy 1983).

Any computing of radiation data out of hemispherical photographs (e.g. Chazdon & Field 1987) was omitted, because such data is susceptible to errors in such grid based approach in a tropical understorey (Becker & Smith 1990). The 10 m sample grid used in this study is an acceptable compromise in order to investigate the structural and spatial variability of certain areas with a manageable number of measurements as affirmed by Chen *et al.* (1991). Thus, a combination of hemispherical photography and quantum sensor measurements are recommended for such assessments.

Other works proposed LAI values higher than recorded in this study for similar vegetation units (Scurlock *et al.* 2001). Hemispherical photography tends to underestimate LAI (Moser *et al.* 2007).

Another possible reason for this phenomenon is that the hemispherical photographs of this study were taken at a height of 1.3 m, discarding vegetation under this level, which can easily reach a LAI of 1 (Cournac *et al.* 2002; Trichon *et al.* 1998). In general, LAI estimation based on hemispherical photographs are problematic when describing realistic leaf area conditions (e.g. for biomass calculations), but nonetheless it is a standardized method to rapidly obtain data to compare canopy conditions of different sites.

Doubtless the sampling area for describing the species composition is too small to provide a complete picture of the woody plant community. But, with regard to an impression of diversity, heterogeneity and the evaluation of these parameters in the plots, this small scale approach is quite suitable.

In summary, small scale structure is subject to high spatiotemporal variability in general. In this context inter-annual PPFD fluctuations in the understorey of the Atlantic rainforest were substantiated and canopy openness seems to be a linking factor of such dynamics. It is not definitely resolved whether canopy openness dynamics are mainly related to certain species composition, or those dynamics are principally linked to stand structure aspects.

This study confirms hemispherical photography and quantum sensor based PPFD measurement as a valid tool for rapid assessment approaches regarding canopy structure and their spatiotemporal heterogeneity and the effect on understorey PPFD fluctuations. The results of this work and the prospective implementation of plant functional traits will help to understand the influence of canopy structure on the community dynamics. Especially, the variability and heterogeneity of canopy structure may help to explain the impact on stand dynamics and the reduced importance of classic gaps in communities identified for some rainforests (Hubbell *et al.* 1999; Lieberman *et al.* 1995; Midgley *et al.* 1995).

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