Original Article

CANOPY STRATIFICATION IN TROPICAL SEASONAL FORESTS: HOW THE FUNCTIONAL TRAITS OF COMMUNITY CHANGE AMONG THE LAYERS

ESTRATIFICAÇÃO DE DOSSEL EM FLORESTAS ESTACIONAIS TROPICAIS: COMO OS TRAÇOS FUNCIONAIS DA COMUNIDADE MUDAM AO LONGO DOS ESTRATOS VERTICAIS

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ABSTRACT. The discussion of the existence and measurement of layers in forests refers to one of the earliest and most controversial concepts of forest ecology, the stratification. Since there is no consensus on the most appropriate methodology to describe the vertical structure of forest communities, we chose for this paper to develop a methodology that was adequate to represent the stratification observed on site. The objective was to determine the species and functional traits characteristic of each vertical layer in the semideciduous seasonal forests (SSF). The study was conducted in ten fragments (10 ha) located in southeastern Brazil. Stratification was performed according to species using the median and the 3rd quartile (non-parametric statistical analysis) of tree heights were used for canopy stratification the (understory, midstory and canopy). This result shows the small range of the midstorey layer, highlighting the dichotomy between the canopy and understory. The variations found for the quartile and median values represent the history of successional stage of each fragment, allowing variations in the vertical occupation by species of certain layers. The analysis of SSF vertical structure allowed a visualization of the division of species and their respective functional traits performing different ecosystem functions in each layers.

KEYWORDS: Ecosystem functions. Forest ecology. Functional groups. Semideciduous seasonal forests. Successional stage.

INTRODUCTION

The discussion of the existence and measurement of layers in forests refers to one of the oldest and most controversial concepts of forest ecology, called canopy stratification (WHITMORE, 1975; RICHARDS, 1996). This discussion occurs firstly due to the variety of ways in which the canopy structure can be conceived, measured, and described, and also due to the multitude of parameters used to describe the canopy and the various levels of integration that can be used as the basis for such descriptions.

Studies of vertical structure began with the elaboration of profile diagrams, aiming to clarify controversies about the canopy stratification in tropical rainforest (DAVIS; RICHARDS, 1933). The method developed by these authors was subsequently used by Richards (1939), Whitmore (1975), and others. However, this method has some problems because it represents only part of the studied community (VALE et al. 2009). Over time, studies about canopy stratification have used different methodologies according to the different questions and focuses of these studies. Based on the mean height of the canopy for each species, Pagano and Leitão Filho (1987) established the existence of two layers in tropical forests. The identification of layers was also performed by preparing frequency histograms of height classes (MARTINS, 1993). However, formulas that take into account the mean height and standard deviation for the identification of layers have also been used (PAULA et al. 2004), as well as multivariate analysis techniques (DCA) like the one used by Guilherme et al. (2004). Nowadays, a new methodology based on profile diagrams and individual tree crown was proposed to the identification of canopy stratification in tropical and temperate forests (BAKER; WILSON, 2000).

Thus, the vertical distribution is not always evident in tropical forests and recognition of the layers in a woody community is, sometimes, imperceptible and/or proceeds from subjective judgments (LATHAM et al. 1998). However, layers have been sampled (ASHTON; HALL, 1992) and normally, for descriptive purposes in tropical forests, one should consider the existence of two or three layers (RICHARDS, 1996; BAKER; WILSON, 2000).

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Few studies have used the same standard procedure for describing and analyzing forest stratification. In part this is due to the different questions and focuses of these studies, but also due the difficulty of standardizing the definition. The term "stratification" has been used to characterize forest in distinct ways, vertical stratification of phytomass, vertical stratification of individual crowns, and vertical stratification of species (BAKER; WILSON, 2000). Furthermore, local characteristics and disturbance history which each studied fragment presents, as well as the successional stage in which the forest is classified (CHAZDON et al. 2010), are also factors that contribute for the difficulty of standardization of methodology.

Studies about the vertical structure in forests, which so far has been less investigated, should be as important as those related to the horizontal structure, and such studies would allow higher correlations between vegetation and functional traits (CHAZDON et al. 2010), especially those related to successional, dispersion, and leaf deciduousness groups, which may be the result of ecological mechanisms (VALE et al. 2009).

This paper aims to identify patterns in the structure of Semideciduous Seasonal Forests (SSF) through a study of vertical stratification of tree components in ten fragments. The aim of this study was to determine the species and the functional traits (successional groups, dispersal mechanism and leaf deciduousness) from each layer found in SSF, attempting to answer the following questions: 1) Is the vertical structure homogeneous among the fragments? 2) How the functional traits are distributed in each vertical layer? 3) Is there a pattern of distribution of functional traits in the layers among the studied SSF? 4) Is it possible, based on the canopy stratification and functional traits, to better sort the forest fragments according to their stage of conservation?

MATERIAL AND METHODS

Database and geographic and climatic factors

This study departed from previous phytosociological tree community studies (DBH ≥ 5 cm) in ten sites of SSF in southeastern Brazil, totaling a sample of 10 ha (Lopes et al., 2012a). The height measurements were taken with the help of a meter stick. Since this paper aimed to study the tree community, with DBH ≥ 5 cm standardized for Seasonal Semidecidual Forests (FELFILI et al. 2011), herbaceous and shrubby species that occured in the understory "*lato sensu*" were not samped. Thus, tested hypotheses are just applicable to the tree community in the understory. More details on the sampling methodology description of the ten sites can be found in Lopes (2012a).

Seasonal semideciduous forest occurs in a climate characterized by the seasonality, with annual rainfall lower than 1,600 mm and with regular drought in five to six months of each year, when the monthly total rainfall is less than 10 mm (GENTRY, 1995). The seasonal climate intensity is related to local variations, such as characteristics of the relief, water retention and soil depth, which determine the trees' level of deciduousness during the dry season (OLIVEIRA-FILHO; RATTER, 2002). The dominant species lose their leaves during the dry period as an adaptation to water stress. The average height of the tree layer ranged among 15 and 35 m. The majority of the trees is upright, with some individuals emerging (LOPES et al. 2012a; LOPES et al. 2012b).

The tropical savanna climate (megathermal Aw) prevails in the region, which is characterized, according to the adaptation of Köeppen-Geiger classification (PEEL et al. 2007) as having dry winters and rainy summers. The average temperature and rainfall are 18ºC and 12.1 mm, respectively. During the rainy season (October to February), the temperature ranges among 20.9ºC and 23.1ºC, and the average rainfall is 228 mm. Half of the annual rainfall (1500 to 1600 mm) are concentrated in the months of December and February. The dry season normally lasts to April and September, and presents a notable decrease in rainfall (average of 35.5 mm per month) (PRADO JÚNIOR et al. 2010).

Vertical structure

We assume the evident existence of a canopy (higher layer) and, consequently, an understory (lower layer). The midstorey layer would be formed by a set of species that are part of a continuum among the shaded understory and the canopy layer (BAKER; WILSON, 2000). Since there is no consensus on the most appropriate methodology to describe the vertical structure of forest communities, we try a characterization of the strata able to differentiate clearly, at least, the forest canopy and the understory. In this way, this classification does not focus on the midstorey layer, due the difficult to evaluate it using a simple method. This analysis of the vertical structure has segmented forest communities in two main layers and the continuum of midstorey. We used only those species that had a minimum of 10 individuals, excluding from the analysis the species with low density.

As the distribution of frequency in heights classes of individual trees usually has a negative exponential pattern (not normal data), the use of the mean heights for layers determination is not allowed. Thus, we used the median and the 3rd quartile (non-parametric statistical analysis) of tree heights for canopy stratification. Moreover, the use of the maximum height to determine the vertical layers alone cannot express the strategy of a species to capture light, because it does not distinguish contrasting strategies between early and late successional stages (FALSTER; WESTOBY, 2005).

The present classification began with obtaining 3rd quartile of the individual heights of the community (Q3c), which delimits 25% of the tallest height values of the community. Later, 3rd quartile of each species heights was obtained (Q3e) to determine species position in the vertical layers. Thus, 3rd quartile was used based on the premise that the tallest 25% of individuals of a species (and not just the maximum height of species) may represent its real position in the vertical structure. It is expected that the tallest individuals of the species represent its reproductive phase (GOURLET-FLEURY et al. 2005) and, consequently, perform processes such as pollination and dispersal, that are important interactions in the ecosystem.

With the values obtained from the 3rd quartile calculated for the community and for selected species, we classified the layers according to the following criteria and limits:

Canopy layer: $Q3e \geq Q3c$;
Understory layer: $Q3e \leq Mc$;
Midstorey layer: $Mc < Q3e < Q3c$;

where: Q3e = 3rd quartile of the heights of the sampled individuals of the species; Mc = median of the heights of the sampled individuals of the community; Q3c = 3rd quartile of the heights of the sampled individuals of the community.

The canopy is formed by the tallest species of the tree community. This means that at least 25% of individuals of a canopy species are higher than 75% of the individuals of the community (Figure 1). Understory species are classified as shade tolerant and have processes of reproduction and growth in shade conditions. This criterion of species separation by different growth strategies in light or shade was described by Hubbell and Foster (1986) and Whitmore (1989). To classify species as understory, 3rd quartile of the heights of its individuals should be less than or equal to the median of the heights of individuals of the entire community. This means that at least 75% of individuals of an understory species are lower than 50% of individuals of the community. Thus, the understory was formed by the lowest species of the tree community included in the sample. The midstorey layer was formed by the species that were not classified as canopy or understory, as described by the classification criteria above, and included all species which 3rd quartile of the individual's height was between the values of median and 3rd quartile calculated for the whole tree community (Figure 1).

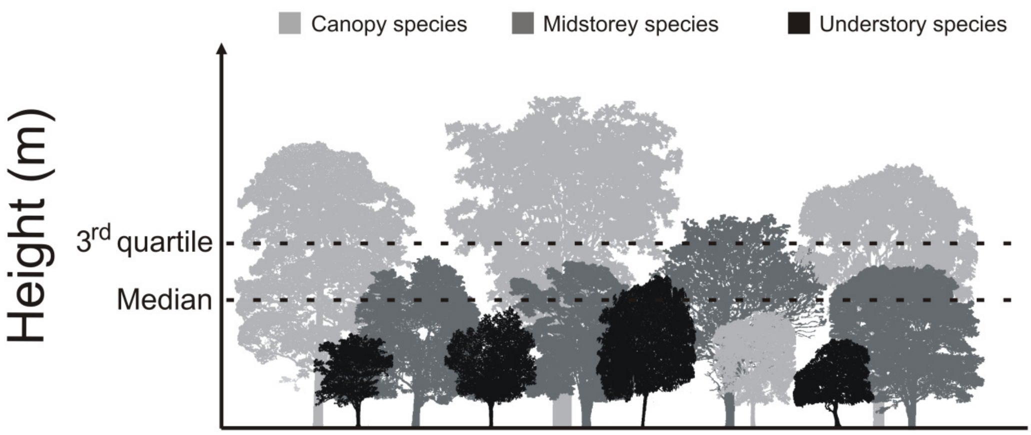

Figure 1. Methodology schematic figure of canopy stratification for SSF in southeastern Brazil. The horizontal lines represent the theoretical bands calculated for each layer, according to the methodology applied.

Functional traits

We also classified the species of each layer with regard to the successional groups, dispersal mechanism, and foliar deciduousness. The classification in successional groups was based on work performed by Gandolfi et al. (1995) and Oliveira-Filho and Scolforo (2008), as well as observations on the occurrence of the species in the field. This classification is subjective in many aspects, however, proves to be very useful for forests works. We separated the species into three successional categories according to the nomenclature established by Gandolfi et al. (1995): pioneer (P), early secondary (ES), and late secondary (LS).

For the dispersal mechanism, we adopted the morphological criteria of fruits defined by van der Pijl (1982) and used in the majority of forest studies (HOWE; SMALLWOOD, 1982, CLARK; POULSEN, 2001; TONIATO; OLIVEIRA-FILHO, 2004). The species were classified as zoochoric (dispersed by animals), anemochoric (dispersed by wind), or autochoric (dispersed by gravity). Regarding leaf deciduousness, we classified the species as evergreen or deciduous based on literature records (CARVALHO, 2006; OLIVEIRA-FILHO; SCOLFORO, 2008; PRADO JÚNIOR et al. 2012; VALE et al. 2013) and the *Royal Botany Garden* database (www.kew.org). To compare all strata into the functional traits, we performed a paried-t test because the separations in layers are interdependent.

Multivariate analysis

We used data sorting by Principal Component Analysis (PCA) processed by PC-Ord for Windows (version 4.0 software, MjM Software Design, Gleneden Beach, Oregon, USA) to investigate the relationships among the functional traits (successional groups, dispersal mechanism, leaf deciduousness) of each layer (canopy, midstorey, and understory) in ten fragments analyzed by species. The PCA forms patterns from the data matrix of quantitative functional traits related to the sampled fragments.

RESULTS

The 3rd quartile (canopy lower limit) and the median (understory upper limit) found for each fragment varied considerable among the fragments, with different heights and bands widths to all the tree strata (Figure 2). The understory upper limit heights ranged from 6 to 13 meters, but most of the areas (80%) had understory below 10 meters. The canopy lower limit varied from 8 to 17 meters, but most of the areas (70%) had canopy higher than 12 meters (Figure 2). Despite the continued distribution of heights in the fragments, this results show that the band width is small in midstorey layer, highlighting the dichotomy between understory and canopy species, where are present emergent trees (tallest individuals of the canopy layer) (Figure 3). The midstorey ranged from 8 to 17 meters.

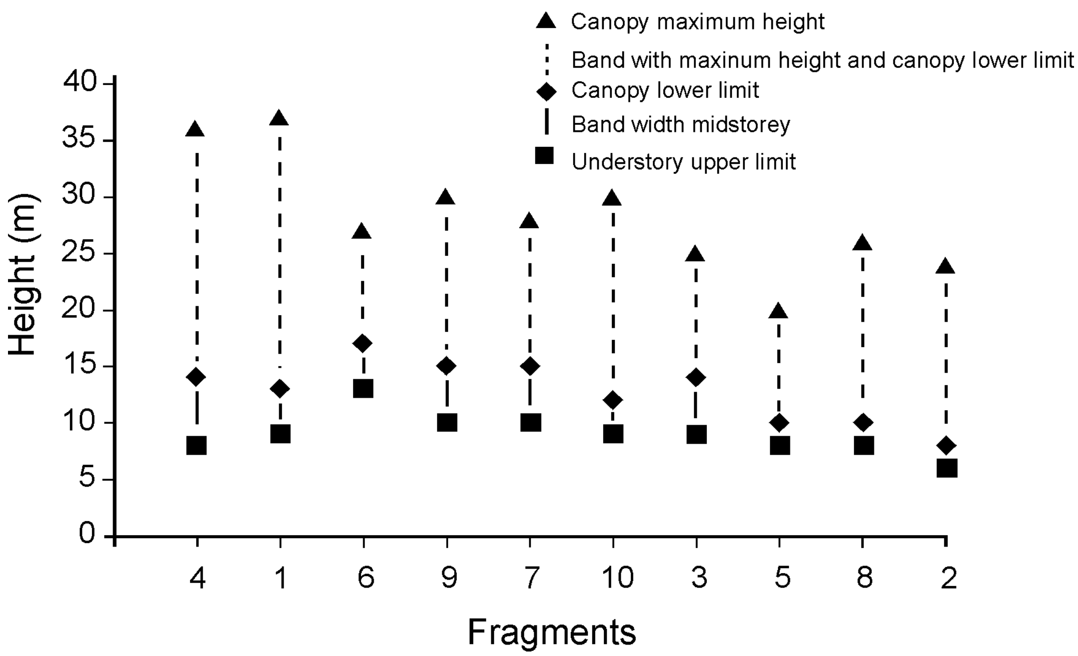

Figure 2. Variation of the quartile and median values for each fragment of sampled SSF.

The distribution of functional traits in the layers in studied SSF showed a pattern formed by species that are early secondary, zoochoric, and evergreen (Figure 4). However, the canopy has the highest percentage of late secondary, pioneer, anemochoric, autochoric, and deciduous species, comparing to other layers. The understory, on the other hand, is composed mainly by shade-tolerant, zoochoric, and evergreen species (Figure 4). Same pattern were found for number of individuals, but for canopy, the percentage of late secondary was high and for dispersion syndrome, the percentage of zoochory was higher in midstorey and understory, compared to the percentage of number of species.

The first two axes of principal component analysis (PCA) have explained 71.44% of the variance of ecological characters among fragments, indicating the formation of an outstanding dichotomy, the canopy (on the right side of figure) and the group formed by species under the canopy (midstorey and understory on the left side) (Figure 5). The axis 1 represents the variation of the characters related to dispersal mechanism and leaf deciduousness, while axis 2 shows the relationship among the successional characters. The canopy is formed mostly by deciduous and anemochoric species (*Astronium nelson-rosae*, *Myracrodruon urundeuva*, and *Anadenanthera colubrina*) and autochorous species (*Micrandra elata*). However, with smaller representation, evergreen species were also found in the canopy (*Psidium sartorianum*, *Ocotea corymbosa*, *Tapirira obtusa*, and *Virola sebifera*).

The comparisons of percentage distributions of species and individuals (Figure 4) and t test (Table 1) among strata for each functional trait proportion confirm a distinct distribution of traits along forest. Specifically for canopy and understory, the first one was higher for pioneers individuals, late secondary species and individuals, anemochoric, autochoric and deciduous species and individuals (Figure 4). Otherwise, understory had more proportion of early secondary, zoochoric and evergreen species and individuals. (Figure 4).

However, in relation to successional groups there was variation in the canopy according to the stage of successional development that the studied fragments are classified in Fragments 2 and 8 were less similar to the others due to a high density in the canopy of early and pioneer secondary species, such as *Enterolobium contortisiliquum*, *Lithraea molleoides*, *Piptadenia gonoacantha*, *Luehea grandiflora*, and *Guazuma ulmifolia.* Fragment 2, although lying in the countryside has a recent history of disturbance as a result of selective logging and the change of surrounding matrix to agricultural areas. Probably this fact was crucial to allow pioneer and deciduous species, such as *Piptadenia gonoacantha* and *Luehea grandiflora,* to achieve high density in this fragment. Fragments 6, 7, and 10 showed the late secondary species in the canopy (*Copaifera langsdorffii*, *Hymenaea courbaril*, *Ocotea corymbosa*) (Figure 5).

Table 1. Results of t paried test between the three layers comparing the traits evaluated in this work, for 10 SSF. The significative difference ($p < 0.05$) are in bold.

	Species			Individuals		
	Und x Can	Und x Mid	Can x Mid	Und x Can	Und x Mid	Can x Mid
	p	p	p	p	p	p
Pioneers	Ns	Ns	Ns	**0.035**	**0.011**	Ns
Early secondary	**0.029**	Ns	Ns	**0.012**	Ns	Ns
Late secondary	**0.046**	Ns	Ns	Ns	Ns	Ns
Zoochoric	**0.001**	Ns	**0.001**	**0.001**	Ns	**0.001**
Anemochoric	**0.001**	Ns	**0.001**	**0.001**	**0.045**	**0.007**
Autochoric	**0.050**	Ns	0.427	**0.029**	Ns	Ns
Deciduous	**0.001**	Ns	**0.004**	**0.001**	Ns	**0.032**
Evergreen	**0.001**	Ns	**0.004**	**0.001**	Ns	**0.032**

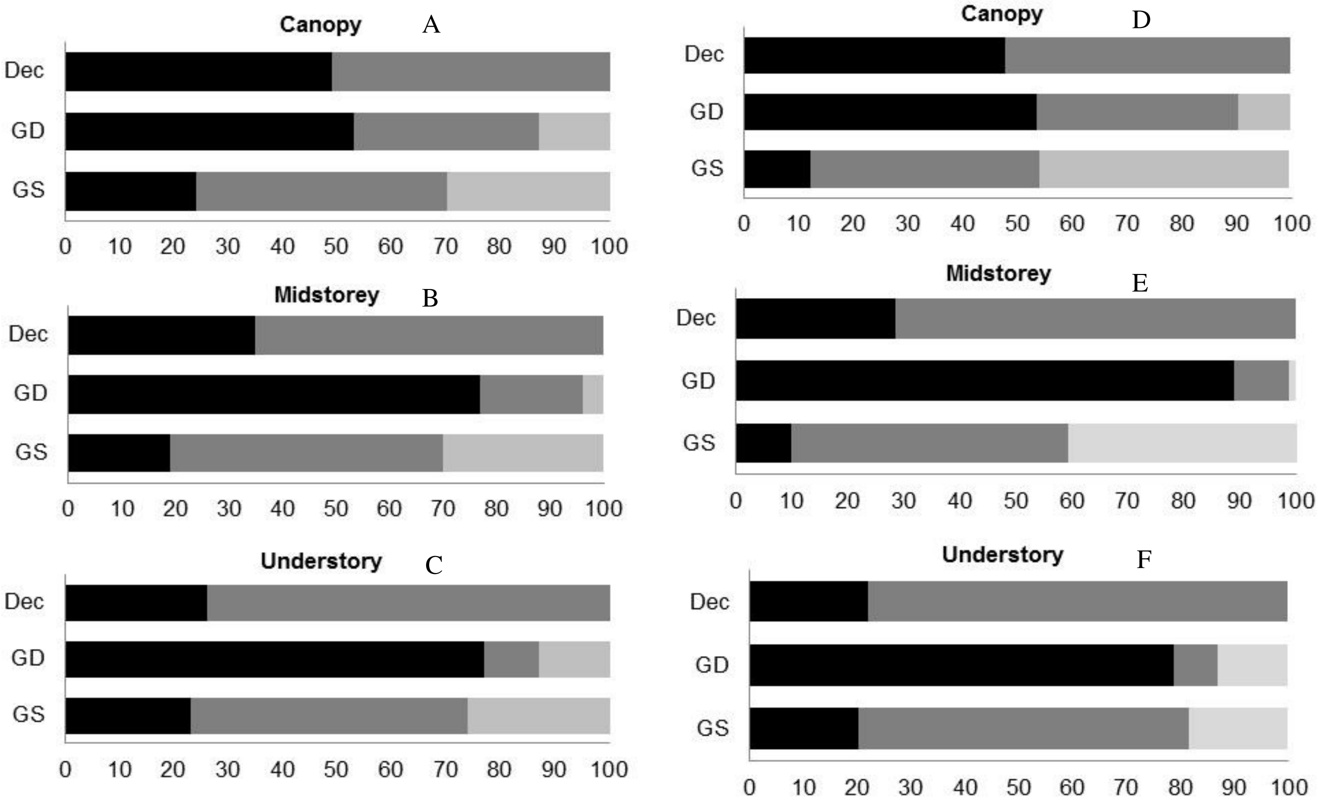

Figure 4. Percentage distribution of number of species (A, B and C) and individuals (D, E and F) of functional traits for each layer of SSF. Dec is the deciduousness, where black is deciduous and dark gray is evergreen. GD is the dispersal syndrome, where black is zoochoryc, dark gray is anemochoryc and gray autochoryc species. GS is the successional groups, where black is pioneer, dark gray is early secondary and gray late secondary species.

The understory is made up of zoochoric, late secondary and perennial species (Figure 5), such as *Cordiera sessilis*, *Myrciaria glanduliflora*, and *Galipea jasminiflora.* The midstorey layer is characterized by the dependence of the successional stage that the fragment is classified (Figure 5). In some areas in advanced stages of conservation, the midstorey layer is formed by late secondary, zoochorous, and perennial species (*Siphoneugena densiflora*, *Ixora brevifolia*, *Duguetia lanceolata*). Fragments 2, 3, 5, and 6 (Figure 5) showed pioneer, early secondary, and deciduous species (*Tabebuia roseoalba, Machaerium brasiliense*).

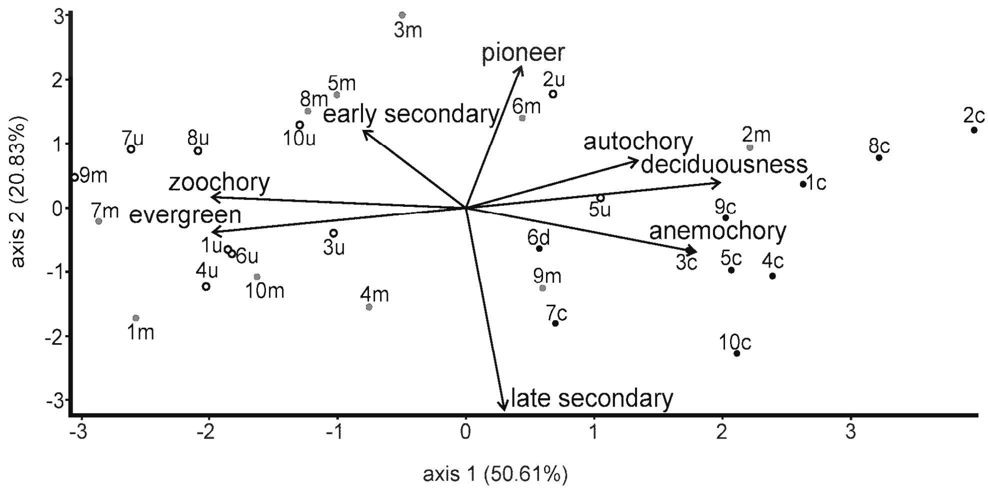

Figure 5. Analysis of main components (PCA), showing the ecological characters per layer that was most representatives for the separation of the sampled fragments of SSF. c = canopy, m = midstorey, u = understory. The numbers represent the fragments (see LOPES et al., 2012a).

DISCUSSION

The methodology applied here for the canopy stratification was effective for the separation of species and functional traits in the two main strata (canopy and understory) in Seasonal Semideciduous Forests. Despite the continuum that exists in the distribution of the height of individual trees in forest fragments, each canopy layer has characteristic species, with specific functional traits. Each particular layer represents a group of species capable to occupy the space, as a result of adaptive responses to different light conditions (GUILHERME et al. 2004).

The layers analyzed after the analysis of the stratification showed distinctions among fragments (Question 1 of introduction). Actually, some fragments had quite differences regarding the stratification, which seems to be a response to perturbations. Many other studies, have evidenced the stage of good conservation of the fragments 1 and 4, and the stage of low conservation of the fragments 5, 8 and 2. Thus, while more conserved fragments had a clear canopy and an understory well shaded (which is visual in the forest), in more disturbed fragments the understory is unclear and it is difficult to detect three layers due the low difference in height among canopy, midstorey and understory. In effect, many other studies have shown that rain and seasonal forests had, at least, two layers commonly classified as canopy and understory (BAKER; WILSON, 2000). Then we consider that the fragments of this study had three layers for comparisons. In this way, the higher and lower height of canopy represent a portion of the history of successional development of each fragment and create variations in vertical occupation by species characteristic of certain layers. For example, some species characteristic of the canopy in most part of fragments may temporarily occupy the midstorey layer of a fragment due to the conditions of natural or man-made disturbances in the site.

The canopy had the highest percentage of late secondary, anemochoric and deciduous species, in relation to other layers. When compared to understory, the canopy had more autochoryc and pioneers species, fact that do not occur when comparing canopy and midstorey. Late secondary species are usually of large size and long longevity, so the predominance of these species indicates an advanced stage of ecological succession. The predominant species in the canopy have slower growth and increased investment in basal area (GANDOLFI et al. 1995), such as *Copaifera langsdorffii,* a large species whose adults predominate in the forest canopy (LOPES et al. 2012a).

The occurrence of more pioneers on canopy and midstorey (the layers above understory) shows the existence of long-lived pioneer species in seasonal forests. According to Gourlet-Fleury et al. (2005), there are two types of pioneer species: those with rapid life cycle, small size, and high replacement rate and those with a long life, long cycle, and low replacement rate, such as *Acacia polyphylla*, *Schefflera morototoni*, and *Virola sebifera*, sampled in the canopy of the studied SSF (1, 3, 6, 9, and 10 fragments).

Most species dispersed by wind under the canopy (HOWE; SMALLWOOD, 1982). The predominance of primary abiotic dispersal (anemo-autochoric) in this layer has already been checked in areas of SSF (YAMAMOTO et al. 2007). The seasonal climate favors wind dispersal, as there is a negative correlation between the percentage of species dispersed by wind in the canopy and precipitation (HOWE; SMALLWOOD, 1982). The frequent occurrence of this mechanism in the canopy occurs because dispersal mechanisms by wind or gravity depend on both, the morphology of the seeds and the height and/or position of the matrix tree (PIRES-O'BRIEN; O'BRIEN, 1995). Despite of no significant differences between canopy and midstorey, the differences between canopy and understory are very clear, with more autochoric species and individuals in the canopy. This result is justified by the efficiency of the mechanism of dispersal by wind or seed launch by the plant itself, as it increases with tree height, which is difficult in lower layers of the forest (NUNES et al. 2003). The efficiency of these dispersal mechanisms, compared to zoochory, may be greater in the upper layer, since the anemo-autochoric species can take a lot of seeds out of the matrix crown (CLARK; POULSEN, 2001), and this should be maximized by the height reached by the individuals of these species. Furthermore, anemo-autochoric species are more numerous among the late secondary species, demanding direct light, and less numerous among shade-tolerant species (NUNES et al. 2003). There was a higher percentage of autochoric species, such as *Micrandra elata* (fragment 4) and *Maprounea guianensis* (fragment 7), in the canopy. The frequency of individual with autochoric dispersal may be related to the degree of conservation of the vegetation, as pointed out by Toniato and Oliveira-Filho (2004). Most conserved areas tend to present higher densities of autochoric species (LOPES et al.

2012a). Deciduous canopy species (e.g. *Astronium nelson-rosae*, *Apuleia leiocarpa*, and *Diospyros hispida*) have long life cycles and can be considered as a group that has the highest biomass increment, since they produce, through photosynthesis, more biomass in a shorter period and can grow rapidly (GANDOLFI et al. 1995).

The midstorey layers, as well as the understory, had a higher percentage of early secondary and zoochoric species than the canopy. The midstorey layers in tropical forests are represented by species more susceptible to large variations in lighting conditions; that is, this layer represents a midstorey condition in the tree community, neither as bright as the canopy nor limited by light like the understory (TERBORGH, 1992). The midstorey layer represents a set of ecological conditions that allow transience in the succession of species over time; thus, in this layer, there are conditions arising from different historical natural and/or man-made disturbances in forest fragments, which cause a direct reflection in the alternation of ecological groups, mainly to pioneer and anemochoric species. Accordingly, each layer has a different floristic composition and, consequently, specific functional traits, as it advances the successional development of the forest (HOWE; SMALLWOOD, 1982).

The understory is dominated by species which individuals are located under the canopy of other trees and can be considered shade tolerant (e.g. *Cheiloclinium cognatum*, *Cordiera sessilis*, and *Siparuna guianensis*). The high density of species of understory in the vegetation under the canopy of other trees may be considered indicative of the mature of the stage of succession of the vegetation, because it shows a relatively closed canopy that is able to filter the direct light that reaches the majority of individuals in this layer.

The understory is composed mainly by shade-tolerant, zoochoric, and evergreen species. But early secondary, zoochoryic and evergreen (species and individuals) were high in proportion compared with the canopy. This layer deserves more attention due to its susceptibility to disturbance and fragmentation processes. Shade-tolerant and animal dispersed species are more sensitive to fragmentation than the claimants of direct light (METZGER, 2000) due, mainly, to the low dispersal ability and because they suffer more from the effects of lack of connectivity among fragments (METZGER, 2000). The efficiency of a disperser is related to its ability to cross among fragments regardless of the vegetation type in which this disperser transits. Thus, dispersers are important for maintaining biodiversity, as they distribute the seeds of a large number of species (CLARK; POULSEN, 2001). The mechanism of dispersal by animal, mainly of heavy fruit and seeds would predominate in the lower layers of the forest, where animal life is more intense and anemochoric and autochoric mechanisms would predominate in the upper layers of tropical forests (ROTH, 1987).

Morellato and Leitão (1992) found differences among the types of dispersal mechanism in each layer in fragments of seasonal semideciduous forest in southeastern Brazil. The diaspore type of dispersal differs among the vertical layers in tropical forest, providing several benefits and resource availability among the layers in the community. Different environmental conditions among forest layers, especially differences in humidity, lighting, and air movement, increase the differentiation among ecological niches (ROTH, 1987).

The species of the understory are generally small; they germinate, grow, reproduce, and die under shaded conditions, unless there is some local disturbance, however sunfleacks and gaps can favor light-demanding species to occupy this strata (WHITMORE, 1989), many of them were considered early successional, because they are small but light demanding. The gaps represent the main possibility of coexistence of different species in tropical forests (BARTON, 1984) and, consequently, a more dynamic relationship among the ecological groups. A forest is a mosaic of different stages of maturity, whose growth cycle begins with a clearing (WHITMORE, 1989).

The comparison of the functional traits among the sampled SSF fragments showed that there are differences in the distribution of groups according to the successional stage of the fragments. The best-preserved areas were grouped in relation to certain functional traits that may define the degree of maturity of the forest community. Although floristic composition have differentiated among ten areas (LOPES et al. 2012a), functional traits and species position in canopy stratification can be more efficient to define differences in sucessional stage among fragments.

The group formed by fragments 1, 4, and 8 have shown as a marked characteristic an understory composed by evergreen, zoochoric, and late secondary species. An area with the presence of late secondary species is indicative of an advanced sucessional stage. The advanced sucessional stage is followed by an increase of late species density and decreasing amount of pioneer species (NUNES et al. 2003). Late secondary species are characterized by longevity, and may be present in either the canopy, represented by individuals of great size, or the understory, represented by individuals with small size, or may be present in both.

Late secondary species typical of the understory have their full development life cycle in shaded conditions. Most preserved areas have a higher density of shade-tolerant species (TONIATO; OLIVEIRA-FILHO, 2004) and late secondary species, which are found in closed understory. An understory with those characteristics, combined with a low density of pioneer species, suggests that natural disturbances occurring in vegetation, such as clearings, are not sufficient to cause great variations in tree community structure. Martins (2004) found a higher density and richness of late secondary species in small clearings formed by natural tree fall. Classical studies consider that pioneer species are more abundant in large clearings (MARTINS, 2004), that was not recorded in the fragments studied.

Moreover, the predominance of pioneer and deciduous species in the understory showed that the fragments are still experiencing constant dynamics in successional development, which may be caused by the fall of one or several trees due to factors including strong winds, thunderstorms, and lightning (WHITMORE, 1989) or by the human action. These actions determine the formation of clearings, and thus the establishment of pioneer species, as fragment 2.

Analysis of the structure of the SSF allowed clear visualization of the species and their ecological groups division exercising their functions in each of the layers. The difference in niches occupation in different layers is one of the crucial factors that explain the high diversity in tropical forests (TERBORGH, 1992). The identified layers are as expected in a tropical forest structure (ROTH, 1987; MORELLATO; LEITÃO FILHO, 1992). Understory consists of early and late secondary, zoochorous, and evergreen species typical of shade conditions, such as *Cordiera sessilis*, *Cheiloclinium cognatum*, and *Siparuna guianensis,* while canopy is formed mostly by large and zoochorous late secondary species such as *Hymenaea courbaril*, *Tapirira obtuse*, and *Copaifera langsdorffii* and wind dispersed and deciduous species, such as *Astronium nelson-rosae* and *Apuleia leiocarpa.* The midstorey layer is formed by environmental groups that differ according to the successional stage of development of each fragment; that is the presence of a higher or lower density of deciduous pioneer species depends on the disturbance history in each fragment.

This analysis of the community structure through canopy stratification enabled identification of ecosystem structural components, since it determines functional traits related to each layer. Different environmental conditions among forest layers increase the differentiation among ecological niches and increase biodiversity.

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RESUMO: A discussão sobre a existência e medição de camadas em florestas refere-se a um dos conceitos mais antigos e mais controversos em ecologia florestal: a estratificação. Como não há consenso sobre a metodologia mais adequada para descrever a estrutura vertical das comunidades florestais, optamos neste trabalho por desenvolver uma metodologia que se mostrou adequada para representar a estratificação observada no local. O objetivo foi determinar as espécies características e traços funcionais de cada camada vertical em florestas estacionais semideciduais (FES). O estudo foi realizado em 10 fragmentos (10 ha) localizadas no sudeste do Brasil. A estratificação foi realizada por espécie, utilizando a mediana e o terceiro quartil (análise estatística não-paramétrica) da altura das árvores, classificando-as em três categorias: dossel, sub-bosque e estrato intermediário. Os resultados mostram a pequena faixa do estrato intermediário, destacando a dicotomia entre o dossel e sub-bosque. As variações encontradas para os valores de quartis e mediana indicaram o estádio sucessional de cada fragmento, permitindo variações na ocupação vertical das espécies em determinadas camadas. A análise da estrutura vertical SSF permitiu uma visualização da divisão das espécies e das suas respectivas características funcionais, mostrando que cada estrato desempenha funções ecossistêmicas diferentes.

PALAVRAS CHAVE: Funções ecossistêmicas. Florestas estacionais semideciduais. Estádio sucessional. Grupos funcionais. Ecologia florestal.

REFERENCES

ASHTON, P. S.; HALL, P. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. **The Journal of Ecology,** London, v. 80, p. 459-481, 1992.

BAKER, P. J.; WILSON, J. S. A quantitative technique for the identification of canopy stratification in tropical and temperate forests. **Forest Ecology and Management,** ELSEVIER, v. 127, p. 77-86, 2000.

BARTON, A. M. Neotropical Pioneer and shade-tolerant tree species: do they partition tree fall gaps? **Tropical Ecology**, London, v. 25, p. 196-202, 1984.

CARVALHO, P. E. R. Espécies arbóreas brasileiras. Brasília, DF: Embrapa Informação Tecnológica; Colombo, PR: Embrapa Florestas, v. 2, 627, (Coleção Espécies Arbóreas Brasileiras), 2006.

CHAZDON, R. L.; FINEGAN, B.; CAPERS, R. S.; SALGADO-NEGRET, B.; CASANOVES, F.; BOUKILI, V.; NORDEN, N. Composition and dynamics of functional groups of trees during Tropical Forest succession in Northeastern Costa Rica. **Biotropica,** Lawrence, v. 42, p. 31-40, 2010.

CLARK, C. J.; POULSEN, J. R. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. **Biotropica**, Lawrence, v. 33, p. 606-620, 2001.

DAVIS, T. A. W.; RICHARDS, P. W. Britsh Guiana: An ecological study of a limited area on tropical rain forest, part I. **The Journal of Ecology**, London, v. 22, p. 106-155, 1933.

FALSTER, D. S.; WESTOBY, M. Alternative height strategies among 45 dicot rainforest species from tropical Queensland, Australia. **The Journal of Ecology,** London, v. 93, p. 521-535, 2005.

FELFILI, J. M.; EISENLOHR, P. V.; MELO, M. M. R. F. Procedimentos e métodos de amostragem de vegetação. In: FELFILI, J. M. et al. (Org.). **Fitossociologia no Brasil: métodos e estudos de casos**. Viçosa, MG: Universidade Federal de Viçosa, p. 86-121, 2011.

GANDOLFI, S.; LEITÃO-FILHO. F.; BEZERRA, C. L. F. Levantamento florístico e caráter sucessional das espécies arbustivo-arbóreas de uma floresta mesófila semidecídua no município de Guarulhos, SP. **Revista Brasileira de Biologia**, São Carlos, v. 55, p. 753-767, 1995.

GENTRY, A. H. Patterns of diversity and floristic composition. In Churchill SP et al. (Eds.) **Neotropical Montane Forest Biodiversity and Conservation**, The New York Botanical Garden, New York, pp 103-126, 1995.

GOURLET-FLEURY, S.; PICARD, N.; SIST, P.; DICK, J.; NASI, R.; SWAINE, M. D.; FORNI, E. Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. **Annual Forest Science,** New York, v. 62, p. 785-796, 2005.

GUILHERME, F. A. G.; MORELLATO, L. P. C.; ASSIS, M. A. Horizontal and vertical tree community structure of Atlantic rain forest in the Intervales State Park, southeastern Brazil. **Revista Brasileira de Botânica**, São Paulo, v. 27, p. 725-737, 2004.

HOWE, H. F.; SMALLWOOD, J. Ecology of seed dispersal. **Annual Review of Ecology and Systematics,** Palo Alto, v. 13, p. 201-228, 1982.

HUBBELL, S. P.; FOSTER, R. B. Canopy gaps and the dynamics of a neotropical forest. In Crawley MJ. (Eds.) **Plant Ecology,** Blackwell Scientific, Oxford, pp. 77-96 1986.

LATHAM, P. A.; ZUURING, H. R.; COBLE, D. W. A method for quantifying vertical forest structure. **Forest Ecology and Management,** ELSEVIER, v. 104, p. 157-170, 1998.

LOPES, S. F.; SCHIAVINI, I.; OLIVEIRA, A. P.; VALE, V. S. An ecological comparison of floristic composition in Seasonal Semideciduous Forest in southeast Brazil: implications for conservation. **International Journal of Forestry Research,** New York, v. 2012, p. 1-14, 2012a.

LOPES, S. F.; SCHIAVINI, I.; VALE, V. S.; PRADO JÚNIOR, J. A.; ARANTES, C. S. Historical review of studies in seasonal semideciduous forests in Brazil: a perspective for conservation. **Brazilian Geographical Journal: Geosciences and Humanities research medium**, Uberlandia, v. 2, p. 21-40, 2012b.

MARTINS, F. R. **Estrutura de uma floresta mesófila**. 2 ed. Editora da Unicamp, Campinas, 1993.

MARTINS, S. V. Colonization of gaps produced by death of bamboo clumps in a semideciduous mesophytic Forest in south-eastern, Brazil. **Plant Ecology, SPRINGER,** v. 172, p. 121-131, 2004.

METZGER, J. P. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. **Ecological Applications,** v. 10 p. 1147-1161, 2000.

MORELLATO, L. P. C.; LEITÃO-FILHO, H. Padrões de frutificação e dispersão de sementes na Serra do Japi. In Morellato LPC (Eds.). **História Natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil.** Editora da Universidade Estadual de Campinas, Campinas, pp. 112-140, 1992.

NUNES, Y. R. F.; MENDONÇA, A. V. R.; BOTEZELLI, L.; MACHADO, E. L. M.; OLIVEIRA-FILHO, A. T. Variação da fisionomia, diversidade e composição de guildas da comunidade arbórea em um fragmento de floresta semidecidual em Lavras, MG. **Acta Botanica Brasilica**, Feira de Santana, v. 17, p. 213-229, 2003.

OLIVEIRA-FILHO, A. T.; RATTER, J. A. Vegetation physiognomies and woody flora of the cerrado biome. In Oliveira, O.S.; Marquis, R.J. (Eds.) **The cerrados of Brazil**. Columbia University Press, New York, pp. 91-120 2002.

OLIVEIRA-FILHO, A. T.; SCOLFORO, J. R. S. **Inventário florestal de Minas Gerais: espécies arbóreas da flora nativa**. Lavras: Editora UFLA, 2008.

PAGANO, S. N.; LEITÃO-FILHO, H. F. Estudo fitossociológico em mata mesófila semidecídua no município de Rio Claro (Estado de São Paulo). **Revista Brasileira de Botânica**, São Paulo, v. 10, p. 49-61, 1987.

PAULA, A.; SILVA, A. F.; MARCO-JÚNIOR, P.; SANTOS, F. A. M.; SOUZA, A. L. Sucessão ecológica da vegetação arbórea em uma floresta estacional semidecidual, Viçosa, MG, Brasil. **Acta Botanica Brasilica**, Feira de Santana, v. 18, p. 407-423, 2004.

PEEL, M. C.; FINLAYSON, B. L.; MCMAHON, T. A. Updated world map of the Koppen-Geiger climate classification. Hydrology. Earth Systematics Science Discussion. v. 4, 439–473, 2007.

PIRES-O'BRIEN, M. J.; O'BRIEN, C. M. **Ecologia e modelamento de florestas tropicais.** Serviço de Documentação e Informação, Faculdade de Ciências Agrárias do Pará, Belém, 1995.

PRADO JÚNIOR, J. A.; VALE, V. S.; OLIVEIRA, A. P.; GUSSON, A. E.; DIAS NETO, O. C.; LOPES, S. F. SCHIAVII, I. Estrutura da Comunidade arbórea em um fragmento de Floresta Estacional Semidecidual localizada na Reserva Legal da Fazenda Irara, Uberlândia, MG. Bioscience Journal, Uberlândia, v. 26, n. 4, p. 638-647, 2010.

PRADO JÚNIOR, J. A.; LOPES, S. F.; VALE, V. S.; SCHIAVII, I. Comparação florística, estrutural e ecológica da vegetação arbórea das Fitofisionomias de um remanescente urbano de Cerrado. Bioscience Journal, Uberlândia, v. 28, n. 3, p. 456-471, 2012.

RICHARDS, P. W. Ecological studies on the rain Forest of southern Nigeria. The structure and floristic composition of the primary forest. **Journal Ecology**, London, v. 27, p. 1-61, 1939.

RICHARDS, P. W. **The Tropical Rain Forest**. Cambridge University Press, Cambridge, 1996.

ROTH, I. **Stratification of a tropical forest as seen in dispersal types**. Dr. W. Junk Publishers, Dordrecht, 1987.

TERBORGH, J. Diversity and the tropical rain forest. Scientific American Library, New York, 1992.

TONIATO, M. T. Z.; OLIVEIRA-FILHO, A. T. Variations in tree community composition and structure in a fragment of tropical semideciduous forest in southeastern Brazil related to different human disturbance histories. **Forest Ecology and Management**, ELSEVIER, v. 198, p. 319-339, 2004.

VALE, V. S.; SCHIAVINI, I.; LOPES. S. F.; DIAS NETO, O. C.; OLIVEIRA, A. P.; GUSSON, A. E. Composição florística e estrutura do componente arbóreo em um remanescente primário de floresta estacional semidecidual em Araguari, Minas Gerais, Brasil. **Hoehnea**, São Paulo, v. 36, p. 417-429, 2009.

VALE, V. S.; SCHIAVINI, I.; LOPES. S. F.; OLIVEIRA, A. P.; DIAS NETO, O. C.; GUSSON, A. E. Functional groups in a semideciduous seasonal forest in Southeastern Brazil. Biotemas, São Carlos, v. 26, n. 2, p. 45-58, 2013.

VAN DER PIJL, L. **Principles of dispersal in higher plants**. Springer-Verlag, Berlin, Heidelberg, 1982.

WHITMORE, T. C. **Tropical rain forest of the far east**. Claredon Press, Oxford, 1975.

WHITMORE, T. C. Canopy gaps and two major groups of forest tree species. **Ecology**, New York, v. 70, p. 536-538, 1989.

YAMAMOTO, L. F.; KINOSHITA, L. S.; MARTINS, F. R. Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. **Acta Botanica Brasilica**, Feira de Santana, v. 21, p. 553-574, 2007.