Environmental heterogeneity caused by anthropogenic disturbance drives forest structure and dynamics in Brazilian Atlantic Forest

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We evaluated how tree community floristic composition, forest structure and dynamics varied over a period of 13 years across a topographic gradient of ravines created by anthropic disturbance in Brazilian Atlantic Forest. The study area is located within a fragment of Atlantic Forest (21° 09' S, 44° 54' W), in Minas Gerais state, Brazil. This work was based on data of tree diameter at 1.3 m from the soil, collected in four inventories. Each individual was recorded as being in one of three stratified topographic classes: hilltop, slope and bottom. We used direct gradient analysis to evaluate floristic compositional changes, phytosociological analysis to evaluate structural variations, and assessed demographic and biomass changes over time through analysis of rates of forest dynamics. The results did not reflect modifications in the patterns of floristic composition and species diversity along the topographic gradient, while differences in forest structural attributes and dynamics may be detected at these smaller spatial scales. Thus, the same species group may employ different strategies against different restrictive environmental factors. Finally, we suggest that floristic composition and species diversity may be less sensitive parameters for post-disturbance responses than forest dynamics and structure.

Keywords: Environmental disturbances. Environmental heterogeneity. Forest dynamics. Species distribution. Spatial scale.

INTRODUCTION

Tree communities are strongly influenced by disturbance events which can modify both biotic and abiotic environmental conditions (Davis & Moritz 2013). Processes resulting from these events can in turn promote habitat heterogeneity at the landscape scale which may lead to dissimilarities in floristic composition and structure between nearby locations (Morellato & Haddad 2000).

Environmental gradients are in general related to the amount of available habitat, resource variability and structural complexity due to increasing availablilty of a broader range of niches and subsequent coexistence of a higher number of species (Begon et al. 2006). However, this mechanism has been questioned, as studies have reported non-significant relationship or negative effects of habitat heterogeneity on the diversity and abundance of species (Laanisto et al. 2013). These results have been attributed to ecological factors such as limitations in the availability ofenergy and dispersion, mass effects (Lundholm 2009) and stochastic extinctions (Kadmon & Allouche 2007).

In rough terrain regions, studies observing variations in tree species distribution and diversity and tree community characteristics along topographic gradients have highlighted their importance in tropical forest ecology (Souza et al. 2013). Topographic gradients are mainly related to changes in soil properties, water regimes and soil fertility (Rodrigues et al. 2007) and other attributes essential for ecological processes that may modify community characteristics (Meireles et al. 2008). For example, lowland areas commonly have more suitable conditions for the plant development, such as higher fertility, higher moisture and lower evapotranspiration demand compared with slope areas and elevated areas (Souza et al. 2017). The very specific role of each environmental variable, combined with the climatic and evolutionary context of the studied vegetation type, drives ecological complexity and subsequent tree community characteristics, promoting diversity within them (Munoz et al. 2014).

As a result of environmental heterogeneity, tree communities may present spatially distinct ecological patterns caused by associations between frequency of disturbances and the point of colonisation by different species, resulting in the occurrence of patches at different stages of restructuring (Begon et al. 2006). In this context, the study of forest dynamics through successive inventories allows detailed analysis of spatial patterns of mortality, recruitment and growth. The set of structural modifications of a single community in response to disturbance occurrences are known as silvigenesis (Hallé et al. 1978), which consists of five phases related to temporal patterns in tree density and biomass within a community: (1) stability; (2) degradation; (3) initial construction with degradation; (4) initial construction, and (5) late construction (Hallé et al. 1978). This process begins with the occurrence of a moderate to severe disturbance, which may cause a reduction in both density and basal area (degradation) and ends with the stability or mature phase, in which the number of individuals and overall biomass may fluctuate moderately under a regime of low-impact disturbances (Hallé et al. 1978). Generally, community changes that occur during silvigenesis are associated with ecological succession of species. As forests recover through the successive replacing of species adapted to the disturbed habitats by others as the community reestablishes its structural and floristic composition (Ricklefs 2010). Thus, studies dealing with temporal behaviour of tree communities enable the understanding of ecological processes and environmental characteristics that control community composition and structure (Corrêa & Van Den Berg 2002), the identification of life strategies used by vegetal populations (Schiavini et al. 2001) and knowledge of population modifications and community variations that may result from disturbances or successional processes (Durigan 2006). In this way, such studies contribute strongly to the improved description of environmental effects on tree communities, and discrimination of distinct stages of the forest successional mosaic (Souza et al. 2013).

Our aim was to evaluate, over a period of 13 years, whether tree community floristic composition, structure and dynamics vary according to the topographic gradient created through an anthropic disturbance event. To do this, we stratified the gradient into three topographic classes: hilltop, slope and bottom for comparison. We hypothesised that the floristic composition would not present differences between topographic classes due to the absence of physical barriers and proximity between the three environment types. In relation to forest structural characteristics and dynamics, we hypothesised that differences between topographic classes would be found due to variation in environmental (physical) factors, including the slope of the terrain and the availability of resources such as light, nutrients and water. Thus, in the hilltop and bottom classes we expected: the tree community to be in the late stage of the silvigenetic cycle due to gentler slopes and higher resource availability. In the slope we expected the tree community to be in the degradation stage due to the greater influence of steeper slopes, in addition to presenting greater variation over time in tree community structure during development towards the initial stability stage.

MATERIALS AND METHODS

Study area

The study area is situated in south-western Minas Gerais state, Brazil (21° 09' S, 44° 54' W). The studied fragment comprises nearly 59 ha of forest, the vegetation being considered as montane seasonal semi-deciduous forest (IBGE 2012) belonging to the Atlantic Domain *sensu latissimo* (Eisenlohr & Oliveira-Filho 2015).

In 18th century, mining has resulted in the removal of soil up to 10 m below the surface, creating a landscape of wide and continuous ravines that remain present today across the entire studied fragment (Appolinário et al. 2005). These ravines create a complex matrix and variety of slopes in which it is possible to observe small-scale environmental variations related to soil attributes and humidity. Vegetation is distributed across the range of different ravines, including extreme inclinations, having different visually exposed soil horizons and consequently distinct soil properties (Figure 1).

Vegetation inventories

In 2003, 15 permanent plots of 20 m × 20 m (0.6 ha, nearly 1% of the total area) were established systematically in five transects 100 m apart, with 50 m between each plot in each transect. The size of the plots was specifically chosen to allow topographic variation within them for classification. In each plot, all trees with diameter at breast height (DBH) ≥ 5 cm were identified, measured for circumference and labelled with numbered aluminum tags. Individuals constituting multiple stems were included when their quadratic mean circumference values (the square root of the quadratic sum of the circumference of each stem) were equal to or higher than 15.7 cm (Carvalho et al. 2007). Circumference measurements were converted to diameters for subsequent analysis. Three further inventory surveys were undertaken in 2005, 2007 and 2015 to monitor surviving individuals, count dead individuals and the record new individuals that achieved the minimum criteria for inclusion (recruits). Within each plot, the topographical position of each individual in the ravine was recorded in one of three subjective classes: hilltop slope and bottom, to represent the topographic gradient (Figure 1).

Data analysis

The differences in floristic composition within the topographical gradient (hilltop, slope and bottom) were verified by multivariate analysis of non-parametric multidimensional scaling, using Bray-Curtis dissimilarity as distance measure (Legendre & Legendre 1998). The presence of plot clusters obtained in non-parametric multidimensional scaling was evaluated through analysis of similarity Anosim (Anderson & Walsh 2013), using p and r values. These analyses were carried out using the PAST software package (Hammer et al. 2001).

In order to analyse the tree community patterns of species abundance and diversity in relation to the topographic gradient, two rarefaction curves were created: one for species abundance and another for the Shannon’s diversity index (H’) (Gotelli & Colwell 2011). The comparison was undertaken using the confidence interval achieved through 999 randomisations per measure. These analyses were made using the EstimateS software package (Colwell 2011). Pielou’s equitability index (J) was used to estimate tree community uniformity (Carvalho & Felfili 2011).

Tree community description in relation to topographic class was performed by phytosociological analysis for the four monitoring periods. The absolute and relative parameters of frequency, density and dominance were calculated and used to obtain the importance value (IV)

(Brower & Zar 1998). Tree abundance and basal area data of the topographic classes were obtained from the inventories of 2003, 2005, 2007 and 2015. Individuals from the Arecaceae family were excluded from calculations for measures of dynamics due to their lack of secondary growth, which may compromise the quality of results and lead to inappropriate ecological inferences. Rates of mortality (M), recruitment of individuals (R) and loss (L) and gain (G) in basal area were calculated according the exponential expressions: $M = \{1 - [(N_0 - N_m)/N_0]^{1/t}\} \times 100$; $R = \{1 - [1 - (N_r/N_t)]^{1/t}\} \times 100$; $L = \{1 - [(Ab_0 - (Ab_d + Ab_m))/Ab_0]^{1/t}\} \times 100$; $G = \{1 - [1 - (Ab_r + Ab_i/Ab_t)]^{1/t}\} \times 100$, where, N_0 corresponds to the number of individuals at the initial time, N_m is the number of dead individuals; t is the temporal period between monitoring; $N_r$is the number of recruited individuals; N_t is the number of individual at the final time; Ab_0 is the initial basal area; Ab_d is decrease in basal area of surviving individuals; Ab_m is the basal area of dead individuals; Ab_r is the basal area of recruited individuals; Ab_i is the increment in basal area of surviving individuals; and Ab_t is the final basal area of arboreal individuals (Sheil et al. 2000).

To account for variation in the length of intervals between inventories, mortality and recruitment rates of topographic classes were corrected according to Lewis et al. (2004). This procedure allows for comparison between intervals, and was achieved using the formula: $\lambda' = \lambda \times t^{0.08}$, where λ' is the rectified dynamic rates; λ is the verified dynamics rates and e; and t is the time interval.

Differences in dynamics between topographic classes were verified by statistical tests. Firstly, data normality within the three studied periods (2003–2005, 2005–2007 and 2007–2015) was tested using the Shapiro–Wilk test (Zar 2010). In order to compare each topographic class over time, tests of Friedman and ANOVA at 5% probability were applied (Zar 2010) for non-parametric and parametric data respectively. To verify differences between topographic classes within the same sampling interval, tests of Kruskall–Waills and ANOVA at 5% probability were used (Zar 2010) for non-parametric and parametric data, respectively.

RESULTS

The rankings produced by non-parametric multidimensional scaling (stress: 0.15) did not show floristic-structural partitioning between topographic classes in all four inventories (Figure 2). This was confirmed by the similarity analysis ANOSIM, that presented p coefficient > 0.05 and r value < 0.25, thus demonstrating no clear separation between groups. Species abundance was not shown to change over time, or between topographic classes (Figure 3a). The same behavior was observed for the Shannon's diversity index (H') (Figure 3b) and Pielou's equitability index (J) (Table 1).

Tree community structure changed significantly over time in relation to hierarchically important species within the different topographic classes using importance values (IV). The species *Protium spruceanum* and *Copaifera langsdorffii* were in 1st and 2nd place respectively, in topographic classes hilltop, slope and bottom. All other species in the top ten IV species in 2003 showed changes in their positions in all subsequent inventories and for all topographic classes. However, *P. spruceanum* was relatively more dominant in the bottom topographic class compared with the other classes. The presence of *C. langsdorffii* was more consistent in comparison, presenting homogeneous behaviour all areas (Table 2).

Low abundance species shift in hierarchical positions, in addition to both the egression and ingression of some species in the topographic classes. A total of 14 species were lost over time in the hilltop topographic class, 8 in the slope and 6 in the Bottom, with only 2 species in common between the three classes. Seven species were accrued over time in the hilltop topographic class, 9 in the slope class and 7 in the bottom class, with no species in common between all of them.

Measures of forest structural dynamics over the topographic gradient are shown in Table 3. In general, the results showed a reduction in the number of individuals and an increase in basal area, implying lower rates of recruitment compared with mortality, and lower basal area loss than rates of basal area gain.

However, the imbalance between rates was spatially heterogeneous. In the Bottom topographic class, this decrease in abundance and increase in basal area was shown for all the three sampling intervals, although the rates of basal area gain and loss were much more similar during the 2005–2007 interval (Table 3). In the hilltop topographic class, recruitment was observed to be higher than mortality during the first interval (2003–2005), as well as an overall increase in basal area, whereas for other intervals (2005–2007, 2007–2015), patterns of structural dynamics were similar to overall trends (Table 3). The slope topographic class did not show similar behaviour to the total sample during any interval. In the first and third intervals, a lower rate of basal area gain compared with loss was observed in conjunction with a lower recruitment rate of individuals in comparison with mortality. Moreover, during the second interval (2005–2007), both a higher recruitment compared with mortality rate and a higher basal area gain compared with loss rate was observed (Table 3).

DISCUSSION

The ordination analysis showed the majority of species to be distributed along the whole gradient. Only some rare species, with abundances varying between one and two individuals were not found across the whole gradient. Additionally, no significant difference was observed in species richness, Shannon´s diversity index (H’) or Pielou’s equitability index (J) between all analysed topographic classes. This result may be explained by the spatial proximity between the different topographic classes (Cruz et al. 2013), and subsequent similarity in general climatic conditions (temperature and rainfall) between them (Nettesheim et al. 2010). It is also necessary to consider that the short distances between topographical classes (hilltop, slope and bottom), combined with an absence of physical barriers, enable the dispersion of propagules between areas (Dalling et al. 2002). Such proximity supports the maintenance of an elevated number of shared species and therefore similar behaviour in floristic composition, diversity and species abundance (Cruz et al. 2013).

The differences in the tree community structure between topographic classes may be explained mainly by the distinct environmental characteristics along the topographic gradient, such as proximity to water and intensity of photosynthetically active radiation. Microclimatic conditions, specifically humidity, degree and extent of exposure to light, are capable of influencing the number of individuals (abundance) and vegetation structure (Small & McCarthy 2002). Thus, the prevalence of the species *Protium spruceanum* in the Bottom class environment type is probably explained by more humid conditions which may favour this species (Rodrigues & Araújo 1997), as its occurrence has been shown to be associated with moist areas of Atlantic Forests, Amazon Forests and riparian forests in the Cerrado biome (Rodrigues et al. 2003). Conversely, *Copaifera langsdorffii* presents similar values across all environment types, which may be explained by its generalist behaviour (Oliveira-Filho & Ratter 2000).

Small-scale environmental variations caused by topographic variations have been reported in numerous studies on vegetation behaviour, including some in the same studied region (Rodrigues et al. 2007, Robinson et al. 2015). In these cases, topographic variables are presented as a synthesis of important soil characteristics for establishment and growth, such as soil physical and chemical attributes that are directly associated with water availability and fertility. For example, throughout topographic profiles or slopes, significant soil variations can also be observed as a function of soil formation processes that imply physical-chemical differences along horizons and also differences in relation to water flow (proximity of the water table) and organic material accumulation (Wang et al. 2017). In addition, characteristics such as slope position provide differential light access (Baldeck et al. 2013), which is a key resource in seasonal forests because it is associated with crown temperature, a crucial factor in the selection of functional groups related to deciduousness and water use (Chou et al. 2018). In this way, each point in the topographic gradient offers different conditions and resources that will give rise to a spectrum of opportunities and restrictions that are recognised as influential in community properties (Putten et al. 2016).

The observed imbalance between rates of measures of dynamics has been shown to be characteristic of seasonal semideciduous forest fragments (Mews et al. 2011). As much as 75% of forest fragments in the southern region of Minas Gerais had both greater rates of mortality compared with recruitment, and basal area gain compared with loss (Garcia et al. 2015). This difference in dynamics has been associated with forest reconstruction during the silvigenetic cycle (Mews et al. 2011), resulting from the disturbance history of the fragment.

Despite the imbalances in dynamic processes for the arboreal community as a whole and topographic classes, there was a spatial heterogeneity of the dynamic processes. The bottom class showed behaviour similar to the whole sample, exhibiting known trends with basal area of individuals increasing mainly within higher diameter classes (Werneck & Franceschinelli 2004) and high mortality rates in lower diameter classes (Kellman et al. 1998). This pattern, known as late construction (Hallé et al. 1978), may result from a scenario of strong competition (Mews et al. 2011), where individuals belonging to lower diameter classes have small competitive capacity when compared with individuals of higher diameters that occupy superior strata (Felfili 1995). Variations in the patterns of mortality and recruitment rates and basal area loss and gain in the successive intervals were observed for the hilltop and slope topographic classes. The pattern observed in the hilltop class for the first sampling interval may be related to the regime of disturbances that a forest is susceptible to (Chazdon et al. 2007). Different perturbation types such as: extraordinary droughts, forest clearings, storms and anthropogenic interventions (Damasceno-Junior et al. 2004) might have caused such alterations in both tree community organisation and biomass (Hallé et al. 1978) by influencing initial stages of the succession process (Oliveira-Filho et al. 2007). Thus, the periods of late construction, 2005-2007 and 2007-2015, might be an indication of the advance of the succession process, allowing the considering of the forest dynamics as a regulating system of the equilibrium status (Felfili 1995). The slope class alternated between the silvigenetic stages of degradation (increase of mortality and loss of basal area) and initial construction. This degradation stage classification may be arising as a result of the deaths of large trees and treefall caused by steep slopes and shallow soils providing difficult conditions for individuals to sustain themselves (Oliveira-Filho et al. 2007). The loss of large individuals causes considerable immediate losses to the standing biomass (Oliveira-Filho et al. 2007), whilst also resulting in tree density reduction (Sheil et al. 2000). These disturbances trigger initial stages of succession commonly associated with the increase of both biomass and number of individuals that is characteristic of the initial construction stage of the silvigenetic cycle (Gomes et al. 2003, Oliveira-Filho et al. 2007, Carvalho & Felfili 2011).

CONCLUSIONS

This study compared tree community attributes and forest structural characteristics of Atlantic Forest over a topographical gradient on anthropogenically disturbed land. Results of this study confirmed that different topographic environments were very similar with respect to floristics, but differred in forest structure and dynamics. Thus, the present work reinforces previous observations that spatial scale is a limiting factor in the differentiation of floristic composition and other forest qualitative parameters. However, for quantitative parameters related to forest dynamics and structure, it is possible to observe significant differences even at reduced spatial scales. Moreover, we suggest that forest structure and dynamics are more sensitive to disturbance than floristic composition, since the same species group may employ different strategies when facing different environmental constraints.

Anthropogenic disturbances can provide a stronger modular force in influencing tree communities when compared with discrete environmental differences. Considering these findings and a progressive increase in the number of modified forests are being observed on the world, the understanding of how tree communities may respond to disturbance before it occurs is crucial.

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Table 1 Equality index of Pielou **(**J) during the four monitoring periods for three topographic classes (H: hilltop; S: slope and B: bottom) of the arboreal community of the Atlantic Forest fragment.

Equality index	Topographic classes	2003	2005	2007	2015
Pielou (J)	H	0.84	0.84	0.84	0.84
	S	0.77	0.77	0.78	0.78
	B	0.71	0.73	0.72	0.74

Table 2 Importance value (IV) and rank for main 10 species for topographic classes over time

Hilltop species	2003		2005		2007		2015	
	IV	Rank	IV	Rank	IV	Rank	IV	Rank
Protium spruceanum	36.71	1	35.67	1	35.38	1	36.36	1
Copaifera langsdorffii	21.71	2	22.17	2	21.93	2	22.85	2
Myrcia pulchra	9.26	3	8.47	4	8.32	5	7.09	11
Clethra scabra	8.57	4	8.41	5	8.27	6	8.23	4
Trichilia pallida	8.56	5	8.70	3	8.68	4	9,19	3
Machaerium villosum	8.14	6	8.09	7	8.70	3	8.02	5
Lamanonia ternata	8.01	7	8.32	6	8.27	7	7.91	6
Protium widgrenii	7.67	8	7.49	8	8.07	8	7.88	7
Styrax camporum	7.00	9	7.06	9	7.22	9	5.65	12
Ixora brevifolia	6.39	10	6.62	10	6.72	10	7.27	9

Slope species	2003		2005		2007		2015	
	IV	Rank	IV	Rank	IV	Rank	IV	Rank
Protium spruceanum	58.39	1	57.19	1	55.14	1	59.02	1
Copaifera langsdorffii	22.12	2	20.97	2	28.30	2	18.12	2
Ixora brevifolia	13.78	3	14.52	3	13.03	3	15.59	3
Protium widgreni	10.78	4	10.96	5	10.94	4	11.23	4
Actinostemon concolor	9.75	5	11.55	4	10.44	5	11.68	5
Tachigali rugosa	8.18	6	9.61	6	8.69	6	10.29	6
Amaioua intermedia	7.84	7	6.28	10	7.53	7	7.98	7
Myrcia pulchra	6.48	8	6.90	7	6.71	8	7.07	8
Clethra scabra	6.23	9	6.58	9	6.40	9	3.88	16
Terminalia glabrescens	5.64	10	6.80	8	4.58	14	0.0	-

Bottom species	2003		2005		2007		2015	
	IV	Rank	IV	Rank	IV	Rank	IV	Rank
Protium spruceanum	91.90	1	89.81	1	88.79	1	91.87	1
Copaifera langsdorffii	12.41	2	13.32	2	14.07	2	15.50	2
Protium widgrenii	11.28	3	10.60	4	9.37	6	8.90	6
Siphoneugena crassifolia	10.93	4	11.35	3	11.61	3	9.77	5

Hyeronima alchorneoides	9.53	5	10.07	5	10.29	4	9.82	4
Myrcia pulchra	8.73	6	6.70	10	7.36	8	5.03	12
Machaerium villosum	8.62	7	9.23	6	9.39	5	8.05	8
Clethra scabra	7.13	8	7.33	8	7.56	9	5.34	10
Faramea hyacinthina	6.95	9	7.38	7	8.75	7	8.07	7
Leucochloron incuriale	6.62	10	6.91	9	7.50	10	13.16	3

Species are ordered according to the importance value in 2003

Table 3 Dynamics rates for three monitoring periods for three topographic classes on the arboreal community of the Atlantic Forest fragment.

Dynamics rate (% year^{-1})	Topographic class	2003–2005	2005–2007	2007–2015
Mortality	H	1.97	2.07	3.02
	S	3.16	2.86	4.09
	B	4.40	1.61	4.11
Recruitment	H	2.07	1.75	2.26
	S	1.49	3.12	3.11
	B	0.89	0.73	1.99
Loss	H	2.14*	2.16*	1.16*
	S	5.59	3.40	3.13
	B	2.78	3.10	1.79
Gain	H	3.31*	3.91*	2.44*
	S	4.19*	8.35*	2.48*
	B	3.18*	3.10*	3.55*

*****Parameters which showed $p < 0.05$, comparison of each topographic class over time; parameters in the topographic classes in the same period all showed $p > 0.05$.

Figure 1 Example of topographic profile and classification within a study plot, where H corresponds to hilltop, S to slope and B to the bottom topographic classes, reflecting characteristics of ravines occurring in the area under study

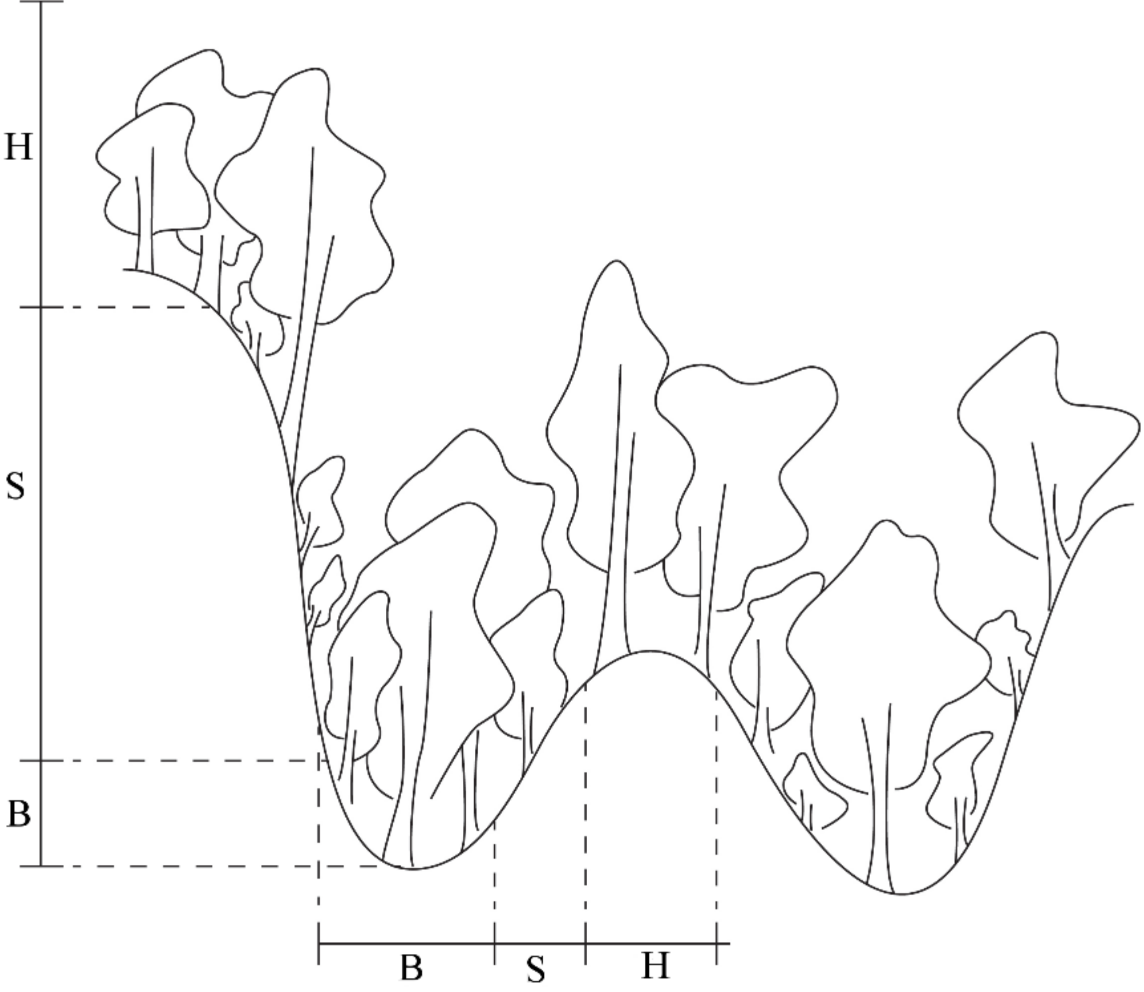
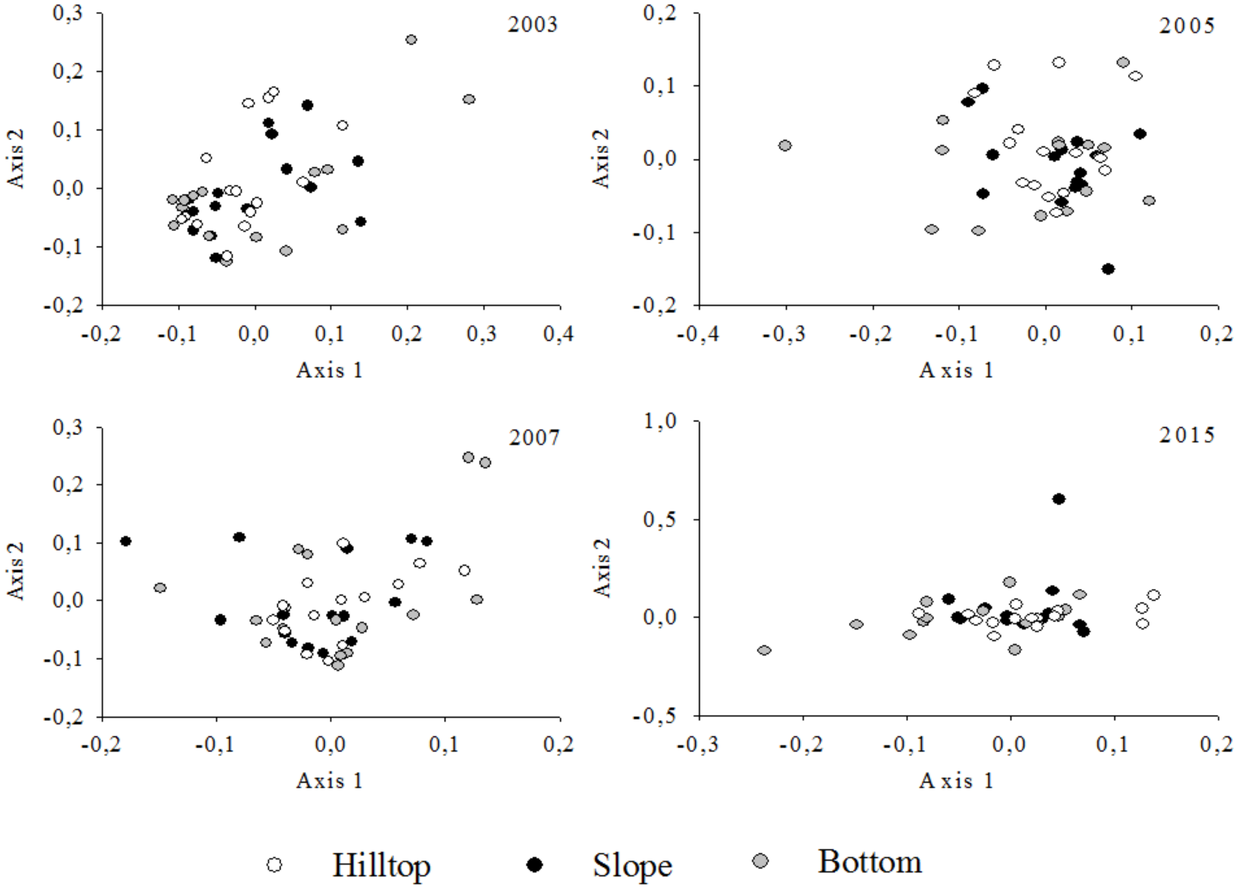


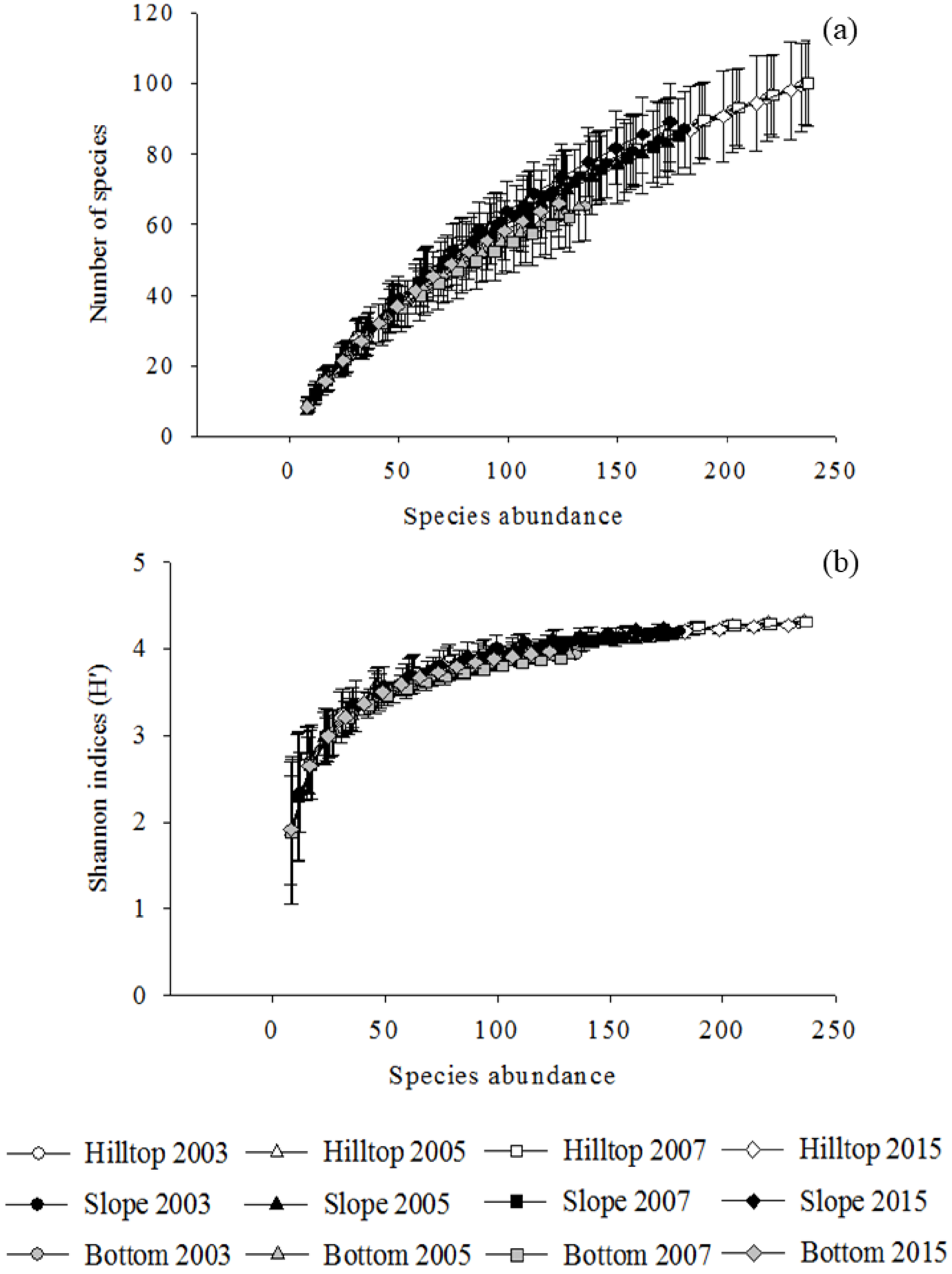
Figure 2 Ordering diagrams resulting from non-parametric multi-dimensional analysis (non-parametric multidimensional scaling), showing the layout of study plots with respect to the quantitative composition (number of individuals of each species present in the parcel), for three topographic classes in four intervals in the studied forest



544

545 **Figure 3** Rarefaction curve for (a) mean specific richness and (b) diversity index of Shannon

546 obtained for topographic classes over time (2003, 2005,2007 and 2015).



547