

FUNCTIONAL CHARACTERISATION OF AN ANTHROPISED ATLANTIC FOREST FRAGMENT

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The present study aimed to evaluate the functional expression of tree sinusiae in three sectors of a forest fragment in relation to different land use histories. The study recorded the number of individuals, number of individuals with multiple stems and number of tillers, calculated the percentages of tillered individuals and species, and then classified the species into regeneration and dispersal guilds. The most anthropised sector of the forest showed higher tillering and a larger proportion of pioneer and light-demanding climax species. The sector with moderate anthropisation presented intermediate tillering and mixed occurrence of light-demanding and shade-tolerant guilds. The non-anthropised sector showed lower tillering and a higher number of shade-tolerant species. The distribution of zoochorous individuals was not significant. In conclusion, the different levels of anthropisation provided distinct patterns of tillering and different compositions in regeneration guilds, highlighting their influence on the ecology of tropical forests.

Keywords: Forest ecology, forest fragmentation, forest succession, functional expression, ecology of tropical forest

INTRODUCTION

Regeneration in tropical forests produces transitions in the composition of species and functional types, which in turn leads to different expressions of the plant community (Chazdon 2012, Lohbeck et al. 2014). Functional characteristics can be understood as the traits developed by species that may influence their survival, growth and reproduction, providing better competitive capacity for resource acquisition (Ackerly 2003, Reich et al. 2003, Ghazoul & Sheil 2010). The shifts that occur in the successional process, such as the substitution of shade-intolerant and fast-growing species by ombrophilous and slow-growth species, for example, tend to increase functional complexity (Reich et al. 2003, Chazdon 2012, Lohbeck et al. 2013).

The different existing types of anthropisation alter composition and structure of forest communities, consequently altering ecosystem functions throughout the successional processes (Ghazoul & Sheil 2010, Chazdon 2012). Thus, forest sectors in early successional stages do not present the same functional diversity as found in more advanced stages (Reich et al. 2003,

Chazdon 2012, Lohbeck et al. 2014). That happens because different types of disturbance, especially those of anthropogenic origin, alter survival and developmental conditions of plants, affecting the structure of species populations and ecosystem processes (Ghazoul & Sheil 2010, Morel et al. 2014, Rodrigues et al. 2016).

Tree species tillering, regarded in light of regeneration, is acknowledged as a key functional trait for spatial occupation and niche maintenance, especially considering that many species in mature tropical forests can resprout in response to anthropogenic impacts (Kammesheidt 1999, Ghazoul & Sheil 2010, Chazdon 2012, Clarke et al. 2013). Lateral expansion and vegetative reproduction may be advantageous strategies for plant species in highly competitive habitats, considering the lower competing abilities of seedlings (Martins et al. 2009, Souza et al. 2012). In such cases, tillering can be an important occupation strategy, since vigorous growth of new sprouts provides large competitive advantage during the early stages of forest succession (Chazdon 2012).

Functionally, trees can also be classified into ecological groups or guilds, which are groups of species that explore resources from the environment in a similar fashion (Giller 1984). Based on regeneration and dispersal traits, guilds' species composition can be understood as an expression of the functional performance of species during the ecological cycles of a forest, since those species present different aptitudes for their establishment and development under different conditions (Reich et al. 2003, Ghazoul & Sheil 2010, Lohbeck et al. 2013). Most studies on ecological succession use an approach that is based on forest structure and/or dynamics (Josse & Balslev 1994, Oliveira-Filho et al. 1997, Addo-Fordjour et al. 2009, Faria et al. 2009). Hence, a perspective that includes ecological guilds as a tool to make inferences about successional stages of tropical forests is valid and has been confirmed as a reliable approach (Tabarelli & Mantovani 1999, Nunes et al. 2003, Oliveira Filho et al. 2004, Corrêa et al. 2014, Rodrigues et al. 2016).

In this study, we aimed to evaluate the functional expression of tree sinusiae in three sectors of a seasonal Atlantic forest fragment in Brazil, in relation to their particular histories of disturbances in an anthropisation gradient, from a most anthropised to an undisturbed sector. Therefore, the study attempted to answer the following questions: i) Are there distinct tillering patterns among the sectors of the forest fragment? ii) Are there differences in the composition of regeneration and dispersal guilds when comparing the three sectors? iii) Do the different types of impacts influence the parameters to the point where they functionally distinguish the fragment sectors?

MATERIALS AND METHODS

Study site and sampling procedure

The study was carried out in a 10 ha forest fragment located at 21°16' S and 44°49' W and 920 to 956 m altitude, in the Municipality of Itumirim, Minas Gerais State, Southeast Brazil. The region falls into the category Cwa of the Köppen climate classification, characterised by dry winters and rainy summers (Dantas et al. 2007). Average annual temperature is 19.4° C (15.8° C in July and 22.1° C in February), and average annual precipitation, 1530 mm (23 mm in July and 296 mm in December)

(Brasil 1992). Being part of the Atlantic forest complex, the surveyed vegetation is classified as Semideciduous Seasonal Forest (IBGE 2012), an intermediate physiognomy between tropical rainforest and tropical seasonal forest. Regarded as a hotspot for biodiversity conservation, the Brazilian Atlantic forests have been extremely devastated since the beginning of colonisation, in centuries XVI and XVII. Human-related disturbances in the region are associated with mining, crop farming and cattle rearing (Dean 1996, Vilela 2007). Currently, most of the original Atlantic forest area is fragmented and exposed to anthropogenic impacts.

The study gathered detailed information about the land use histories of each sector through a structured interview with locals. Due to their distinct histories of disturbance, the fragment presented different successional stages, and was consequently divided into three sectors (Figure 1). Sector A suffered land clearing and burning in 1965, and after one year of cultivation and two subsequent years serving as pasture, the area was abandoned. The vegetation that established in sector A has suffered selective cutting and is now susceptible to occasional access by cattle. Sector B was part of a larger forest prior to 1965, when part of the once continuous vegetation was submitted to clear cut. The cleared land was later used alternately for cultivation and pasture, which allowed for cattle to frequently enter the sector B area. In contrast, sector C, influenced by riparian vegetation, was not submitted to anthropogenic interventions.

In order to obtain parameters of the tree sinusiae, 24 plots, totaling 72 plots, 10 × 10 m each, was established in each sector. Within each plot, all arborescent individuals with diameter equal or greater than 5 cm at 1.30 m height was measured. For example, part of the tree sinusiae, those that form the community between the understory and the forest canopy, which may include pteridophytes and palm trees were considered as arborescent individuals. Plant identification was based on the criteria from Angiosperm Phylogeny Group (APG III 2009).

Tillering assessment

To determine the number of multiple stems (tillers), the numbers of stems of every individual that met the inclusion criterion were counted. In each plot, the number of individuals, number of

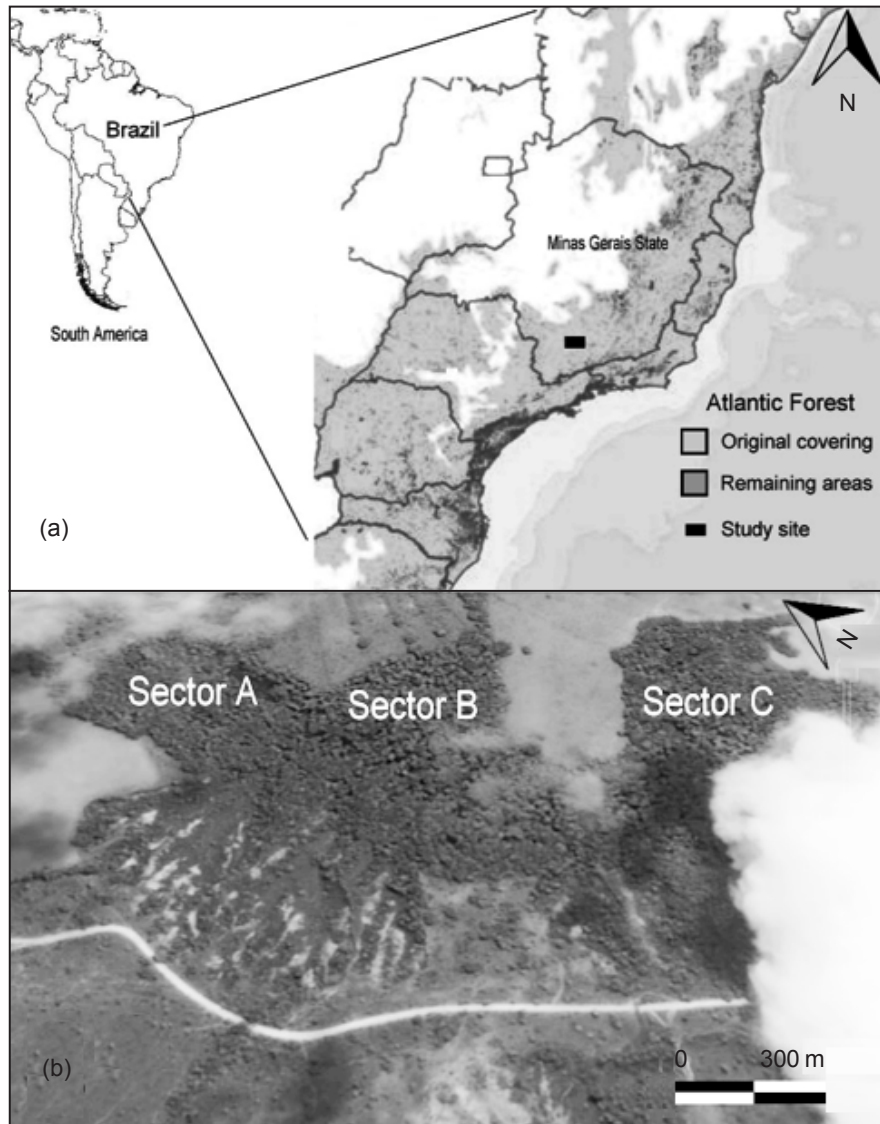


Figure 1 Study site map, a = geographic location of the fragment, featuring the original cover of Brazilian Atlantic Forests and their current remaining distribution, b = location of the three sampled sectors in relation to the forest fragment

tillered individuals and number of tillers were recorded. To evaluate the degree of tillering, percentages of tillered individuals and tillered species by sector were calculated.

Guild systems and species classification

Species were classified into two guild systems: one regarding their regeneration characteristics based on optimal light conditions, and another concerning dispersal, based on main dispersal agents (Denslow 1980, Wheelwright 1985). Classification was based on previous knowledge on behavior, field observations and the literature (Lorenzi 2000, 2002, Nunes et al. 2003, Silva Júnior et al. 2005).

Species classification into regeneration guilds followed Swaine and Whitmore (1988) as follows: (i) pioneer—species that demand full light for germination and establishment, (ii) light-demanding climax—species able to germinate under shaded conditions, but demand abundant light to grow in height and reach the canopy and (iii) shade-tolerant climax—species that germinate and grow under shaded conditions, reaching maturity in the understory or at the canopy layer. Species classification into dispersal guilds followed Pijl (1982). In this case, the following categories were used: (i) anemochorous—species that produce wind-dispersed seeds, (ii) autochorous—species that produce seeds dispersed by gravity or explosive

dehiscence and (iii) zoochorous—species with seeds dispersed by animals. To compare the species distribution within regeneration and dispersal guilds, categories ‘pioneer’ and ‘light-demanding climax’ were merged into ‘light species’, while ‘anemochorous’ and ‘autochorous’ were combined into ‘abiotic dispersal species’. The reason for this fusion is the short number of species found in these groups.

Statistical analyses

Normality of data was verified by a D’Agostino-Pearson test. To compare the numbers of individuals, tillered individuals and tillers between the sectors, Student’s t-tests was performed (Zar, 1999). Analysis of individuals’ distribution in the guilds was performed using a Chi-square test on contingency tables, crossing data from the regeneration and dispersal guilds with fragment sectors. A Chi-square test was also performed on species level to confirm if species distribution in the guilds is independent in relation to the sector. The analyses were performed in BioEstat 5.0 and Microsoft Excel 2010 (Ayres et al., 2007).

RESULTS

Tillering assessment

A total of 1228 individuals belonging to 154 species were sampled: 533 individuals in the most anthropised sector (A = 95 species), 358 in the intermediate sector (B = 79 species) and 337 in the undisturbed sector (C = 88 species). Sector A had the largest number of tillered individuals and tillers, and the highest percentage of tillered individuals and species, followed by sectors B and C (Table 1). According to the t-test results, the number of individuals in sectors B and C were not significantly different ($t = 0.6782$; $p = 0.2505$). The test showed significant differences regarding number of individuals, number of tillered individuals and number of tillers in every other comparison between sectors A, B and C (Table 2).

Species composition of regeneration and dispersal guilds

The light-demanding and zoochorous guilds presented the highest numbers of individuals

Table 1 Number of individuals (N), number of tillered individuals (Nti), number of tillers (Nt) and tillering percentage for individuals and species in three sectors of a forest fragment in the Municipality of Itumirim, Minas Gerais State, Southeast Brazil

Sector	Ni	Nti	Nt	Tillering (%)	
				Individuals	Species
A	533	92	226	17,26	42,11
B	358	37	85	10,34	29,11
C	337	14	34	4,15	12,50

Table 2 Comparison of Student’s t-test results for the number of individuals (Ni), number of tillered individuals (Nip) and number of tillers (Np) in three sectors of a forest fragment in the Municipality of Itumirim, MG

Sectors	Ni		Nti		Nt	
	t	p	t	p	t	p
A – B	4,5338	< 0,0001	3,6359	0,0005	3,5085	0,0007
A – C	4,8784	< 0,0001	5,4658	< 0,0001	4,9675	< 0,0001
B – C	0,6782	0,2505	3,2569	0,0012	3,0975	0,0018

on sector A, accounting for 52.72% and 61.17%, respectively. On sector B, the most frequent guilds were shade-tolerant (61.17%) and zoochorous (79.89%). Sector C had shade-tolerant (76.56%) and zoochorous individuals (92.58%) at the highest frequency (Table 3).

According to the Chi-square test results, the frequency distribution of the sampled individuals within regeneration guilds is not independent from the sectors (Table 4). The only exception

was the zoochorous category, which showed to be non-significant ($\chi^2 = 3.264$; $p = 0.181$). The analyses also presented statistically significant results when we compared the distributions of each guild within each sector. The proportion of pioneer individuals was higher than expected in sectors A and B. Likewise, light-demanding species on sector A and shade-tolerant species on sectors B and C were at a higher-than-expected proportion. Concerning dispersal

Table 3 Number of individuals, species and percentage values of regeneration and dispersal guilds in three sectors of a forest fragment in the Municipality of Itumirim, Minas Gerais State, Southeast Brazil

Sectors	Individuals						Species					
	Regeneration			Dispersal			Regeneration			Dispersal		
	Guilds	Ni	%	Guilds	Ni	%	Guilds	Ns	%	Guilds	Ns	%
A	Pio	41	7.69	Ane	76	14.26	Lig	59	62.11	Abi	19	20.00
	Ldc	281	52.72	Aut	9	1.69	Sha	36	37.89	Zoo	76	80.00
	Sha	211	39.59	Zoo	448	84.05						
B	Guilds	Ni	%	Guilds	Ni	%	Guilds	Ns	%	Guilds	Ns	%
	Pio	28	7.82	Ane	22	6.15	Lig	45	56.96	Abi	15	20.00
	Ldc	111	31.01	Aut	50	13.97	Sha	34	43.04	Zoo	64	81.00
C	Guilds	i	%	Guilds	Ni	%	Guilds	Ns	%	Guilds	Ns	%
	Pio	5	1.48	Ane	19	5.64	Lig	37	42.05	Abi	11	12.50
	Ldc	74	21.96	Aut	6	1.78	Sha	51	57.95	Zoo	77	87.50
	Sha	258	76.56	Zoo	312	92.58						

Ni = number of individuals, Ns = number of species, Pio = pioneer, Luz = light-demanding climax, Sha = shade-tolerant climax, Lig = light species, Ane = anemochorous, Aut = autochorous, Zoo = zoochorous and Abi = abiotic dispersal

Table 4 Observed and expected frequencies of individuals and species sampled in three sectors of a forest fragment in the municipality of Itumirim, MG

Sector	Individuals						Species							
	Observed frequency			χ^2	p	Expected frequency			Observed frequency		χ^2	p	Expected frequency	
	Regeneration					Regeneration			Regeneration				Regeneration	
	Pio	Ldc	Sha			Pio	Ldc	Sha	Lig	Sha			Lig	Sha
A	41	281	211	27.991	0,000	32.12	202.26	298.62	59	36	0.763	0.328	54.29	40.71
B	28	111	219	3.412	0,017	21.57	135.85	200.57	45	34	0.007	0.974	45.14	33.86
C	5	74	258	36.208	0,000	20.31	127.88	188.81	37	51	7.585	0.004	50.29	37.71
χ^2	14.613	56.914	52.010						3.580	4.770				
p	0.000	0.000	0.000						0.141	0.073				
Sector	Dispersal						Dispersal		Dispersal		χ^2	p	Dispersal	
	Dispersal			χ^2	p	Dispersal			Dispersal				Dispersal	
	Ane	Aut	Zoo					Ane	Aut	Zoo	Abi	Zoo		
A	76	9	448	641.388	0.000	7.38	28.21	454.00	19	76	0.009	0.975	19.12	75.88
B	22	50	286	105.595	0.000	4.96	18.95	304.94	15	64	0.013	0.800	15.90	63.10
C	19	6	312	50.314	0.000	4.67	17.84	287.05	11	77	2.729	0.074	17.71	70.29
χ^2	725.162	68.872	3.264						2.198	0.554				
p	0.000	0.000	0.181						0.273	0.721				

Pio = pioneer, Ldc = light-demanding climax, Sha = shade-tolerant climax, Lig = light species, Ane = anemochorous, Aut = autochorous, Zoo = zoochorous and Abi = abiotic dispersal

guilds, anemochorous individuals on sectors A, B and C and autochorous individuals on sector B were found at a larger-than-expected number.

Comparing the number of species in the guilds, sector A presented a higher percentage of light species (62.11%, $\chi^2 = 0.763$, $p = 0.328$) and zoochorous species (80.00%, $\chi^2 = 0.009$, $p = 0.975$). These guilds also had the largest number of species on sector B, with proportions of 56.96% ($\chi^2 = 0.007$, $p = 0.974$) and 81.00% ($\chi^2 = 0.013$, $p = 0.800$), respectively. On sector C, the most species-rich guilds were shade-tolerant, with 57.95% ($\chi^2 = 7.585$, $p = 0.004$), and zoochorous, with 87.50% ($\chi^2 = 2.729$, $p = 0.074$) (Table 3). Nonetheless, species distributions within regeneration and dispersal guilds in each sector were not significantly different (Table 4). The values were significant only when we compared species distribution in regeneration guilds on sector C, with a lower-than-expected value for light species, and a higher-than-expected value for shade-tolerant species.

DISCUSSION

A previous study carried out on the same forest fragment identified floristic and structural differences among sectors A, B and C (Morel et al. 2016). Such differences were attributed to anthropisation rather than soil features, since sectors A and B are very similar regarding soil type, soil chemical and textural variables. This study evaluated the functional expression of tree *sinusiae* through tillering and species composition of regeneration and dispersal guilds, and further verified the influence of anthropisation over these parameters.

By considering tillering as an adaptive trait that favors post-disturbance occupation (Ghazoul & Sheil 2010, Chazdon 2012, Clarke et al. 2013), it was found that the most anthropised area (sector A) had the highest number of tillers and tillered individuals. Sector A, which also showed a significantly higher number of individuals compared with the other sectors, can be considered the most disturbed. This can be attributed to its historical association with land clearing and burning in 1965 (Morel et al. 2016). Distinctly, tillering was less expressive in sector B, an area exposed to milder disturbances, and even less so in sector C, which was unaffected by anthropogenic disturbances. The percentages

of tillered individuals and species in the three sectors can be acknowledged as occupation strategies that further confirm the three levels of anthropisation acting upon the fragment.

Tillering derives from a plant's resprouting capacity, and is a common trait in tropical forests (Paciorek et al. 2000, Chazdon 2012), especially following damage caused by natural or anthropogenic impacts (Kammesheidt 1999, Ghazoul & Sheil 2010, Clarke et al. 2013). In locations where there is limited condition for seed colonisation, for example, resprouting from stumps and basal shoots can represent an important adaptive strategy throughout the entire regeneration process (Uhl et al. 1988, Vesk & Westoby 2004, Martins et al. 2009, Ghazoul & Sheil 2010, Clarke et al. 2013).

The importance of resprouting in the colonisation of disturbed areas has been documented in several successional ecology studies. For example, Ewel (1977) and Murphy & Lugo (1986) observed quick forest recomposition through root budding in an area previously submitted to coppicing in Central America (Chazdon 2003). Uhl & Murphy (1981) showed that resprouting was a common regeneration strategy in a forest subjected to logging in San Carlos, Venezuela, and Kammesheidt (1999) found that resprouting strongly contributed to the regeneration of arborescent vegetation following logging and burning on eastern Paraguay (Chazdon 2003).

Since numerous species remain present in logged forests through the maintenance of buds (Vesk & Westoby 2004, Chazdon 2012, Clarke et al. 2013), many of the tillered species from sector A are likely to have persisted from the pre-clear-cut forest. Such strategy may have played an important role in the resilience manifested in sector A, providing elements for the recovery of species composition. In a different manner, the tillering pattern found in sector C may be intrinsic to the species or a response to natural disturbances, since occupation by tillers is not a common strategy in preserved forests (Kammesheidt 1999, Chazdon 2012, Clarke et al. 2013).

Species composition of the guilds was influenced by the levels of anthropisation that affected each sector. Moreover, the distribution of individuals in the regeneration guilds emphasises that sector A, owing to its history of intense

anthropisation, still has features associated with early regeneration stages, as observed by Nunes et al. (2003). This is further corroborated by the finding of a higher-than-expected percentage of light-demanding individuals, since pioneer and light-demanding climax species are the main groups to colonise large gaps, pastures and degraded or disturbed areas (Chazdon 2012, Braga et al. 2015). Besides, sector A was the only one not to present shade-tolerant species at a higher proportion.

Furthermore, it was understood that sectors B and C, the ones with higher percentages of shade-tolerant individuals, are in more advanced successional stages. Shade-tolerant species tend to develop under competitive conditions in shaded environments, with increasing importance toward the maturing stages of forest succession (Tabarelli & Mantovani 1999, Chazdon 2012, Braga et al. 2015). Hence, the largest percentage of shade-tolerant individuals found on sector C, unaffected by anthropisation, in relation to B, indicates that the former presents a more favorable environment for the development of such species, confirming its more advanced state of conservation (Chazdon 2012, Rodrigues et al. 2016).

The proportion of individuals in the species corroborates the existence of functional patterns that respond to the histories of anthropisation in each sector, with expressive number of pioneer and light-demanding species in sector A, and shade-tolerant species in sector C. Likewise, the higher-than-expected proportions of pioneer and shade-tolerant species on sector B indicate an intermediate state of anthropisation, reached through the influence of cattle and absence of tree logging in this sector.

The finding of zoochorous species in high percentages in every sector, with non-significant differences, can be considered natural, as other studies obtained similar results when assessing distinct successional stages (Oliveira-Filho et al. 2004). That is mostly because seed dispersal by animals predominates in tropical forests and tends to have increased importance with increasing humidity (Howe & Smallwood 1982, Chazdon 2012, Braga et al. 2015). Studies have shown that in secondary Atlantic forests, there is an increment in the number of zoochorous individuals throughout the successional process (Tabarelli & Mantovani 1999, Oliveira Filho

et al. 2004, Corrêa et al. 2014). Despite not finding such pattern in this study, the largest proportion of zoochorous individuals, although not significantly distinct, was found in the undisturbed sector C (92.58%).

Concerning the species, the only comparison with significant results was related to regeneration guilds in sector C, and it can be further interpreted from the successional perspective. Sector C had lower-than-expected values for light species and higher-than-expected values for shade-tolerant species, which, considering the predominance of the latter group in conserved forests (Tabarelli & Mantovani 1999, Chazdon 2012, Corrêa et al. 2014, Rodrigues et al. 2016), reaffirms this sector's higher state of conservation. On the other hand, the non-significance of all other comparisons reflects the typical mixture of species found in tropical forests, which simultaneously comprise different groups representing distinct regeneration stages and dispersal syndromes (Chazdon 2012, Rodrigues et al. 2016).

CONCLUSIONS

The distinct levels of anthropisation observed in the forest fragment contributed to the maintenance of contrasting functional expressions of the tree sinuiae in their respective sectors, leading to different tillering patterns and multiple compositions of regeneration guilds. On the most anthropised sector (A), the considerable occupation by tillers and higher proportion of light species are consistent with a highly anthropised situation. The intermediate sector (B), submitted to moderate anthropisation, reflected such condition with intermediate tillering and mixed distribution of light and shade-tolerant individuals. Distinctly, the undisturbed sector (C) showed a higher conservation status as a result of tillering being a less important strategy and the finding of shade-tolerant individuals at a higher proportion. Thus, it was shown that over 50 years succeeding logging and burning on sector A and moderate impacts on sector B, the two sectors were not at an advanced state of succession. Our findings highlight the influence of anthropisation on tropical forests, indicating that different sorts of impacts contribute to the occurrence of multiple processes of regeneration.

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