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Post-fire regeneration of vegetation on sandy oligotrophic soil, in Itabaiana, Sergipe, Brazil

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ABSTRACT. Two models of post-disturbance regeneration of vegetation in areas of oligotrophic soils have been proposed for temperate regions. The first model is characterized by rapid recovery of the floristic composition, due to the fire resistance of plants; while in the second model, the fire causes extensive mortality and the recovery occurs by recruitment from the seed bank. Since these models have been rarely tested in tropical oligotrophic environments, we applied them in the analysis of floristic compositions in three areas with different post-fire regeneration times in Sergipe State, Brazil. The regeneration followed the seed bank recruitment model in places of bare ground, with a progressive increase in plant density and changes in the relative abundance and dominance of the populations along the successional process. The parameters that best allowed the succession evaluation were the floral similarity, plant height and density, which increased as regeneration progressed. The stem diameter and tillering were inconclusive as parameters for assessing the regeneration progress.

Keywords: succession, disturbance, burning, resilience, models.

Regeneração vegetacional pós-queimada em solos arenosos oligotróficos, Itabaiana, Sergipe, Brasil

RESUMO. Dois modelos de regeneração pós-distúrbio em vegetação sobre solos oligotróficos têm sido propostos para as regiões temperadas. O primeiro modelo caracteriza-se pela rápida recuperação da composição florística, devido à resistência das plantas ao fogo; enquanto no segundo modelo, o fogo provoca grande mortalidade e a recuperação ocorre por meio do recrutamento do banco de sementes. Uma vez que estes modelos têm sido raramente testados em ambientes oligotróficos tropicais, nós os aplicamos a análises de composição florística em três áreas com diferentes tempos de regeneração pós-fogo em Sergipe, Brasil. Como resultados, identificou-se que a regeneração seguiu o modelo de recrutamento do banco de sementes em locais de solo desnudo, com um aumento progressivo na densidade de plantas e mudanças na abundância relativa e dominância das populações ao longo do processo sucessional. Os parâmetros que melhor permitiram uma avaliação da sucessão foram a similaridade florística, altura e densidade, que aumentou com o progresso da sucessão. Diâmetro do caule e o número de perfilhamentos foram inconclusivos como parâmetros para avaliar o progresso de regeneração.

Palavras-chave: sucessão, distúrbios, fogo, resiliência, modelos.

Introduction

Anthropic disturbances are increasingly common around the world and, depending on the type, intensity and frequency may alter the floristic composition and the relative abundance of plant populations (ACCATINO et al., 2010; KREYLING et al., 2011). Anthropic disturbances are considered an extremely worrying factor since they change the environmental conditions, threatening the successional status of forests and the conservation of the biological diversity. In many areas, anthropic activities are discontinued and the native vegetation is regenerated. The knowledge on the ability and time required to regenerate a vegetation similar to that preceding the disturbance is scarce (D'OLIVEIRA et al., 2011), especially on sandy soils in seasonally dry tropical environments (DALY; MITCHELL, 2000). Studies on the successional process in anthropic areas monitoring the qualitative and quantitative sequential changes in the community composition and structure are increasingly important (PICKETT et al., 2009) because they may guide actions for conservation, restoration and sustainable management of the vegetation (BAASCH et al., 2010; MAZANCOURT et al., 2013).

Throughout the succession process there are inter- and intraspecific interactions in the community that reflect the abiotic environmental conditions. Unpredictable changes in the species composition and/or environmental conditions may modify the sequence of the successional process (PICKETT at al., 1989; KREYLING et al., 2011). In areas with low water and nutrient availability, such as oligotrophic sandy areas, the vegetation regeneration post-disturbance may vary depending on the disturbance factor and local abiotic conditions (KEELEY et al., 2005). The post-disturbance successional dynamics in vegetation on oligotrophic soils in Mediterranean climates is well known and follows two distinct models (LLORET et al., 2005; BIGANZOLI et al., 2009), which can occasionally be complementary (BAEZA et al., 2007).

The first of these models suggests a quick recovery of the plants present before the disturbance (CAPITANIO; CARCAILLET, 2008), resulting in a rapid restoration of the plant density and floristic composition (KEELEY et al., 2005). The model is based on species tolerant to disturbances and on the high resilience of the vegetation on oligotrophic soils (MAGUIRE; MENGES, 2011; MARZANO et al., 2012). In the second model, the post-disturbance regeneration occurs through germination from the seed bank due to the lack of tolerant species (KEELEY et al., 2005; MAIA et al., 2012). This model resembles the general model of secondary succession in tropical environments (RICHARDS et al. 1996; CHAZDON, 2008), which implies replacement of species and decrease in plant density with increase in the successional time towards later stages, due to competition, mainly for space (CROTTEAU et al., 2013; SANTANA et al., 2012).

Despite the evidences recorded on the successional dynamics in temperate oligotrophic areas, the low number of studies does not allow to determine which model corresponds to the succession in tropical regions (UHL, 1987; MENEZES; ARAÚJO, 2004). Thus, this study aimed to describe the successional process in tropical oligotrophic areas disturbed by fire, in order to assess if it fits the existing successional models for temperate regions and to determine which parameters best allow to understand the dynamics of the successional process in oligotrophic tropical areas.

Material and Methods

Study site

The study was conducted in the Serra de Itabaiana National Park in the state of Sergipe, northeastern Brazil. The park covers a total area of 7,966 ha and encompasses three continuous mountains: Serra do Cajueiro, Serra Comprida and Serra de Itabaiana (the highest of them), with a maximum altitude of 670 m. The climate is tropical, with a dry summer and moderate water surplus in winter, with Thornthwaite moisture index (Im) between - 1.3 and 8.8 Im, characterized by a mean annual rainfall between 1,100 and 1,300 mm and mean annual evapotranspiration of 800 mm (DANTAS et al., 2010). The park is protected by law since 1978 and has monitoring programs in order to prevent fire and deforestation.

In the park, there are areas with Quartzipsamments formed by dystrophic quartz sands, being excessively drained, from moderately to highly acidic and of low fertility, classified as areas of ecological tension between savannah park and seasonal forest (VELOSO et al., 1991). These sandy areas are locally called Areias Brancas (White Sands) and, within the park, they occur as separate fragments on the east side of the Serra Comprida and Serra da Itabaiana, between the ridge and forests at the bases of the mountains, in elevations around 200 m (DANTAS; RIBEIRO, 2010a). Areias Brancas has a sclerophyllous vegetation established that seems the resting vegetation (DANTAS et al., 2010). Fire does not occur naturally in the vegetation, but the surrounding communities use it in order to clear areas for activities of hunting and farming, occasionally entering the park boundaries.

Three areas with one hectare of Areias Brancas were selected, with fire disturbances of similar intensity but at different times, and thus with different post-disturbance regeneration times (WHITE; RIBEIRO, 2011). The size of the areas was based on the most reliable records on fires, which were reported for units with one hectare. The area that suffered the most recent burning, in 2005, is designated as being 'young', representing the early stage of succession. The second area was burned in 1994, being designated as 'intermediate'. The third area, called 'mature', is located near the headquarters of the Chico Mendes Institute for Biodiversity Conservation (ICMBio). This latter area has not been disturbed by fire for over 30 years and is in the most advanced succession stage.

The three areas have different physiognomies and surrounding matrices. The 'young' area is located at the edge of the park and is surrounded by seasonal forests, agricultural fields, and pastures. In addition, a dense grass cover characterizes its physiognomy with many shrubs sparsely distributed or in small groups, under which the vegetation litter accumulates. The 'intermediate' area is inserted in an array of seasonal forests and sloping fields. The grass cover is less dense and the woody vegetation is more developed than in the 'young' area. The shrubs group in dense thickets, where the litter builds up. The 'mature' area is near the seasonal forests and has a continuous coverage of woody vegetation so that the shrub clusters cannot be seen as in the other two areas.

Sampling protocol

In each of the three areas, 20 plots with 10 x 10 m were delimited and randomly drawn from the geographical coordinates of the total area of physiognomies under analysis. All plants in the plots, with at least equal circumference to one of the stem branches (tillers), measuring 30 cm in height from the ground level (C_{gl}), larger than or even equal to 10 cm, had their heights and C_{gl} for all branches measured and the number of tillers counted.

As for the three selected areas with fire records, the sampling covered around 20-25% of the total area. The plot size followed the same pattern of previous studies in the area (DANTAS et al., 2010) and was considered sufficient for individuals sampled per plot (15-25 ind/plot) in the mature area, although it was lower in the Intermediate and Young areas. The criterion for inclusion of the individuals was similar to several studies where the shrub component is dominant and the measurement of the trunk circumference at the ground level is more appropriate (BARREIRA et al., 2002; BHUYAN et al., 2003).

Data analysis

In order to characterize the vegetation structure, the following parameters were calculated for each area: density, frequency, basal area and the Importance Value index (IV – average of relative density, frequency and basal area) of each species (MUELLER-DOMBOIS; ELLEMBERG, 1974). The ratio of richness/density of species of each area was compared using the rarefaction curves with 95% confidence interval and the analytical formulas of Colwell et al. (2004), through the software EstimateS. Differences among areas, concerning the mean diameter and height, were evaluated using the Kruskal-Wallis test (H) and then compared to the SNK (Student-Newman-Keuls) tests. Differences in the proportion of individuals per diametric and height classes were evaluated by the chi-square test for independence and homogeneity (χ^2). The H and χ^2 were evaluated at a significance level of 0.05.

In order to assess the existence of significant differences among communities with different regeneration times, it was used a one-tailed analysis of similarity (ANOSIM). The ANOSIM was carried out with the software Primer E-v.6 (PRIMER-E Ltd., Plymouth, UK), using the Bray-Curtis similarity matrix, with the abundance data normalized and transformed into quadratic root. The significance was tested with 999 random permutations and a significance level of 0.1%.

Results

Richness and floristic similarity

The 'young' area was the richest with 26 species, followed by the 'mature' area, with 23 species, and the 'Intermediate' area, with 20 species. Together, the three areas had a total of 33 species belonging to 31 genera and 24 families. The families with the greatest diversities were the Fabaceae and Myrtaceae, with four and three species, respectively. The rarefaction graph (Figure 1) showed a higher ratio of richness/density of species in the 'young' area, while the 'intermediate' and 'mature' areas had lower and similar ratios, respectively.

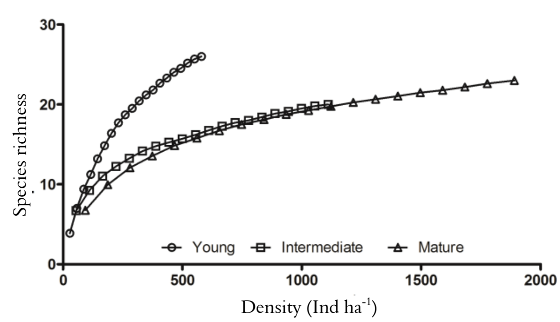

Figure 1. Rarefaction curves for the surveys in the three areas with increasing post-fire regeneration times in Serra de Itabaiana National Park, Sergipe State, Brazil.

The Analysis of Similarity (ANOSIM) resulted in a global R value of 0.41 ($p < 0.01$), indicating significant differences among the areas. The 'young' and 'intermediate' areas were relatively less dissimilar ($R = 0.29$, $p < 0.01$), followed by the 'young' and 'mature' areas ($R = 0.38$, $p <0.01$) and by the 'intermediate' and 'mature' areas ($R < 0.59$, $p = 0.01$), which were less similar.

Vegetation structure

There were significant differences in plant density in the three sampling areas ($H = 24.6$, $p = 0.00$). The 'young' area had 580 plants ha^{-1}, which was significantly lower than the 'intermediate' (1100 plants ha^{-1}) and 'mature' (1890 plants ha^{-1}) areas, corresponding to only 53 and 31% of density in these areas, respectively. There was a progressive increase in the abundance of the plants in the classes of stems of larger diameters with increasing regeneration times (Figure 2a). However, the mean diameter ($H = 1.93$, $p = 0.37$) and proportion of individuals per class ($\chi^2 = 12, 8$, $p = 0.54$) in the three areas did not differ.

The average height (3.5 m) in the 'mature' area was significantly higher ($H = 74.38$; $p = 0.00$) than those of the 'young' (2.5 m) and 'intermediate' (2.8 m) areas, which were not significantly different. The main difference in the plant average height was due to the proportion of shrubs and trees with heights of up to two meters (Figure 2b), which was lower in the areas of higher regeneration time ($\chi^2 = 60.53$; $p = 0.00$). Less than 1% of the individuals were larger than 6 m in height.

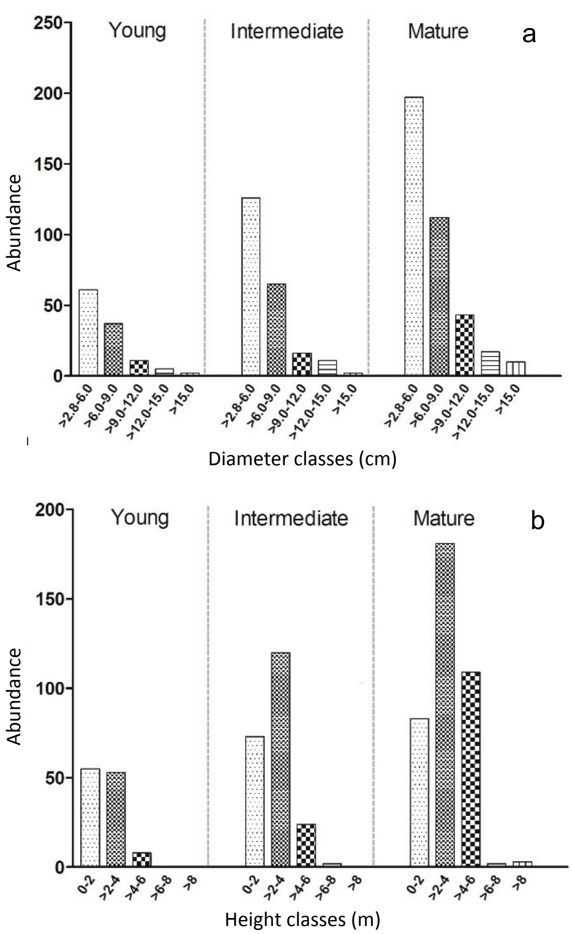

Figure 2. a) Distribution of plants by diameter classes (cm); b) Distribution of plants by height classes (m) in three areas with increasing post-fire regeneration times in Serra de Itabaiana National Park, Sergipe State, Brazil.

The stem ramification near the steam base (tillering) was common in all three areas. Approximately 54% of all plants had at least one stem ramification (two branches) at ground level. The 'young' area had an average number of tillers (2.76) significantly higher ($H = 13.24$, $p = 0.00$) than those in the 'intermediate' (2.16) and 'mature' (2.34) areas, in which these last two did not differ. This superiority in the 'young' area was mainly a reflection of more tillers in *Kielmeyera rugosa* and *Ouratea cuspidate*, among the most abundant species, while other species had no significant differences in the number of tillers between the three areas (Table 2).

Table 2. Average number of stem per individual of the species with highest plant density in three areas with increasing post-fire regeneration times in Serra de Itabaiana National Park, Sergipe State, Brazil.

Species	Young	Intermediate	Mature
Coccoloba laevis Casar.	3.8^{a}	4.3^{a}	4.0^{a}
Guettarda platypoda DC.	4.3^{a}	3.5^{a}	3.4^{a}
Kielmeyera rugosa Choisy	2.5^{b}	1.6^{a}	1.5^{a}
Diptychandra epunctata Tul.	1.2^{a}	1.2^{a}	1.6^{a}
Coccoloba rosea Meisn.	1.6^{a}	4.0^{a}	1.9^{a}
Ouratea cuspidata Tiegh.	3.8^{b}	-	1.1^{a}
Total	2.76^{a}	2.16^{b}	2.34^{b}

Means followed by the same letter in the row do not differ when tested by the SNK test at 5% probability.

In the three areas, few species had high Importance Values (Table 3). In the 'mature' area, three species accounted for more than 50% of the IV, while in the 'young' and 'intermediate' areas this proportion was only reached with the sum of the IVs of five and four species, respectively. *Coccoloba laevis* was the species with the highest IV in all three areas, mainly due to the contribution of density to the IV index, but its density was lower than that of *Kielmeyera rugosa* in the 'intermediate' area. The rank of importance of the species was different in each area, reflecting differences in density and basal area of their populations in the areas.

Discussion

Biotic attributes: floristic similarity, richness and community structure

The differences among the areas regarding aspects of the arbustive-arboreous community, including plant density and the rank of importance of the species, indicate that the regeneration in the areas best fits with the post-disturbance model, showing germination from the seed bank and replacement of species over time, as described by Gleeson and Tilman (1990), Keeley et al. (2005) and Marzano et al. (2012). The adequacy to this model may be a result of the type of disturbance to which the vegetation was subjected.

Table 3. Phytosociological parameters of species in three areas with increasing post-fire regeneration times in Serra de Itabaiana National Park, Sergipe State, Brazil. RD = relative density (%); RF = relative frequency (%); RB = relative basal area (%); IV = Importance Value index (average of RD, RF and RB).

	Young				Intermediate				Mature			
Species	RD	RF	RB	IV	RD	RF	RB	IV	RD	RF	RB	IV
Acosmium bijugum	0.86	1.28	0.57	0.91	0.45	0.85	0.87	0.73	1.59	2.8	4.93	3.10
Acritopappus confertus	4.31	6.41	1.49	4.07	-	-	-	-	0.26	0.7	0.07	0.34
Agarista revoluta	-	-	-	-	0.91	1.71	0.18	0.93	11.9	11.19	16.49	13.20
Bauhinia acuruana	3.45	3.85	2.89	3.40	-	-	-	-	-	-	-	-
Jacaranda obovata	1.72	2.56	0.98	1.76	5.00	8.55	3.26	5.60	-	-	-	-
Bonnetia stricta	0.86	1.28	0.83	0.99	-	-	-	-	0.26	0.7	0.05	0.34
Byrsonima sericea	3.45	3.85	8.11	5.13	-	-	-	-	-	-	-	-
Chamaecrista cytisoides	1.72	1.28	1.44	1.48	7.27	7.69	4.68	6.55	21.69	12.59	20.01	18.10
Clusia nemorosa	-	-	-	-	-	-	-	-	1.06	2.1	1.03	1.40
Coccoloba laevis	21.55	14.1	28.34	21.33	15.91	14.53	27.9	19.45	26.98	13.99	36.08	25.68
Coccoloba rosea	4.31	6.41	2.77	4.50	2.27	1.71	1.8	1.93	9.79	9.09	4.16	7.68
Davilla flexuosa	-	-	-	-	0.45	0.85	0.16	0.49	-	-	-	-
Diptychandra epunctata	6.9	5.13	4.17	5.40	8.64	9.4	5.18	7.74	5.03	7.69	3.32	5.35
Esenbeckia grandiflora	0.86	1.28	0.66	0.93	0.91	1.71	0.27	0.96	-	-	-	-
Guapira opposita	-	-	-	-	2.73	4.27	6.26	4.42	1.06	2.1	1.4	1.52
Guettarda platypoda	7.76	11.54	6.11	8.47	2.73	4.27	1.74	2.91	2.12	4.9	0.93	2.65
Hancornia speciosa	1.72	2.56	4.05	2.78	3.18	5.13	4.76	4.36	0.26	0.7	0.06	0.34
Humiria balsamifera	1.72	2.56	0.79	1.69	0.91	0.85	0.51	0.76	6.08	7.69	4.21	6.00
Kielmeyera rugosa	9.48	7.69	4.71	7.29	20.45	12.82	14.33	15.87	3.7	4.2	2.27	3.39
Lafoensia sp.	-	-	-	-	-	-	-	-	0.26	0.7	0.11	0.36
Lantana lucida	0.86	1.28	0.23	0.79	-	-	-	-	-	-	-	-
Manilkara salzmannii	8.62	6.41	13.79	9.61	-	-	-	-	0.79	2.1	0.41	1.10
Myrcia falax	0.86	1.28	0.17	0.77	-	-	-	-	0.26	0.7	0.2	0.39
Myrcia guianensis	-	-	-	-	11.36	7.69	9.55	9.53	0.53	1.4	0.8	0.91
Myrcia guianensis	0.86	1.28	0.84	0.99	-	-	-	-	-	-	-	-
Myrcia lundiana	0.86	1.28	0.87	1.01	3.18	3.42	5.7	4.10	0.26	0.7	0.5	0.49
Ocotea gardneri	0.86	1.28	1.81	1.32	-	-	-	-	1.06	2.8	0.45	1.44
Ouratea cuspidata	11.21	7.69	11.2	10.03	0.91	0.85	0.62	0.79	3.17	6.99	1.55	3.91
Pera ferruginea	0.86	1.28	0.57	0.91	-	-	-	-	-	-	-	-
Protium heptaphyllum	1.72	2.56	0.93	1.74	-	-	-	-	-	-	-	-
Salzmannia nitida	-	-	-	-	0.45	0.85	0.12	0.48	-	-	-	-
Sapium sp.	1.72	2.56	1.17	1.82	-	-	-	-	-	-	-	-
Schwartzia brasiliensis	0.86	1.28	0.5	0.88	-	-	-	-	0.26	0.7	0.13	0.36
Tetragastris occhionii	-	-	-	-	11.82	11.97	11.99	11.92	1.59	3.5	0.84	1.97
Vochysia lucida	-	-	-	-	0.45	0.85	0.12	0.48	-	-	-	-

In the regeneration model through germination and species replacement in oligotrophic soils (KEELEY et al., 2005; MAIA et al., 2012) the anthropic factor which induces the succession usually causes death of pre-existing plants. In the succession model, through the recovery of the floristic composition and then by the rapid re-establishment of the density (CAPITANIO; CARCAILLET, 2008; MAGUIRE; MENGES, 2011), the disturbance factor does not completely damage the plants, allowing the survival and recovery of some plants. In the studied area, the disturbing factor was the fire, which varies greatly in effect, depending on the frequency and intensity. Fire can cause changes in soil fertility (PIVELLO et al., 2010), in the seed bank dynamics (NAVARRA et al., 2011) and in the number of tillers of surviving plants (LAWES; CLARKE, 2011) and may promote the selection of tolerant species (MAGUIRE; MENGES, 2011).

The differences among the areas could be a reflection of the effect of the succession time but could also indicate some level of heterogeneity among them. The evident environmental differences are restricted to the differences in concentrations of some soil nutrients and the presence of pasture fields adjacent to the 'young' area. In contrast, the areas did not differ in climatic conditions, anthropic influence or origin and time for substrate formation (DANTAS et al., 2010).

The pasture near the 'young' area may have contributed to seeds or seedlings of species not found in the 'intermediate' and 'mature' areas, for instance, *Sapium* sp. and *Bonnetia stricta*, species that are not typically seen in the sandy areas at Serra de Itabaiana National Park (DANTAS et al., 2010). This indicates that the surrounding matrix may be a factor influencing the post-disturbance regeneration process on oligotrophic soils.

Considering that the heterogeneity effect of the surroundings and fertility are relatively small on the dissimilarities in composition and abundance of shrubs and trees in the areas, the main influence came from the disturbance/succession processes, except for the possibility of stochastic colonization. It can be inferred that the bush-tree species in the area have low tolerance to fire and the decimation of their populations hinders the rapid restoration of the species richness and population density.

The differences in species richness strengthen the models of germination and species replacement. The 'young' area had more species and a higher ratio of richness/density of species than the other two areas with longer regeneration time, showing that the vegetation succession in oligotrophic soils involves loss of species. According to Catford et al. (2012), the elimination of dominant species and the temporary improvement of fertility due to ashes, coal and organic fragments (NEARY et al., 1999) favor a greater species richness in the early stage of the successional process, including the allochtonous and fertility-demanding species.

The main structural difference among the three areas was the increased plant density as the successional process progressed. The same occurred in other oligotrophic areas (DAI et al., 2009) and the authors reported that the plant populations under stressful conditions such as drought or low soil fertility tend to have a clustered pattern, and the vegetation presenting many open spaces among the groups. The low nutrient availability limits the recruitment and survival, while the greatest fertility below the canopy of the plants that colonize open spaces seems to facilitate the interactions among plants (CALLAWAY, 2007), contributing to the increased density and aggregation throughout the succession (SCARANO, 2002; DANTAS; RIBEIRO, 2010b). These aspects differ from the general model of succession suggested for tropical forests, which assumes a progressive reduction in density due to the accumulation of aboveground biomass and competition for space (RICHARDS et al. 1996; CHAZDON, 2008).

The highest plant abundance for the classes of smaller diameters is commonly associated with the vegetation in the early successional stages (CHAZDON, 2008). However, in this study, the 'mature' area had an abundance of plants with thin stems significantly higher than the other areas with shorter succession time. This characteristic contrary to the general models of succession is due to the continuous recruitment in open areas and the increased density under the canopy throughout the succession, confirming the importance of the recruitment in the regeneration process in these oligotrophic sandy soils. Despite the differences in abundance per diameter class, the ratio between classes remained unchanged, showing that the diameter distribution cannot always be used as a parameter to assess the structural differences in the successional process for this type of vegetation. Unlike the diameter distribution, the plant height were significantly different among areas, with the 'mature' area presenting the highest mean, however, no stratification were observed as has been recorded in some mature tropical forests (RICHARDS et al., 1996).

Except for *Coccoloba laevis*, there were changes in the rank of ecological importance of species among the areas. The dominant species in the last stage of succession (*C. laevis*, *Chamaecrista cytisoides* and *Agarista revoluta*) are both scleromorphic and dominant species of the early stages, which do not corroborate the hypothesis assumed by Berendse (1998), who suggests the replacement of the most scleromorphic species by less scleromorphic species as the succession time progresses. This disagreement may have occurred due to differences in fertility that would have promoted the replacement of more scleromorphic species by less scleromorphic species, but such differences were relatively small in the study areas.

A frequent characteristic in the structure and physiognomy of the three areas was the tillering of stems, probably caused by injuries from burning (KENNARD et al., 2002), although it may also occur without any sort of disturbance (LAWES; CLARKE, 2011). This is a frequent characteristic in less productive environments such as sites with oligotrophic soils or water deficit (BELLINGHAM; SPARROW, 2009) and it is seen in both tropical (ALMEIDA JR. et al., 2011) and temperate vegetation (CAPITANIO; CARCAILLET, 2008; NZUNDA; LAWES 2011). The largest number of tillers in the 'young' area occurred due to the increased tillering of species such as *Kielmeyera rugosa* and *Ouratea cuspidata*, possibly as a response to fire. Other species did not show increase but many species also presented branched stems, indicating that this may be a natural characteristic of most species of this environment, regardless of the effect of fire. Thus, the tillering may not be a good parameter to assess the successional stage of this vegetation.

Conclusion

The post-fire succession in the sandy areas at the Serra de Itabaiana National Park fits the succession model of germination and species replacement. The fire causes mortality of the most plants, and the recolonization process occurs by recruiting species from the seed bank followed by progressive changes in the population abundances and community density as the regeneration time advances. The parameters that best characterized the structural changes were the Bray-Curtis species similarity, the rank of importance of species, and plant density and height. In contrast, the diametric distribution and tiller numbers were not efficient parameters to separate areas with different regeneration times in the vegetation developing in the oligotrophic soils of the area.

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