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Cibele de Cássia Silva

ESTRUTURA FILOGENÉTICA E VARIAÇÃO DE CARACTERES FUNCIONAIS EM CERRADOS RUPESTRES DO BRASIL CENTRAL

Orientadora: Drª. Rosane Garcia Collevatti
Coorientador: Dr. Marcus Vinicius Cianciaruso

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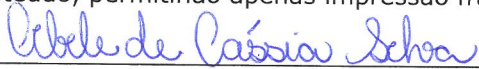|				
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"Diante da vastidão do tempo e da imensidão do universo, é um imenso prazer para mim dividir um planeta e uma época com você".

Carl Sagan

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RESUMO GERAL

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Neste trabalho, procuramos entender a influência de processos evolutivos subjacentes na estrutura filogenética de assembleias de árvores e arbustos de um tipo de habitat do Cerrado: o cerrado rupestre. Além disto, avaliamos se espécies que ocorrem tanto em cerrado rupestre quanto em cerrado *sensu stricto* apresentam variação de atributos funcionais em nível intraespecífico em resposta as diferentes condições ambientais. Para isso, dividimos esta dissertação em dois capítulos. No primeiro capítulo, buscamos compreender o papel das contingências histórico-evolutivas, padrões de diversificação e distribuição de diferentes clados na formação da diversidade atual do componente arbustivo-arbóreo do cerrado rupestre. Além disto, buscamos compreender também a influência da escala e do *pool* de espécies na estrutura filogenética de assembleias de arvores e arbustos do cerrado rupestre. No segundo capítulo, novamente utilizando o componente arbustivo-arbóreo como modelo de estudo, nós investigamos a ocorrência estratégias ecológicas distintas em indivíduos de uma mesma espécie, de acordo com o tipo de habitat em que estavam inseridos. Especificamente, avaliamos a variação de atributos funcionais em espécies que ocorriam tanto em cerrado rupestre quanto em cerrado *sensu stricto* adjacente.

ABSTRACT

In this study, we investigate the role of underling evolutionary process in current phylogenetic structure of tree and shrub assemblages from rocky savanna, which is a habitat type from Cerrado biome. Besides, we analyzed whether species that occurr in both contrasting habitats types from Cerrado biome: rocky savanna and savannas, have varying functional traits in intraspecific level in response to different environmental conditions. For this, we splitted this dissertation in two chapters. In the first chapter, we aimed to understand the role of historical and evolutionary contingencies, diversification patterns and different clades distributions in shaping the current diversity of trees and shrubs from rocky savannas. Furthermore, we also seeked understanding the role of scale and species pool in phylogenetic structure of tree and shrub assemblages from rocky savanna. In the second chapter, again using trees and shrubs as study model, we investigated the occurrence of different ecological strategies in individuals of the same species, according to the type of habitats in which they occurred. Specifically, we addressed the variation of functional traits in species occurring both in rocky savannas such as in geographically adjacent savannas.

SUMÁRIO

INTRODUÇÃO GERAL

A diversidade de espécies nas comunidades biológicas remete a processos ecológicos. Competição, facilitação, dispersão e filtragem ambiental são alguns dos mecanismos e processos comumente explorados com intuito de entender a distribuição das espécies nas comunidades (Ricklefs, 1987; Weiher & Keddy, 1999). Entretanto, a estrutura atual de uma comunidade também é resultado de processos históricos e evolutivos (Webb et al., 2002; Gerhold et al., 2015), que durante muito tempo foram ignorados nos estudos ecológicos (Weeb et al., 2002; Warren et al., 2015). Atualmente, com a crescente disponibilidade das relações de parentesco entre as espécies é possível incorporar um contexto evolutivo nos estudos de estruturação das comunidades ecológicas.

Ainda no contexto evolutivo, mas dentro de uma visão populacional, uma questão antiga, mas que até hoje inspira muitos ecólogos evolutivos é a plasticidade fenotípica. A variação do fenótipo entre indivíduos de uma mesma espécie é "matéria-prima" para seleção natural (Mousseau & Fox, 1998). Ao longo de gradientes ambientais ou dentro de ambientes altamente heterogêneos, a plasticidade fenotípica possui um papel-chave ao permitir que o indivíduo siga seu "*fitness*" ótimo (Charmantier et al., 2008). Sendo assim, a plasticidade fenotípica é um mecanismo importante para entender os padrões de distribuição de populações em ambientes altamente heterogêneos (Valadares et al., 2014) como o Cerrado.

O Cerrado apresenta uma grande variedade de habitats (Eiten, 1972) associada a diferentes padrões de solos, paisagens e clima (Eiten, 1992; Ribeiro & Walter, 2008). Dentre as várias fitofisionomias do Cerrado (ver Ribeiro & Walter, 2008), a fitofisionomia "cerrado *sensu stricto*" é considerada dominante no bioma (Silberbauer-

Gottsberger & Eiten, 1987; Ribeiro & Walter, 2008). Associado com o cerrado *sensu stricto,* ocorre um determinado tipo de habitat restrito a afloramentos rochosos denominado de cerrado rupestre. Os cerrados rupestres ocorrem de forma insular ao longo do Cerrado geralmente em altas altitudes (serras e chapadas) sobre afloramentos rochosos de origem quartízica ou arenítica (Furley & Ratter, 1988; Ribeiro & Walter, 2008). Apesar de apresentarem distribuição geográfica interligada com o cerrado *sensu stricto,* os cerrados rupestres diferem do cerrado *sensu stricto* em aspectos relacionados ao microclima, pedológicos, intensidade e frequência de fogo (Furley & Ratter, 1988). Os cerrados rupestres apresentam solos rasos (o que reduz a capacidade de retenção de água) e com menor teor de nutrientes do que os solos de cerrado *sensu stricto*. Os ventos são incessantes e a amplitude térmica é alta nesses ambientes, com dias quentes devido ao sobreaquecimento e noites frias (Rapini et al., 2008).

Neste trabalho, procuramos entender a influência de processos evolutivos subjacentes na estrutura filogenética de assembleias de árvores e arbustos de um tipo de habitat do Cerrado: o cerrado rupestre. Além disto, avaliamos se espécies que ocorrem tanto em cerrado rupestre quanto em cerrado *sensu stricto* apresentam variação de atributos funcionais em nível intraespecífico em resposta as diferentes condições ambientais. Para isso, dividimos esta dissertação em dois capítulos. No primeiro capítulo, buscamos compreender o papel das contingências histórico-evolutivas, padrões de diversificação e distribuição de diferentes clados na formação da diversidade atual do componente arbustivo-arbóreo do cerrado rupestre. Além disto, buscamos compreender também a influência da escala e do *pool* de espécies na estrutura filogenética de assembleias de arvores e arbustos do cerrado rupestre. No segundo capítulo, novamente utilizando o componente arbustivo-arbóreo como modelo de estudo, nós investigamos a ocorrência estratégias ecológicas distintas em indivíduos de

uma mesma espécie, de acordo com o tipo de habitat em que estavam inseridos. Especificamente, avaliamos a variação de atributos funcionais em espécies que ocorriam tanto em cerrado rupestre quanto em cerrado *sensu stricto* adjacente.

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CAPÍTULO I

Phylogenetic structure in trees and shrubs from rocky savannas: evaluating the role of evolutionary history in a habitat type from Cerrado

Introduction

Understanding why ecological communities differ in species diversity and composition is a key objective in ecology. Ecological processes such as competition, dispersion and environmental filtering are commonly explored to understand the distribution of species in communities (Gause, 1934; MacArthur & Levins, 1967; Weiher & Keddy, 1995). However, evolutionary history may also influence the current structure of communities (Webb et al., 2002; Pausas & Verdú, 2010; Gerhold et al., 2015). In contrast to early works, when a genetic approach was not incorporated into ecological studies (Warren et al., 2015), nowadays, the use of species phylogenetic relationships is a powerful tool to understand the role of evolutionary processes on current community structure in different scales (e.g., Webb et al., 2002; Ackerly,2003, 2004; Cavender-Bares et al., 2004; Vamosi et al., 2009; Fine & Kembel, 2011; Gerhold et al., 2015).

Time calibrated phylogenies provide insights about the origin and diversification of lineages (Pennington et al., 2004; Morlon, 2014). Diversification can vary through time due to diversity-dependent processes, geological and environmental effects (Morlon, 2014). Different diversifications patterns associated with long-distance dispersal events shape lineage pools in large scales (Ricklefs & Schluter, 1993; Vamosi et al., 2009), which have profound effects in species composition and turnover among contemporary communities (Graham & Fine, 2008; Fine & Kembel, 2011). Thus, analysis of diversification patterns and historical contingencies using a community phylogenetic approach allows a deeper understanding about the underling evolutionary and biogeographic mechanisms determining current diversity patterns and communities composition (Graham & Fine, 2008; Morlon, 2014; Gerhold et al., 2015).

The community phylogenetic approach yield information about the role of macroevolutionary processes in different habitats (Pennington et al., 2006; Graham & Fine, 2008; Gerhold et al., 2015), such as centres of recent diversification (Pennington et al., 2004b). In this manner, this approach allows evaluating the role of evolutionary process for the origin and maintenance of the variation in species composition, as well as different diversification patterns between habitats within a single biome (Pennington et al., 2006; Souza-Neto et al., 2016). Indeed, understanding the variation of species composition between specific habitats in species-rich biomes is the first step for the deeper interpretation of the entire biome diversity (Simon et al., 2009). In this way, due to the high habitat heterogeneity with different woody plant communities associated with different soils types, the Cerrado biome affords an interesting study model to explore the patterns of phylogenetic structure of trees and shrubs assemblages in specific habitats.

The Cerrado biome is a mosaic of habitats, consisting of different formations such as forest, savanna and grassland (Eiten, 1972; Coutinho, 2006). The habitat heterogeneity is mainly due to the high spatial and environmental heterogeneity (Eiten, 1992) associated with different climates, landscapes and soil (Ribeiro & Walter, 2008). Cerrado biome has the most diverse flora among all tropical savannas (Silva et al., 2006). The savannas, known as *"cerrado sensu stricto",* are the predominant vegetation type in the Cerrado occurring in deep dystrophic soils (Ribeiro & Walter, 2008). They are characterized by trees and shrubs distributed in more or less continuous layer of grass and herbaceous species (more details see Ribeiro & Walter, 2008). Based in geographical patterns of the flora distribution, Ratter *et al.* (2003) proposed the classification of savannas in phytogeographical provinces or regions within the Cerrado biome (see Fig 1 for detail and Ratter et al., 2003). Phytogeographical regions differ in

geomorphology and mainly in species composition and co-occurrence (Ratter et al., 2003). According to Ratter et al. (2003), the Cerrado has six phytogeographical areas (Figure 1): Disjunct Amazonian savannas; Central and Southeastern; Central-Western; North and Northeastern; Southern and Far Western Mesotrophic sites (FWM) (Figure 1). Associated with the savannas, the rocky savannas ('cerrado rupestre', in Portuguese) are habitats restricted to mountains and hills, where the relief is hilly and steep and the soils are shallow and covered by rocky outcrops (Furley & Ratter, 1988; Ribeiro & Walter, 2008).

Rocky savannas have an insular distribution, mainly in the highlands of Central Brazil (Furley & Ratter, 1988). It occurs on rocky outcrops of quartzite and sandstone formation, over shallow and generally acid soils with low nutrient and organic matter content and show sharper night-to-day temperatures fluctuations than typical cerrado (Furley & Ratter, 1988; Ribeiro & Walter, 2008). On the one hand, during the day heat can be increased due to the sun-light reflected on the rocks. On the other hand, in the night rocky savannas can become quite cold environments due to winds and rock cooling (Rapini et al., 2008). Therefore, rocky savannas may be considered a more stressful habitat for colonization and survival of plants than ordinary savannas. However, those environmental conditions may favour plant diversification in rocky savannas, such as the species-rich genera *Mimosa* (Simon & Proença, 2000). Rocky savannas are considered centres of *Mimosa* endemism within Cerrado biome (Simon & Proença, 2000). Furthermore, floristic studies in rocky savannas show many trees and shrubs habitat-specialist, such as *Mimosa claussenii*, *Schwartzia adamantium* and *Wunderlichia cruelsiana* (Ratter et al., 2000; Pinto et al., 2009; Lemos et al., 2013), as well as endemic species. The shrub *Tibouchina papyrus*, for instance, is an endemic species from rocky savannas (Marachipes et al., 2012). Nevertheless, the endemism in

rocky savannas is mainly related to the herbaceous component of vegetation (Pinto et al., 2009).

Dated phylogenies show that the Cerrado flora lineages started to diversify less than 10 million years ago, with most lineages diversifying at 4 million years ago or less (Simon et al., 2009). *In situ* diversification and habitats shifts in some lineages were important process in shaping the Cerrado flora diversity (Simon et al., 2009; Batalha et al., 2011; Souza-Neto et al., 2016). Additionally, a recent study highlighted the importance of considering the Cerrado biome habitats separately due to significant phylogenetic structure (Souza-Neto et al., 2016). However, studies using this approach are still scarce, mainly considering rocky savanna habitat type (Hughes et al., 2013). Phylogenetic analysis focusing in specific habitats of Cerrado biome, such as rocky savannas, could help to evaluate the relative importance of macroevolutionary diversification process occurring in specific habitats, in shaping the current high Cerrado flora diversity.

In the present work, we aimed to understand the role of historical contingencies, diversification patterns of different clades and evolutionary processes in shaping the current rocky savannas flora diversity, at different spatial scales: biome, phytogeographical and local scale. For this, we used a community phylogenetic framework (Webb et al., 2002; Graham & Fine, 2008; Gerhold et al., 2015) with shrubs and trees as study group, to test the hypothesis that rocky savannas are centres of recent diversification of plants within Cerrado biome. If our hypothesis holds, we predicted that rocky savannas shrubs/trees assemblages are phylogenetically clustered. Furthermore, we expected to find more recent diversification patterns in rocky savannas than in savannas and higher lineages turnover between rocky savannas and savannas. Additionally, we addressed the following questions:

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1- Do rocky savanna and savanna assemblages from the same phytogeographical region exhibit similar patterns of phylogenetic structure at regional and local scale?

2- Are the diversification patterns of tree and shrub species similar in rocky savannas and savannas? Which are the most important clades that colonized rocky savannas and savannas?
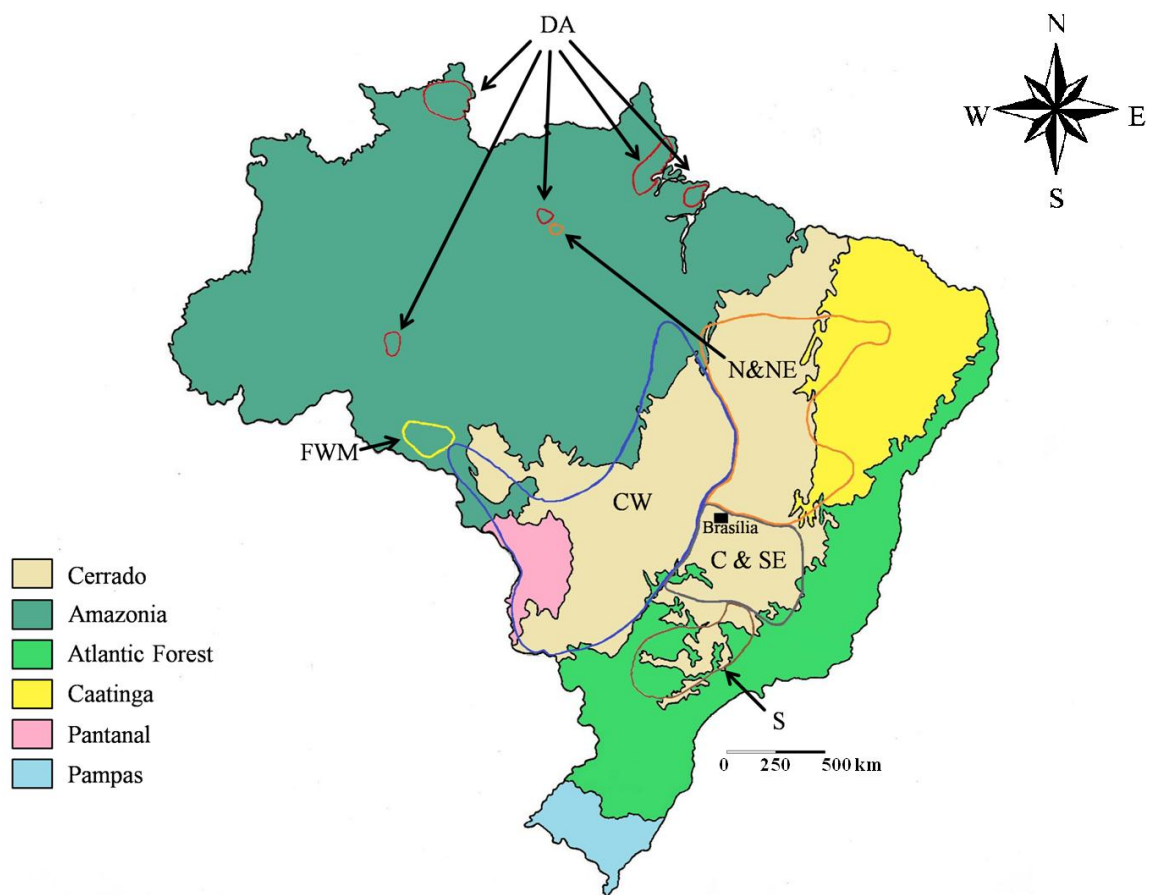
Figure 1: Distribution of Brazilian biomes (modified from IBGE, 2004) and the six Phytogeographical areas proposed by Ratter *et al.* (2003). **DA**: Disjunct Amazonian savannas; **C & SE**: Central and Southeastern, **CW**: Central-Western; **N & NE**: North and Northeastern; **S**: Southern and **FWM**: Far Western Mesotrophic sit

Material and Methods

Species pools and occurrence data

Species pools were defined at three spatial scales: biome scale (full pool), regional scale (regional pools) and local scale (local pool). The full pool was composed by shrubs and trees species occurring in savannas habitat type from Cerrado biome, i.e. savanna pool. We obtained the occurrence data of 867 trees and shrubs occurring in savannas from data set of Ribeiro et al. (2008). The occurrence data was updated with data on further 55 species occurring in rocky savannas based in floristic studies (Table 1). Regional scale was defined using the phytogeographical areas from Cerrado biome, proposed by Ratter et al. (2003). Phytogeographical areas (see Fig 1 and for detailed description, see Ratter et al., 2003). differ from each other mainly in species composition and co-occurrence patterns Besides species composition, those areas also differ in soil and climate patterns. As mentioned above, Cerrado biome features six phytogeographical areas (Ratter et al., 2003; see Figure 1): Disjunct Amazonian savannas (DA); Central and Southeastern (C & SE); Central-Western (CW); North and Northeastern (N & NE); Southern (S) and Far Western Mesotrophic sites (FWM). We used three phytogeographical areas for analyses: (1) N&NE, (2) C&SE and (3) CW (Figure 1). For regional species pools, i.e. full pool split by regions, we also used the data set from Ribeiro *et al.* (2008) and floristic papers, which included these phytogeographical areas. In local scale, species pool was by shrubs and trees species occurring in rocky savannas and savannas geographically adjacent. To construct local species pool, we gathered data of shrubs and trees species occurring in rocky savannas and savannas surrounding from

floristic studies (Table1).We based mainly in recent surveys conducted by Mews (2014a) which contained plant occurrence data from almost all rocky savannas communities and also geographically adjacent savannas communities from central Brazil. Synonymies were checked based on the List of Brazilian Flora (2015).

Tree phylogeny

We reconstructed the phylogenetic tree of shrubs and trees from Cerrado biome of Souza-Neto et al. (unpubl.) using only the species occurring at savannas and rocky savannas obtained from the floristic studies.
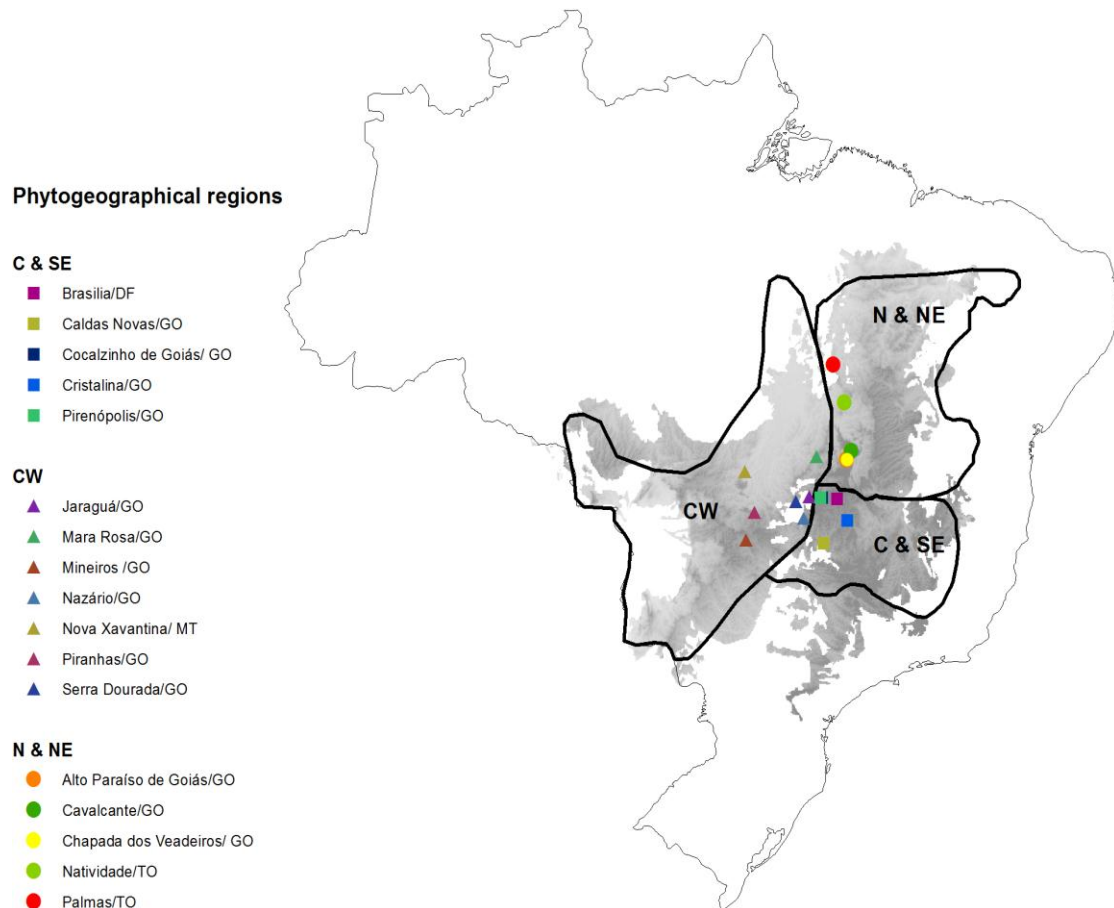
Figure 2: Rocky savannas communities used in our study and their respectives phytogeographical regions. **C & SE** (squares): Central and Southeastern; **CW** (triangles): Central-Western and **N & NE** (circles): North and Northeastern. In gray the Cerrado biome distribution**.**

Table 1: Localities and altitude from rocky savannas and savannas communities included in this study. Besides, their respective phytogeographical region and data source (floristic studies).

Localities of pairs communities	Altitude (m)	Phytogeographical Region	Floristic studies
Brasília/DF**	1.050	C&SE	Amaral et al., 2006
Caldas Novas/GO	901	C&SE	Santos et al., 2012; Mews et al.,2014a
Cristalina/GO	1.123	C&SE	Santos et al., 2012; Mews et al.,2014a
Pirenópolis/GO	1.179	C&SE	Moura et al., 2010; Mews et al.,2014a
Cocalzinho de Goiás/ GO**	1.2	C&SE	Pinto et al., 2009
Jaraguá/GO	790	CW	Santos et al., 2012; Mews et al.,2014a
Mara Rosa/GO	577	CW	Santos et al., 2012; Mews et al.,2014a
Mineiros /GO	800	CW	Santos et al., 2012; Mews et al.,2014a
Nazário/GO	735	CW	Santos et al., 2012; Mews et al.,2014a
Nova Xavantina/ MT	340-400	CW	Maracahipes et al.,2011; Gomes et al., 2011
Piranhas/GO	750	CW	Abreu et al., 2012; Mews et al.,2014a
Serra Dourada/GO	-	CW	Miranda, 2008
Alto Paraíso de Goiás/GO	1.162	N&NE	Santos et al., 2012; Mews et al.,2014a
Cavalcante/GO	900	N&NE	Santos et al., 2012; Mews et al.,2014a
Chapada dos Veadeiros/GO**	1.180 - 1.210	N&NE	Lenza et al., 2011
Natividade/TO	1.000	N&NE	Lemos et al.,2013
Palmas/TO	400	N&NE	Lemos et al.,2013

 * For detailed description, see Ratter et al. (2003).

** Brasília/DF, Cocalzinho de Goiás/GO and Chapada dos Veadeiros/GO did not have paired data of savanna local communities.

Phylogenetic structure

We evaluated the phylogenetic structure of rocky savannas, using the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) (Webb, 2000;Webb et al., 2002). To calculate NRI and NTI we used *ses.mpd* and *ses.mntd* functions respectively, from Picante package (Kembel et al., 2010) implemented in the software R (R Core Team, 2015). The NRI and NTI results were multiplied by -1. NRI of an assemblage is represented by the average distance between each species and all others on the phylogeny of species pool) and indicates the phylogenetic clustering of taxa over the whole pool phylogeny. In other words, NRI represents deeper divergences in phylogenetic tree (Webb, 2000). NTI is based on the mean nodal distance to the closest relative on the phylogeny of species pool, and represents the extent to which taxa are "locally clustered" within particular terminal clades (more recent divergences) (Webb, 2000). Both NRI and NTI increase with increasing phylogenetic clustering and become negative with phylogenetic overdispersion (Webb et al., 2002). To access the phylogenetic structure in biome scale, we compared observed values of NRI and NTI of rocky savannas assemblage with those randomly generated by a null model to full pool (biome scale). The null model randomizes the data matrix and species occurrence frequency and species richness are maintained. In regional scale spatial, the phylogenetic structure was measured in a way analogous to biome scale. Specifically, we evaluated whether rocky savannas assemblages and their geographically adjacent savannas are phylogenetically clustered or overdispersed compared to regional pools, i.e. phytogeographical areas which they belong (Table 1, Figure 2). To access phylogenetic structure in local scale, we performed a paired t-test between rocky savannas local communities and their paired savanna local communities, to test whether NRI and NTI

were significantly different from what one would expect by chance. Besides, we calculated the ratio between observed values of MPD (pairwise phylogenetic distance, metric from NRI) from rocky savanna local community and observed value of MPD from geographically adjacent savanna local community (paired date): $R_{MPD}= MPD_{observed}$ *(Alto Paraíso from rocky savanna)/ $MPD_{observed}$ (Alto Paraíso from savanna).* Using these ratio values, we performed a one-sample t-test to test whether values were significantly different from 1.0. When $R_{MPD} < 1$ rocky savanna species are more phylogenetically related than savanna species, when $R_{MPD} > 1$ rocky savanna species are less phylogenetically related than savanna species, and when $R_{MPD}=1$ rocky savanna and savanna species have similar phylogenetic distances. For three local communities (Brasília, Cocalzinho, and Chapada dos Veadeiros; Table 1) we did not have paired data (rocky savanna - savanna communities). Thus, we excluded these sites from that analysis.

Lineages through-time and clades diversification

To evaluate how speciation rates have varied through time in each assemblage: rocky savannas and savannas, we performed the lineages through-time plot (LTT plot) using *llt.plot* function from Picante package (Kembel et al., 2010) implemented in R software (R Core Team, 2015). To determine whether diversification patterns are similar or distinct between rocky savannas and savannas, we identified the most important clades that colonized each assemblage. For this, we used the Nodesig analysis, implemented in Phylocom 4.2 (Webb et al., 2008). This analysis compares the total observed number of taxa of each habitat descended from each internal node in the phylogenetic tree from the species pool, to the number expected under a null model. The null model was generated

by random draws taxa across the tips of phylogenetic tree (Webb et al., 2008). Overrepresented clades in each assemblage were those with observed number of descendant taxa in the top 5% of the null model (Fine & Kembel, 2011).

Taxonomic and phylogenetic beta diversities

To better understand the roles of evolutionary processes in shaping flora diversity in rocky savannas, we used an integrated approach of evolutionary and taxonomic information (Graham & Fine, 2008). To estimate taxonomic and phylogenetic dissimilarity between rocky savannas and savannas (biome scale) such as between rocky savannas and their respective phytogeographical areas (regional scale), we used the Sørensen (Baselga, 2010).and Phylosor (Leprieur et al., 2012) indexes, respectively.

The dissimilarity Sørensen index is a pairwise metric that ranges from 0.0 (when two assemblages are composed by the same taxa) to 1.0 (when both assemblages are composed by totally different taxa) (Baselga, 2010). Total Sørensen dissimilarity values were decomposed into turnover and nestedness components following Baselga (2010) and were obtained using *beta.pair* function from betapart package (Baselga & Orme, 2012), in R software (R Core Team, 2015). We quantified phylogenetic beta diversity (i.e. dissimilarity in the phylogenetic composition of assemblages) using the PhyloSor dissimilarity index (1 minus PhyloSor similarity index) (Bryant et al., 2008), with *phylosor* function from betapart package (Baselga & Orme, 2012) implemented in R software (R Core Team, 2015). Phylosor dissimilarity index is a pairwise metric that represents the proportion of shared branch lengths between assemblage pairs. PhyloSor dissimilarity varies from nearly zero 0 to 1, which nearly to zero values means that the phylogenetic composition is identical in assemblages, and 1 means that communities

share just a small proportion of basal branches. To test whether assemblage pair was more or less phylogenetically dissimilar than expected by chance, we test statistical significance of PhyloSor indices using randomizations. In the randomizations, we maintained species richness in each assemblage, but randomizing species shared between rocky savannas and savannas. Each species was sampled from the species pool with equal probability. The phylogenetic beta diversity was also partitioned into turnover and nestedness components (Leprieur et al., 2012) to distinguish between lineage filtering from species pool and in situ diversification in rocky savannas.

Furthermore, we compared the measures of taxonomic and phylogenetic beta diversity between local pairs of communities (e.g, Alto Paraíso rocky savanna community and Alto Paraíso savanna local community).

Results

Phylogenetic structure

Rocky savanna was phylogenetically clustered (positive NRI value) i.e., composed of species that are more related than expected by chance with respect to the savannas species pool- biome scale (Table 2). The lower mean phylogenetic distance (MPD) observed for co-occurring species in rocky savannas than expected under a null model (Table 2), is consistent with the idea that high rate of diversification in rocky savannas. However, phylogenetic structure of rocky savannas assemblage, according NTI, did not differ from that expected by chance (NTI= -0.690, p=0.761; Table 2), at biome scale.

Across all phytogeographical regions, NRI was significant to almost all assemblages analyzed (Table 3). To NTI just one savanna assemblage differed from that expected by chance (Table 3). Rocky savanna assemblage did not differ from that

expected by chance just in C&SE phytogeographical region, using the NRI, whereas NRI did not differ from that expected by chance for all rocky savannas assemblages (Table 3).

In local scale, the phylogenetic structure (NRI and NTI mean) of local communities from rocky savannas and geographically adjacent savannas did not differ ($t_{NRI} = 0.326$, p = 0.749; $t_{NTI} = -0.252$, p = 0.804; Table 4). Consistent with this pattern, we found no difference in phylogenetic distance among species from rocky savannas and savannas ($t_{MPD} = 0.574$, p = 0.575).

Table 2- Phylogenetic structure (NRI and NTI) of rocky savanna compared to the savanna species pool- biome scale. ***n***, number of species in species pool; **MPD**, mean observed phylogenetic distance; **MPD$_{null}$**, mean phylogenetic distance for the null model; **NRI**, Net relatedness index. **MNTD**, mean observed phylogenetic distance to closet relative; **MNTD$_{null}$**, mean phylogenetic distance to closet relative for the null model; **NTI**, Nearest taxon index.

Scale	Species Pool	*n*	Assemblage	MPD	MPD$_{null}$	NRI	p
	Savannas	922					
			Rocky savannas	192.211	195.122	1.661*	0.045
Biome				**MNTD**	**MNTD$_{null}$**	**NTI**	**p**
	Savannas	922					
			Rocky savannas	26.438	25.613	-0.690	0.761

*p<0.05

Table 3- Phylogenetic structure (NRI and NTI) of rocky savanna and savannas assemblages compared to their respectives phytogeographical regions (regional species pools). **n**, number of species; **MPD**, mean observed phylogenetic distance; **MPD$_{null}$**, mean phylogenetic distance for the null model; **NRI**, Net relatedness index. **MNTD**, mean observed phylogenetic distance to closet relative; **MNTD$_{null}$**, mean phylogenetic distance to closet relative for the null model; **NTI**, Nearest taxon index.

| Scale	Species Pool	Assemblage	*n*	MPD	MPD$_{null}$	NRI	p	MNTD	MNTD$_{null}$	NTI	p
	C&SE		239								
		Rocky savannas	133	191.643	195.133	1.178	0.134	38.428	36.940	-0.503	0.687
		Savannas	88	184.946	195.2492	1.744*	0.043	49.5933	46.551	-0.701	0.757
Regional	**CW**		359								
		Rocky savannas	149	192.781	197.435	1.659*	0.051	33.310	35.046	0.720	0.241
		Savannas	148	191.567	197.456	1.845*	0.035	34.446	36.030	0.641	0.261
	N&NE		287								
		Rocky savannas	150	191.250	197.845	2.369*	0.013	33.330	34.701	0.582	0.283
		Savannas	129	188.722	197.880	2.704*	0.008	32.636	37.927	1.816*	0.029

*p<0.05.

Table 4- Paired t-test for the NRI/NTI (**metrics**) observed values between paired data of local communities: rocky savannas and savannas. **_n,_** number of local communities (rocky savannas and savannas).

Scale	Communities	_n_	Metrics	Mean	t	p
	Rocky savanas	14	NRI	0.051	0.326	0.749
	Savannas	14	NRI	0.192		
Local						
	Rocky savanas	14	NTI	0.265	-0.252	0.804
	Savannas	14	NTI	0.374		

Lineages through-time and clades diversification

Lineages-through time (LTT) showed that rocky savannas and savanna species started to diversify at almost the same time about _c._ 100 Ma (Figure 2), with a higher rate of speciation in rocky savannas than savannas at about _c._ 50 Mya. Although rocky and savannas showed similar patterns of speciation rates through time, _Aspidosperma_, _Byrsonima_, Myrtales and _Stryphnodendron_ were dominant clades within the rocky savannas, whereas within savannas no clade was overrepresented.
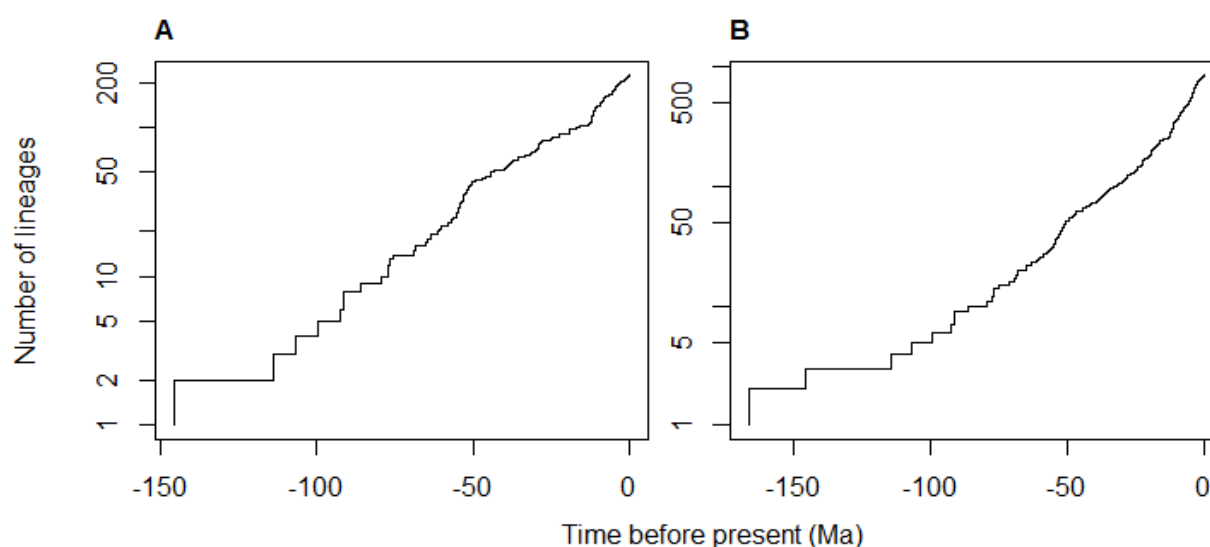
Figure 3- Speciation time of shrubs and trees species obtained from lineages through time plot –LLT plot. Log numbers of lineages reported in millions of years before present (Ma), in (**A**) rocky savannas and (**B**) savannas.

Taxonomic and phylogenetic beta diversities

The rocky savannas and savannas assemblages were more dissimilar in species composition (Sørensen index, Table 7) than in species relatedness (Phylosor index, Table 7). Taxonomic and phylogenetic dissimilarities were mainly due to turnover component (Table 7).

Overall, among pairs of communities (rocky savanna community and geographically adjacent savanna comunity), taxonomic dissimilarities were also higher (Table 8) than phylogenetic dissimilarities (Table 9). Both beta diversities (taxonomic and phylogenetic) were mainly due to the turnover of species and lineages (Table 8 and 9, respectively).
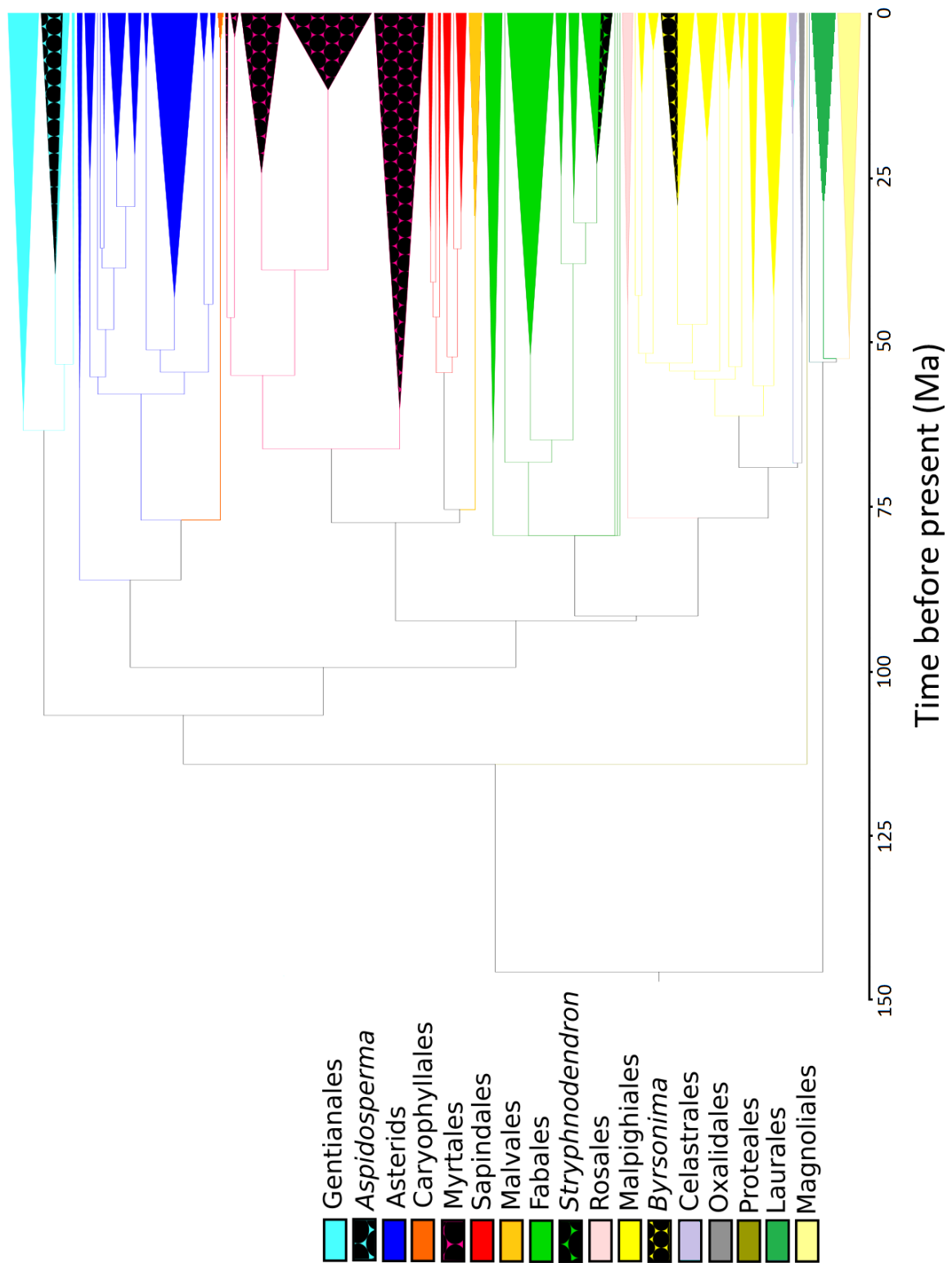
Figure 4: Clades diversification obtained from Nodesig analysis. Bayesian dated phylogenetic tree showing clades with overrepresented of 922 shurbs-tree species occurring in rocky savannas and savannas habitat types. In bold with colored triangles, clades that were overrepresented in rocky savannas: *Aspidosperma*, Myrtales, *Stryphnodendron* and *Byrsonima*.

Table 7- Taxonomic and phylogenetic beta diversities (Sørensen and PhyloSor dissimilarity indexes) between rocky savanna and savannas.

Taxonomic Beta diversity	Sørensen	Turnover	Nestedness	p
	Savannas			
Rocky Savannas	0.684	35.27%	64.73%	
Phylogenetic beta diversity	**Phylosor**			
	Savannas			
Rocky savannas	0.427	21.03%	78.97%	p=0.001

Table 8: Taxonomic beta diversity (Sørensen dissimilarity index) among pairs of local communities: rocky savanna and savanna.

Taxonomic beta diversity	Sørensen		
Rocky savannas communities	Paired local communities of savannas	**Turnover**	**Nestedness**
Pirenópolis	0.496	59.86%	40.42%
Caldas Novas	0.466	89.17%	10.83%
Cristalina	0.406	97.85%	2.15%
Mineiros	0.370	90.12%	9.88%
Palmas	0.410	81.33%	18.67%
Jaraguá	0.244	91.97%	8.03%
Mara Rosa	0.358	79.10%	20.90%
Nazário	0.350	84.55%	15.45%
Nova Xavantina	0.353	85.45%	14.55%
Piranhas	0.450	88.98%	11.02%
Cavalcante	0.479	95.35%	4.65%
Natividade	0.556	88.24%	11.76%
Serra Dourada	0.480	72.33%	27.67%
Alto Paraíso	0.558	99.29%	0.71%

Table 9: Phylogenetic beta diversity (Phylosor dissimilarity index) among pairs of local communities: rocky savanna community and savanna.

Phylogenetic diversity Rocky savannas communities	Phylosor Paired local communities of savannas	Turnover	Nestedness	p
Pirenópolis	0.283	43.34%	56.66%	0.001
Caldas Novas	0.235	85.46%	14.54%	0.001
Cristalina	0.254	94.40%	5.60%	0.001
Mineiros	0.182	90.39%	9.61%	0.001
Palmas	0.202	61.66%	38.34%	0.001
Jaraguá	0.176	73.42%	26.58%	0.001
Mara Rosa	0.193	64.24%	35.76%	0.001
Nazário	0.201	92.97%	7.03%	0.001
Nova Xavantina	0.188	74.57%	25.43%	0.001
Piranhas	0.290	94.85%	5.15%	0.001
Cavalcante	0.236	88.28%	11.72%	0.001
Natividade	0.345	78.52%	21.48%	0.036
Serra Dourada	0.267	56.81%	43.19%	0.001
Alto Paraíso	0.323	80.67%	19.33%	0.010

Discussion

Rocky savannas and savannas- biome scale: Deep divergences, "recent" mixing of lineages and similar diversification patterns

Deep divergences (i.e. older) in phylogenetic tree evinced by NRI, suggest that rocky savannas are centres of diversification within Cerrado biome. Indeed, high rate of diversification is represented by low distances among closely related species (Gerhold et al., 2015), as observed for rocky savannas. In more restricted spatial scales, such as at the habitats within a single biome, centres of recent diversification might result in phylogenetic clustering of co-occurring species (Pennington et al., 2004; 2006). On the other hand, the lack of phylogenetic structure when considered more recent divergences patterns, evinced by NTI value, indicates evolutionary differences between rocky savannas and savannas, probably in whole clades and not only in specific lineages. Indeed, the phylogenetic similarity of terminal taxa between rocky savannas and savannas was high (low patterns of lineages turnover between rocky savannas and savannas) suggesting recent mixing of lineages between these habitat types.

The rocky savannas are isolated mainly in highlands of Central Brazil, such as Chapada dos Veadeiros, Serra dos Pireneus, Serra Dourada and Serra da Natividade (Figure 2), which may favour the high differentiation of lineages with typical geographically adjacent savannas. However, the cooler and drier climate in Pleistocene glacial cycles may have allowed expansion of highland vegetation, such as the rocky savannas of central Brazil, to lower altitudes (Fairbridge, 1979; Simon & Proença, 2000; Collevatti et al., 2009, 2013). With the warmer and moist conditions of interglacial periods, savannas expanded fragmenting highland vegetation (Simon & Proença, 2000), such as rocky savannas. Thus, the cycles of expansion and retraction of rocky savannas and savannas due to Quaternary climate changes might have connected the vegetation and hence, allowed the mixing of "recent" lineages between them. These

findings are consistent with the lack of recent divergences between rocky savannas and savannas. Moreover, the current interconnected distribution of rocky savannas and savannas favors that recent lineages remain phylogenetically intermingled (Hughes et al., 2013). In fact, the lack of phylogenetic structure at local scales (NRI and NTI), confirms that rocky savannas communities are not phylogenetically isolated.

In addition, rocky savanna and savanna assemblages had similar diversification ages and shared relatively similar speciation patterns through time (Figure 3), suggesting that these specific habitats from Cerrado biome had similar origin and exhibited low difference in speciation rates through time. However, rocky savannas had a higher increasing in speciation rate than savannas at ~50Ma, long before mixing of lineages in Quaternary. These findings are consistent with the divergence deep in the past between both habitat types, which may explain the phylogenetic clustering of rocky savannas when measured across the whole depth of the phylogeny (NRI).

The increase of diversification rate in rocky savannas at ~50Ma coincides with the start of Myrtales clade diversification, which was overrepresented in these habitat type (Figure 4). We believe that overrepresentation of Myrtle clade may be attributed mainly to high diversity of Melastomataceae in rocky savannas. Highlands of Central Brazil are centers of diversity of Melastomataceae family (Santos et al., 2012b). On the one hand, Melastomataceae seems to be favoured in rocky environments from Cerrado, mainly the species-rich genera *Miconia, Tibouchina* and *Trembleya* (Romero & Martins, 2002; Lenza et al., 2011; Marachipes et al., 2012). On the other hand, *Byrsonima*, Apocynaceae (Aspidosperma clade) and others species-rich families of Myrtales clade as Myrtaceae and Vochysiaceae are widely distributed and overrepresented across Cerrado biome (Ratter et al., 2003).

Regional scale and local scale: rocky savannas and savannas are phylogenetically intermingling

The similar (NRI) and random patterns (NTI) of phylogenetic structure for rocky savannas and savannas assemblages within phytogeographical regions (*sensu* Ratter et al., 2003) and the lack of phylogenetic structure at local scales (NRI and NTI), reinforce the idea of mixing of lineages as well as dispersion events between these assemblages due to geographical proximity. The mixing of lineages between both habitats through time may have influenced the formation of regional lineages pools (phytogeographicals pools). Species composition in contemporary assemblages in both habitat types might correspond to lineage-pool of these phytogeographical regions, which associated with current dispersion events might lead to the similar patterns of phylogenetic structure.

Taxonomic and phylogenetic beta diversities: taxonomically different but phylogenetically intermingled

The centres of endemism and habitat-specialist species within rocky savannas (Simon & Proença, 2000; Pinto et al., 2009; Lenza et al., 2011; Lemos et al., 2013), led to high taxonomic dissimilarity between rocky savannas and savannas (biome scale). On the one hand, the high habitat heterogeneity in Cerrado biome may produce assemblages restricted to specific habitats types, which may result in high taxonomic beta diversity between specific habitats types within this biome (Bridgewater et al., 2004; Ratter et al., 2006; Souza-Neto et al., 2016). This is especially due to the environmental differences among habitats types and different physiological requirements of species (Oliveira-Filho & Ratter, 2002). However, the Cerrado flora is also characterized by species that occur in nearly all habitats in the Cerrado biome (Ratter et al., 2006), which may led to which may led to high taxonomic nestedness component, as observed at biome scale (see also Souza-Neto et al., 2016). However,

the high values of both taxonomic and phylogenetic turnover components in local scale corroborate the view of centres of endemism for some clade in rocky savannas. Besides, rocky savannas are considered as floristic refuges at local scale, due to the current human transformation of savannas (see Mews et al., 2014). Thus, the high observed turnover components at local scale may also be the outcome of the recent anthropic disturbance in savannas, highlighting the importance of rocky savannas conservation (Pinto et al., 2009; Lenza et al., 2011; Santos et al., 2012; Mews et al., 2014b). Although the higher phylogenetic turnover components in local scale, the low phylogenetic dissimilarity between rocky savannas and savannas local communities is consistent with our findings of the lack of phylogenetic structure at local scales, reinforcing that in general those communities are phylogenetically intermingled with some lineages restrict to rocky savannas (turnover component).

In biome scale, rocky savannas and savannas may have different tree and shrub species but, many species are from the same lineages. The higher taxonomic dissimilarity than phylogenetic dissimilarity indicates that rocky savannas and savannas have similar evolutionary history due to the recent mixing of lineages between them, as discussed above. Furthermore, the recent vegetation connection between rocky savannas restricted to highlands and savannas suggest the absence of enough time to evolve many novel lineages in each specific habitat, resulting in the low observed lineage turnover at biome scale.

Conclusion

Overall, our results show that rocky savannas and savannas share very similar evolutionary history and are recently phylogenetically intermingled at regional and local scales, as result of recent mixing of lineages and their current inter-digitated distribution

in Cerrado (Hughes et al., 2013). Deeper divergences between these two assemblages may be the outcome of ancient higher speciation rate in rocky savannas than savannas, due a possible isolation of rocky savanna assemblage in highlands. However, climatic changes in quaternary allow the connection of these two assemblages. Nevertheless, this study showed that evaluate origin and diversification process within specific habitats types of a single biome, can be the first step to deeper understanding diversity pattern in species-rich biomes.

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CAPÍTULO II

When the same is not the same: intraspecific trait variation reveals different ecological plant strategies in contrasting habitats

Introduction

Plants are among the most plastic organisms because, given their sessile nature, they should be capable to cope with the environment in which they have been dispersed (Fridley & Grime, 2010). Intraspecific variation may be the result of genetic factors such as genetic drift and spatially varying selection, which causes heritable differentiation. Spatial structure on environmental pressures may result in local adaptive changes or phenotypic plasticity (Mayr, 1963; Endler, 1977). Phenotypic differences among individuals of same species play a key role in determining population distribution patterns across environmental gradients because they allow species to adapt across heterogeneous and variable environments within their range and even expand it (see Valadares et al., 2014 and references within). Therefore, to improve the acquaintance of mechanisms that govern the structure of higher organizational levels, it is firstly essential understanding the importance of population performance (McGill et al., 2006; Cianciaruso et al., 2009; Siefert et al., 2015).

Several ecological strategies that can be understood via functional traits are well documented for terrestrial plants (Grime, 1977; Westoby, 1998; Adler et al., 2014). Adult maximum height and leaf traits have been widely exploited to access the variation in plant ecological strategies mainly due to their ecological significance (Westoby et al., 2002) and data availability (Ackerly, 2009). Traits values inherited through evolution define the capacity of species to survive in a specific environment (Graham et al., 2009) and strongly influences individual performance (McGill et al., 2006; Violle et al., 2007). Evaluating differences in functional traits at different habitat types allows the understanding of the underlying mechanisms of trait–environment relationships (Ackerly, 2004) and resulting adaptive trade-offs between traits (Westoby et al., 2002).

Abiotic factors such as topography, elevation, water availability, depth and soil fertility play a key role in determining the spatial distribution patterns of functional traits of individuals in plants (Ackerly et al., 2004; Ackerly & Cornwell, 2007). In savannas, which are highly heterogeneous environments, the presence of different edaphic patterns associated with periodic occurrence of fire (Coutinho et al., 1990) constantly changing across space, may act as environmental filters (Goodland, 1971). Therefore, differences in soil properties and seasonal fire may determine different ecological strategies at different habitat types and consequently different distribution patterns of population functional traits.

The Cerrado, which is the richest savanna region in world (Silva & Bates, 2002; Silva et al., 2006) is notable for its diversity of vegetation types with forest, savanna and grassland formations occurring together in a natural mosaic landscape (Oliveira-Filho & Ratter, 2002). The Cerrado domain bears the widest area of savanna in South America distributed mainly in Central Brazil (Furley, 1999). The savannas occur over nutrient poor soils, mainly with low concentration of nitrogen and phosphorus (Bustamante et al., 2004). It is a fire-prone environment, wherein the fire plays a key role in structure and function of plants communities (Bustamante et al., 2004). It is therefore an interesting region to explore functional variation within plant species, even at small spatial scales. The seasonal savanna woodland (*cerrado sensu stricto*, in Portuguese) is usually the dominant vegetation of the Cerrado landscape (Silberbauer-Gottsberger & Eiten, 1987), which occur over well drained and acid soils, with low availability of nutrients and a medium to low level of organic matter (Haridasan, 2008). Associated with the savanna woodland, a particular vegetation community occurs, restricted to mountains hills (Ribeiro & Walter, 2008), the rocky savannas (*cerrado rupestre*, in Portuguese). Although being associated with savanna woodlands, the rocky savannas

present unshared environmental features. Rocky savannas occur usually at higher altitudes over shallow and nutrient poor rocky soils (Furley & Ratter, 1988). It differs from close savanna woodlands in micro climate and soil water availability (higher at savanna woodland than in rocky savannas) as well as the intensity and frequency of fire (higher intensity and frequency of fire in savanna woodlands than in rocky savannas). The difference in frequency of fire between the two habitat types occurs due to the higher dominance of flammable C4 grasses in savanna woodlands and due to the outcrops that are safe sites for shrubs-trees in fire-prone environments (Carlucci et al., 2011).

To better understand the role of abiotic characteristics in determining different patterns of ecological strategy and use of resources, in this study we investigate how functional traits are distributed in different habitats types at individual level, in fine spatial scale. Specifically, we addressed whether different patterns of ecological strategies and use of resource cause variation in functional traits between individuals from rocky savanna and savanna woodland. For this, we measured functional traits that are related to environmental features, resource use strategy and fire response in both habitat types (Table 1). Our hypothesis and predictions related to traits we measured are summarized in Table 1.

Table 1 - Hypotheses and their predictions about the ecological strategies in woody species of savanna woodland and rocky savanna.

Ecological Strategies	Hypothesis	Predictions
Defense against fire	H1: Defense against fire will be higher in savanna woodland individuals than rocky savanna individuals due lower frequency of fire in rocky savanna.	H1: Rocky savanna individuals will have lower bark thickness.
Water use efficiency and resistance to lower water availability	H2: Water use efficiency and resistance to lower water availability will be higher in rocky savanna individuals, due the shallow soils and lower moisture availability of rocky savanna.	H2: Rocky savanna individuals will have lower specific leaf area and higher leaf thickness and dry leaf mass. H2: Rocky savanna individuals will have higher leaf carbon concentration and stem specific density.
Competitive vigour and growth potential	H3: Competitive vigour and growth potential will be higher in savanna woodland individuals, due to the deeper soils and higher soil nutrient availability of nutrients than in rocky savanna.	H3: Rocky savanna individuals will have lower maximum height than savanna woodland individuals. H3: Rocky savanna individuals will have higher stem specific density due the low relative growth rate.
Response to soil resource	H4: Response to soil resource will be lower in rocky savanna individuals, due to the nutrient poor rocky soils in rocky savanna habitats.	H4: Rocky savanna individuals will have lower leaf nutrient concentrations than savanna woodland individuals.

Material and Methods

Study area

We carried out this study in two locations with nearby rocky savanna and savanna woodland pairs. In the first, the rocky savanna was located at 340m altitude at Bacaba

Park (14°42′-47,4″S,52°-21′04,2″W) and the savanna woodland was at 324m altitude (14°42′-27,3″S,52°-21′06,0″W). In the second sampled location the rocky savanna occurred at 380m of altitude (13°00′-09,6″S,51°-45′09,9″W) and the savanna woodland at 320m (12°49′-05,1″S,51°46′11,4″W). Both locations are under a seasonal climate that exhibit a well-defined dry (May to September) and wet (November to March) seasons (Maracahipes et al., 2011).

Sampling

We selected 62 shrub and tree species pairs belonging to 28 botanical families for our study. Pairs of species were constituted by individuals from savanna woodland and rocky savanna (Table 2). For each species pair, we measured 10 functional traits (Table 3), closely related with the ecological strategies under investigation. We sampled up to 10 individuals from each species, with a stem circumference greater than 5 cm at soil level in 10 plots of 20x20m in each habitat type (savanna woodland and rocky savanna), in both localities. We identified the species in the field, but we collected exsiccates for comparison with those available in the Herbarium NX (Nova Xavantina, Federal University of Mato Grosso). We checked for synonymies using the List of Brazilian Flora (2015).

We followed the methods presented in Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013) to sample and measure all functional traits. For each ecological strategy we selected key functional traits (Table 3), but some traits are related to more than one strategy.

Defense against fire

To evaluate defense against fire we measured bark thickness (Table 3). For trees exposed to burning, bark thickness play a key role in defense against fire because, it protects vital tissues against high temperatures (Cornelissen et al., 2003; Paine et al., 2010; Pausas, 2015). We estimated bark thicknesses by removing a bark sample and we measured its thickness with a digital caliper.

Water use efficiency and resistance to lower water availability

To address the water use efficiency question, we used specific leaf area (SLA), leaf thickness, dry leaf mass, and leaf carbon concentration (Table 3). These traits are considered good traits to identify ecological strategies for water use efficiency (Wright et al., 2001; Ackerly, 2004). We collected 15 expanded leaves of individuals belonging to the species previously chosen in each plot. Then, 3 to 5 leaves of each individual of each environment were scanned to calculate leaf area (cm²) and oven dried (during 48h at 60°C). After drying, we calculate dry leaf mass. SLA (cm² g-1) was obtained by dividing leaf area by leaf dry mass. We measured leaf thickness (mm) by taking the average thickness of 3 to 5 leaves with a digital caliper. Leaf carbon concentration was obtained analysing 5 or more dry leaves for each individual. Analyses were performed by *Análise de Solo, Tecido Vegetal e Fertilizante* (Federal University of Viçosa) laboratory facility.

Competitive vigor and growth potential

We used maximum height and stem specific density to address competitive vigor and growth potential strategies between habitat types (Westoby, 1998; Reich, 2000; Cornelissen et al., 2003) (Table 3). For this, we measured plant height in the field by choosing the tallest individual of the species within each plot (i.e. the maximum height

for the species) in each habitat type. To measure woody density, we collected a woody cylindrical sample of the plant and after we removed all the bark, and measured its diameter and length to estimate the volume of the sample. We obtained woody density by dividing the dry mass of the sample by its fresh volume.

Response to soil resource

To evaluate the response to soil resources, we measured leaf nutrient concentrations (Cornelissen et al., 2003; Hoffman et al., 2005; Rossato et al., 2013). Specifically, we used leaf nitrogen, potassium and phosphorus concentrations (Table 3). Sampling and analyses followed the same protocol used to calculate leaf C.

Data analyses

To evaluate trait variation between indivuduals occurring in both rocky savanna and savanna habitats we used a paired t-test. We performed this test in computational statistic environment R (R Development Core Team, 2015).

Table 2 – The 62 species included in this study with populations occurring in both rocky savanna and savanna habitats.

Family	Species
Anacardiaceae	*Anacardium occideantale*
	Astronium fraxinifolium
Annonaceae	*Annona coriacea*
	Xylopia aromatic
Apocynaceae	*Aspidosperma macrocarpon*
	Aspidosperma tomentosum
	Hancornia speciosa
	Himathanthus obovatus
Bignoniaceae	*Tabebuia aurea*
Calophyllaceae	*Kielmeyera coriacea*
	Kielmeyera rubriflora
Celastraceae	*Salacia crassifolia*
Chrysobalanaceae	*Hirtella glandulosa*

Combretaceae	*Buchenavia tomentosa*
Connaraceae	*Connarus suberosus*
Dilleniaceae	*Curatella Americana*
	Davilla elliptica
Erythroxylaceae	*Erythroxylum suberosum*
	Erythroxylum tortuosum
Euphorbiaceae	*Maprounea guianensis*
Fabaceae	*Andira cuiabensis*
	Bowdichia virgilioides
	Copaifera langsdorffii
	Dalbergia miscolobium
	Dipteryx alata
	Hymenaea stigonocarpa
	Leptolobium dasycarpum
	Luetzelburgia praecox
	Mimosa laticifera
	Plathymenia reticulate
	Pterodon pubescens
	Tachigali aurea
	Vatairea macrocarpa
Icacinaceae	*Emmotum nitens*
Lauraceae	*Mezilaurus crassiramea*
Lythraceae	*Lafoensia pacari*
Malpighiaceae	*Byrsonima coccolobifolia*
	Byrsonima pachyphylla
	Heteropterys byrsonimifolia
Malvaceae	*Eriotheca gracilipes*
	Pseudobombax longiflorum
Melastomataceae	*Mouriri elliptica*
	Mouriri pusa
Myrtaceae	*Eugenia aurata*
	Eugenia gemmiflora
	Eugenia punicifolia
	Myrcia lanuginose
	Myrcia splandens
Nyctaginaceae	*Guapira graciliflora*
Ochnaceae	*Ouratea hexasperma*
	Ouratea spectabilis
Olacaceae	*Heisteria ovate*
Opiliaceae	*Agonandra brasiliensis*
Rubiaceae	*Cordiera sessilis*
	Tocoyena Formosa
Sapindaceae	*Magonia pubescens*
Sapotaceae	*Pouteria ramiflora*
Vochysiaceae	*Qualea grandiflora*
	Qualea multiflora

Qualea parviflora
Salvertia convallariodora
Vochysia rufa

Code	Trait	Main functional role *
BT	Bark Thickness (mm)	Protection of vital tissue against high temperatures associated with fire
SLA	Specific Leaf Area (cm^2 g-1)	Maximum photosynthetic rate, potential growth rate and related the environment disturbance.
LT	Leaf Thickness (mm)	Resistance to lower water availability, nutrient poor soil
DLM	Dry Leaf Mass (g)	Resistance to physical hazards (e.g. herbivory, wind, hail)
MH	Maximum Height (cm)	Access to light and competitive vigour and is related the environment disturbance level.
SSD	Stem Specific Density (mg mm–3)	Stability, defense, architecture, growth potential and hydraulic capacity
C Leaf	Leaf carbon (C) concentration (%)	Water use efficiency, potential photosynthetic rate, architecture and potential growth.
N Leaf	Leaf nitrogen (N) concentration (g/kg (%))	Response to soil resources
P Leaf	Leaf phosphorous (P) concentration (g/kg (%))	Response to soil resources
K Leaf	Leaf potassium (K) concentration (g/kg (%))	Response to soil resources

*Adapted from Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013).

Results

Rocky savanna and savanna woodland individuals did not differ in bark thickness (Table 4). Individuals from rocky savanna had values of specific leaf area 9.343 lower and leave 0.050 more thick than those individuals occurring in savanna woodlands (Table 4). Leaf dry mass was 0.111 lower in rocky savannas individuals than savanna woodland. Leaf carbon concentration was 2.310 higher in rocky savanna than savanna woodland individuals (Table 4).

Rocky savanna individuals have maximum height about 1.78 lower values of than savanna woodland (Table 4) and stem specific density was just 0.037 lower in rocky savanna individuals (Table 4). We detected contrasting patterns in leaf nutrient concentrations. The leaf nitrogen and potassium concentrations did not differ between both habitats. Leaf phosphorus concentration was 0.020 higher in savanna woodland than in rocky savanna individuals (Table 4).

Table 4 - Result of the paired t-test for the traits measured and their related ecological strategies for two habitat types. **RS-** Rocky savanna and **SW-** savanna woodland. **N**=62, **Diff-** Difference**, Std. DV-** Standard Deviation**.**

Habitat type	Ecological Strategies/traits	Mean	Diff.	Std.Dv.	t	p-value
	Defense against fire					
RS	Bark Thickness (mm)	6.141	0.636	2.999	-1.383	p = 0.171
SW		6.778		4.732		
	Water use efficiency and resistance to lower availability					
RS	Specific Leaf Area (cm2 g-1)	76.741	9.343	19.122	-4.519	p < 0.001
SW		86.085		24.788		
RS	Leaf Thickness (mm)	0.285	0.050	0.069	9.687	p < 0.001
SW		0.234		0.067		
RS	Dry Leaf Mass (g)	1.404	0.111	2.225	-2.287	p.=.0.025
SW		1.516		2.476		
RS	Leaf C concentration (%) CR	55.833	2.310	1.230	18.527	p < 0.001
SW		53.522		0.752		
	Competitive vigour and growth potential					
RS	Maximum Height (cm)	522.419	119.194	171.116	-5.445	p < 0.001
SW		641.612		214.951		
RS	Stem-Specific Density (mg mm–3)	0.512	0.037	0.097	-5.35	p < 0.001
SW		0.549		0.081		
	Response to soil resource					
RS	Leaf N concentration (g/kg (%))	1.754	0.024	0.441	0.524	0.601
SW		1.729		0.414		
RS	Leaf P concentration (g/kg (%))	0.083	0.020	0.031	-6.459	p < 0.001
SW		0.103		0.025		
RS	Leaf K concentration (g/kg (%))	0.574	0.007	0.295	-0.192	0.847
SW		0.581		0.204		

Discussion

Overall, our results support that the individuals occurring in different habitat types have plastic responses that are reflected in the intraspecific level variation in their functional traits. This indicates that functional traits may respond to different patterns of topography, slope, soil moisture availability and soil fertility in the Cerrado biome. Nevertheless, some strategies evaluated here showed no difference between individuals from savanna woodland and rocky savanna (i.e., defense against fire and response to soil resources).

Defense against fire

Our findings did not support the hypothesis that defense against fire could be higher in savanna woodland than rocky savanna individuals. We found a similar response to the defense against fire (bark thickness), despite differences in fire frequency in these two habitats (Ribeiro & Walter, 2008). Nevertheless, this result can be explained by the *in situ* diversification of fire adaptations in the Cerrado biome (Simon et al., 2009, Simon & Pennington, 2012) such as thick bark. A range of functional traits are similar among individuals co-occurring in areas with low fire frequencies in Cerrado (Cianciaruso et al., 2012). Overall, species living in habitats where fire regimes are rare (e.g., forests) exhibit thinner bark than savannas congeners species (Hoffmann et al., 2003; Simon & Pennington, 2012; Lawes et al., 2013). However, fire is an abiotic factor shared between habitat types here evaluated, so, the investment in protection of cambium heating is critical to survival of plants in all Cerrado biome. Although bark thickness is the best single descriptor of defense against fire, other important functions are also addressed to bark thickness, such as reduction of water loss, defense against pests, pathogens and mechanical injury (Cornelissen et al.,

2003; Paine et al., 2010; Pausas, 2015). On the one hand, the lack of difference of bark thickness may be reflecting other ecological strategies, such as pathogen defense and water loss, and not only fire frequencies. On the other hand, savanna individuals have other adaptations against fire, such as protected gems, rooting depth, and regeneration organs that allow them to sprout after fire occurrence (Coutinho, 1990; Paine et al., 2010; Simon & Pennington, 2012). These adaptations were not measured here.

Water use efficiency and resistance to lower water availability

The lower SLA, higher leaf thickness and leaf carbon concentration in rocky savanna individuals are possibly related to a high investment in structural tissues, which allow these plants to maintain leaf turgor even in an environment with low soil water availability (Niinemets, 2001; Hoffmann et al., 2005). Lower SLA is related to greater stress tolerance, and is commonly found in individuals occurring under dry and nutrient poor soils (Westoby, 1998; Cornelissen et al., 2003;), leading to a longer leaf life span and increasing water and nutrient use efficiency (Reich et al., 1992; but see Cianciaruso et al., 2013). Our result is similar to Hoffmann et al. (2005), who found higher C values in savanna species compared to congeneric forest species, indicating higher water use efficiency in environment with lower water availability.

Thicker leaves are advantageous strategy for plant survivorship in restrictive habitat such as rocky savanna, because they are more resistant to lower water availability and nutrient poor soils and because they generally have longer life span (Westoby et al., 2002; Cornelissen et al., 2003; but see Cianciaruso et al., 2013). Longer leaf life span decreases continued investment in new leaves, resulting in greater tolerance to stressful conditions. Thicker leaves also play a key role in protection of overheating (Rozendaal et al., 2006) by high irradiances. Indeed, high irradiances are a factor present in both environments. However, in rocky savanna the investment in

thicker leaves is fundamental, because besides having lower tree canopy, the sun reflected on the rocks can cause overheating on the abaxial surface of the leaves.

Higher leaf dry leaf mass is related to regulation of water loss through leaves (Poorter et al., 2009) increasing the water use efficiency. Here, the lower leaf dry mass showed by rocky savanna individuals is possibly related to the poor availability of others nutrients needed to actually increase dry matter mass such as nitrogen, phosphorus and potassium. On the other hand, the lower specific leaf area and higher leaf thickness in rocky savanna individuals could also minimize loss of water through leaves, counteracting the lower leaf dry mass. Indeed, the regulation of water loss through leaves can be expressed by leaf functional traits (Ackerly, 2004).

Water use efficiency is also positively correlated with leaf nitrogen concentration (Hoffman et al., 2005). Higher concentrations of N and P on drier habitats are related to greater photosynthetic efficiency combined with lower stomatal conductance, resulting in greater water-use efficiency (Wright et al., 2001; Hoffman et al., 2005). However, here we did not find differences in leaf N concentration between the two habitat types and leaf P concentration was lower in rocky savanna individuals. The lack of differences in leaf concentration of N and lower P concentration in rocky savanna individuals may be due to the low nutrient availability in soils of both habitats. Therefore, the accumulation of high concentration of these nutrients in the leaves could be an unfeasible strategy.

Competitive vigour and growth potential

It has been widely recognized that height reflects the major axis of trade-off between competitive vigor and construction costs (Westoby, 1998). In this way, the significantly lower height in rocky savanna individuals is in agreement with our

prediction of higher competitive vigor in savanna woodland individuals. Shorter stature could be an advantageous strategy in rocky savanna, because the survival of plants with a high height might be limited in environment with shallow and nutrient poor soils (Westoby, 1998) . Additionally, taking in account the lower water availability in rocky savanna, the lower height in rocky savanna individuals may be an "economic strategy".

Although stem density is a conserved trait within species (Chave et al., 2006; Swenson & Enquist, 2007; Fajardo & Piper, 2011) here we found differences between individuals from the two habitats, with rocky savanna individuals showing lower stem specific density. Stem specific density reflects a relevant trade-off between relative grow rate and defense against abiotic factors and herbivores (Cornelissen et al., 2003). Low relative growth rate is also related with high SSD (Cornelissen et al., 2003), thus, we expected that rocky savanna individuals with slow growth rate had higher SSD than savanna woodland individuals, corroborating our findings of height. We hypothesize that shallow and nutrient poor rocky savanna soils could not provide sufficient resources for plants to invest in high stem density values. Firstly, we expected that pattern of lower stem specific density in rocky savanna individuals, could be a response to lower availability of water in rocky savanna. Indeed, soil moisture is an important environmental factor that affects woody density (Fajardo & Piper, 2011). However, previous studies showed an opposite pattern, with higher SSD been considered an adaptation to lower water availability (Hacke et al, 2001; Fajardo & Piper, 2011).

Additionally, higher stem specific density found in savanna woodland individuals could be related to defense to physical damage caused by abiotic factors (e.g., fire) that are more frequent in savanna woodlands than in rocky savanna individuals. However, savanna woodland shows no substantial water deficit during the prolonged dry season

(Hoffmann et al., 2005). Furthermore, this observed pattern is likely to be a consequence of the trade-off between traits and resource availability.

Response to soil resources

Leaf nutrient concentration is a highly plastic response to resource availability at intraspecific level (Siefert et al., 2015). However, here we found difference leaf nutrient concentration just for one of the three macronutrients analyzed. Leaf phosphorus concentration was higher in savanna woodland individuals, which corroborates our prediction. Whereas nitrogen and potassium that are commonly referred to limit the vegetation growth in all Cerrado biome did not exhibit difference between habitat types (Bustamante et al., 2004; Haridasan, 2008). The lack of difference in leaf N concentration may be due to the other sources of N than the soil. The interplay between N fixation by atmosphere and biotic interactions (e.g, symbioses with mycorrhizal fungi) could offset the lower nutrients availability in soils of rocky savanna. These mechanisms could also confound the interpretation of the response of plants to soil nitrogen resource (Bustamante et al., 2004).

These contrasting results may also reflect local adaptation and plasticity to nutrient availability in soils that includes the lower SLA, which is considered a mechanism of nutrient conservation (Reich et al., 1992). Strategies of litter accumulation could also decrease the disparity in soil nutrient concentrations (Hoffmann et al., 2005). As nitrogen and potassium are abundant components in plant tissue decomposition, the litter accumulation in soil may ensure an enough supply of these macronutrients. Additionally, the shortfall deeper knowledge about mineral nutrition of native plants of savannas and their adaptations hinders the most accurate interpretations of the present results (Haridasan, 2008).

Conclusion

Our findings show different ecological strategies at individual level between savanna woodland and rocky savanna, and this could be an advantageous mechanism in highly heterogeneous environment such as the Cerrado biome. We believe that the interaction between functional traits and habitat type at intraspecific level has a central role in patterns of diversity and distribution in savannas ensuring the survival of species in restrictive environments such as rocky savannas. Nonetheless, more investigations regarding the relationship between defense against fire and response to soil resource and functional traits are necessary to better understanding the role of soil nutrients and fire frequency in these specific habitat types and whether these differences are so significant.

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Conclusão Geral

Ao final desta dissertação, concluímos que cerrado rupestre e cerrado *sensu stricto* compartilham uma história evolutiva muito semelhante. No entanto, estes apresentam divergências filogenéticas, de modo geral, profundas na filogenia. Além disso, o Cerrado rupestre apresenta clados superabundantes enquanto o cerrado sensu stricto não. Evidenciamos também que as espécies que ocorrem tanto em cerrado rupestre quanto em cerrado *sensu stricto* adjacente, apresentam diferentes estratégias ecológicas em respostas a mudanças nas características ambientais. Ou seja, as populações "apresentam respostas plásticas", refletida em características funcionais, de acordo com o ambiente o qual ocorrem (cerrado rupestre ou cerrado *sensu stricto*).