Environmental severity promotes phylogenetic clustering in *campo rupestre* vegetation

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ABSTRACT

The stress-dominance hypothesis postulates that the importance of competition in plant communities declines with increasing environmental stress while the importance of environmental filters increases. To test this hypothesis for *campo rupestre* vegetation, we analyzed phylogenetic diversity and community structure of angiosperm communities at two study sites within the Itacolomi State Park, Minas Gerais, Brazil. Plots representing more favorable habitats, such as those with a higher percentage of rocky outcrops that might permit the tapping of deeper water and nutrient resources as well as higher contents of clay and loam thereby increasing water and nutrient availability, show higher phylogenetic diversity and therefore lower phylogenetic clustering than plots with more sever habitats. This observation is consistent with the stress-dominance hypothesis if we assume ecological niches to be conserved within evolutionary niches. However, more comprehensive studies including tests for phylogenetic signal of ecological niches are necessary before generalizations for larger regions may be carried out.

Keywords: angiosperm community composition, environmental filtering, Faith's Index of phylogenetic diversity, Mean Nearest Taxon Index, Mean Pairwise Distance, Nearest Taxon Index, Net Relatedness Index, phylogenetic community analysis

Introduction

Different types of neotropical rocky field vegetation displace tropical forests and savannas above certain altitudes (Alves & Kolbek 2010). *Campo rupestre* is a species-rich and diverse vegetation found on quartzite and sandstone outcrops or white sand soils in the highlands of southeastern Brazil (Giulietti *et al.* 1987; Conceição & Giulietti 2002; Caiafa & Silva 2005; Jacobi *et al.* 2008; Messias *et al.* 2011; Gastauer *et al.* 2012). *Campos rupestres* are exposed to intense solar radiation, high evapotranspiration, and large daily temperature variation; their soils retain little water and provide low nutrient availability (Jacobi *et al.* 2007). Although this diverse ecosystem is endangered by various man-made pressures (Pirani *et al.* 2003), little is known about the mechanisms that determine richness, taxonomic or phylogenetic diversity of these ecosystems (Mourão & Stehmann 2007; Messias *et al.* 2011; Gastauer *et al.* 2012).

Topological variations in *campo rupestre* ecosystems form a small-scale relief of cracks, pontoons, valleys, rocky outcrops and depressions, each with a particular microclimate. Additionally, differences in soil composition, ranging from pure sand to completely organic layers (Benites *et al.* 2003), contribute to a high amount of environmental heterogeneity, resulting in a diversified mosaic of different environments (Scolforo & Carvalho 2006). The stress-dominance hypothesis (Swenson & Enquist 2009) postulates that the importance of competition and further density dependent factors in plant communities declines with increasing environmental stress (Grime 1977) while the importance of environmental filters increases. Environmental filters are abiotic constraints that restrict the presence of organisms within a community to individuals possessing certain morphological, physiological or phenological feature values (Simberloff 1970; Kraft *et al.* 2015). Competitive exclusion and further density dependent factors, in contrast, limit the coexistence of ecologically similar species with a large niche overlap (Elton 1927; Hutchinson 1957).

If we assume the ecological niche to be conserved within evolutionary lineages, closely related species are ecologically more similar. Under this assumption, environmental filters cause phylogenetic clustering, promoting the co-existence of closely related species within communities (Webb *et al.* 2002; Hardy 2008; Cianciaruso *et al.* 2009; Silva *et al.* 2011), while competition and further density dependent factors cause phylogenetic overdispersion (Harms *et al.* 2001;

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Cavender-Bares *et al.* 2004). Although the assumption of niche conservatism in evolutionary lineages is discussed critically (e.g., Cavender-Bares *et al.* 2009; Kraft & Ackerley 2010), there is evidence that ecological niches show phylogenetic signal (e.g., Davies *et al.* 2004; Díaz *et al.* 2004; Baraloto *et al.* 2012). Therefore, we expect higher phylogenetic clustering where environmental conditions are less favorable for plants, i.e., in areas with higher soil acidity, lower nutrient availability or higher sand content in the soil (Gastauer & Meira-Neto 2014).

The aim of this study is to test if environmental severity reduces phylogenetic diversity and increases phylogenetic clustering in *campo rupestre* vegetation as expected by the stress-dominance hypothesis. For that, we analyzed the phylogenetic diversity and community structure of two study sites located in Itacolomi State Park in the Southern Espinhaço Mountain Range, Minas Gerais, Brazil and correlated them with different environmental variables.

Methods

Study sites

Both study sites are located in Itacolomi State Park in the municipalities of Mariana and Ouro Preto, in the southeastern region of Minas Gerais, Brazil (Fig. 1). Encompassing approximately 7,000 ha, the Itacolomi State Park covers the *Serra do Itacolomi* in the southern part of the Espinhaço Mountain Range that extends northwards until the Brazilian State of Bahia. The region is characterized by Köppen as a Cwb climate, with cold and dry winters as well as hot and rainy summers (Peel *et al.* 2007). The southern part of the Espinhaço Mountain Range in general and Itacolomi

State Park in particular have been highlighted as a local hotspot of biodiversity due to a diverse landscape and the occurrence of many endemic species (Batista *et al.* 2000; Dutra *et al.* 2014).

A mosaic of grassland vegetation, small shrubs and outcrops of quartzite rocks characterizes the study sites Calais (20°25' S and 43°30'W, 1270 m ASL) and Lagoa Seca (20°26'S and 43°29'W, 1600 m ASL). In Calais, sandy soil dominates, while Lagoa Seca is formed by clayey sands (Gastauer *et al.* 2015).

Data collection

In each study site, 15 plots of 10 x 10 m were delimited. The percentage of rocky outcrop was estimated. Soil samples were collected within each plot. From these samples, we analyzed the soil acidity (pH), the concentration of potassium, phosphorus, magnesium, calcium and aluminum, the cation exchange capacity, the saturation of bases and aluminum (see Gastauer *et al.* 2015 for details).

All angiosperm species within those plots were identified (Gastauer *et al.* 2015). Nomenclature and classification follow that of the Missouri Botanical Garden (2015) and were carried out as suggested by Boyle *et al.* (2013).

Phylogenetic community analysis

We defined all species from within this study as the *campo rupestre* metacommunity. Species from this metacommunity were inserted into the megatree R20120829mod.new using the phylomatic function from the Phylocom 4.2 package (Webb & Donoghue 2005). The calibration of the community phylogeny was performed by the BLADJ algorithm using exponentially distributed age estimates of Bell
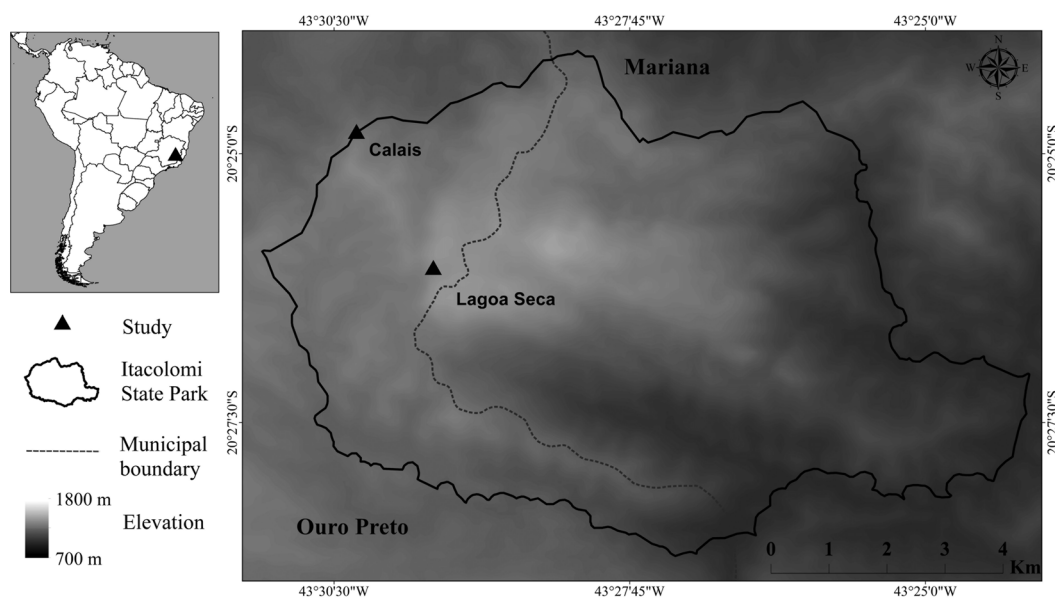

Figure 1. Localization of the study sites in relation to Itacolomi State Park and the South American continent.

et al. (2010) with the BLADJ algorithm from Phylocom 4.2 (Webb *et al.* 2002), as suggested by Gastauer & Meira-Neto (2015) (Fig. 1 in Supplementary Material).

From this metacommunity, the Faith's Index (FI) of phylogenetic diversity (Faith 1992), the Mean Pairwise Distance (MPD) and the Mean Nearest Taxon Distance (MNTD) (Webb *et al.* 2002) were computed for each plot using the Phylocom 4.2 package. To detect phylogenetic clustering or overdispersion, we calculated the Net Relatedness Index (NRI) and the Nearest Taxon Index (NTI) as the negative standard effective sizes of the MPD and MNTD using the unconstrained null model (Kembel & Hubbell 2006), randomizing the composition of each plot 10,000 times. Values of zero are expected for the NRI and NTI in plots without phylogenetic structure, while positive values of these indices indicate phylogenetic clustering and negative values indicate phylogenetic overdispersion.

Data analysis

We checked normal distribution of phylogenetic diversity (FI, MPD, MNTD) and community structure indices (NRI, NTI) by the Shapiro-Wilk test. To achieve normal distribution, FI, MPD and MNTD were log-transformed using natural logarithm.

Two-tailed t-tests were used to identify the differences between the study sites. To detect whether the phylogenetic community structure differed significantly from zero, we used one-tailed t-tests.

To outline the influence of the environment variables of each plot, i.e., the percentage of rocky outcrops, the soil's content of small particles (i.e., sum of percentage of clay and loam), the acidity (pH), cation exchange capacity as well as aluminium availability, on the phylogenetic diversity and community structure, we built General Linearized Models (GLM) without any type of interactions using the "glm" command (Zuur *et al.* 2009) in the R Environment, version 3.1.0 (R Development Core Team 2014). We choose soil's content of small particles as a proxy for water retention (Saporetti-Junior *et al.* 2012), while pH, cation exchange capacity and the availability of toxic aluminium resume chemical soil properties by strong correlations with available nutrient concentrations (Gastauer *et al.* 2015). To detect the influence of different study sites on phylogenetic diversity and community structure, we added 'site' as a further categorical variable.

We used the dredge function from the "MuMIn" package (Bartón 2014) in the R Environment to test all possible combinations of the variables included in the global models as well as the null model. To determine which combinations of explanatory variables were the most parsimonious, we used an information-theoretic approach based on the Akaike Information Criterion of the Second Order (AICc). The best model was indicated by the lowest AICc value (Burnham *et al.* 2011). Nevertheless, the models that differ by, at most, two counters from the lowest AICc value were considered equally good models. From these models, we defined that one(s) with the lowest number of variables as the most parsimonious.

Phylogenetic resolution

To verify whether the lack of phylogenetic resolution in the phylogenetic hypothesis of our metacommunity influences the outcomes of phylogenetic diversity and community structure, we randomly resolved all polytomies in the phylogeny 1000 times. Each fully resolved phylogeny was calibrated with BLADJ as described above, before the indices FI, MPD, MNTD, NRI and NTI were calculated.

Indices derived from fully resolved phylogenies were correlated with that from the unresolved phylogeny as suggested by Swenson (2009). The closer the coefficients of correlation, as well as the correlations' slopes, are to 1, the smaller the influence from the lack of phylogenetic resolution on the results and their interpretation.

Results

Altogether, we found 156 angiosperm species from 43 families. With 103 angiosperm species, species richness in Calais was higher than in Lagoa Seca (74 species). The phylogenetic diversity in Calais was higher than in Lagoa Seca (Tab. 1). Nevertheless, we detected no difference in the structure of the phylogenetic community between the study sites; the NRI and NTI values indicated phylogenetic clustering for both study sites (Tab. 1).

The best models indicate that the phylogenetic diversity measures FI, MPD and MNTD increased with the percentage of rocky outcrops. MPD and MNTD increased furthermore with the percentage of fine soil content, while FI and MPD were influenced by some differences between the study sites (Tab. 2). Due to the negative standard effective size transformation, the NRI and NTI showed inversed tendencies as MPD and MNTD.

Table 1. Comparison of the phylogenetic diversity and community structure (mean values ± SD) of two *campo rupestre* sites in Itacolomi State Park, southeastern Brazil. P values indicate the significance level of the difference between the study sites according to a two-tailed t test (for logtransformed values of FI, MPD and MNTD). FI is Faith's index, MPD is the Mean Pairwise Distance, MNTD is the Mean Nearest Taxon Distance, NRI is the Net Relatedness Index and NTI is the Nearest Taxon Index. Bold values indicate the NRI and NTI values that differ significantly from zero (p <0.05) according to a one-tailed t-test.

Variable	Calais	Lagoa Seca	P
FI	2186.4 ± 349.6	1797.9 ± 330.0	0.007
MPD	219.1 ± 11.9	207.9 ± 14.7	0.030
MNTD	90.1 ± 13.3	86.2 ± 7.9	0.337
NRI	**0.855 ± 0.502**	**1.078 ± 0.319**	0.157
NTI	**1.149 ± 0.761**	**1.369 ± 0.428**	0.337

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Table 2. Fitting parameters, the Akaike Information Criterion of the Second Order (AICc) and the percentage of explained variance of the best model(s) explaining the phylogenetic diversity and community structure of two *campo rupestre* study sites from Itacolomi State Park, southeastern Brazil. * is $p < 0.05$, ** is $p < 0.01$.

Variable	Intercept	Area	% Rocky outcrops	% Fine soil	Aluminium availability	pH	df	AICc	Explained variance
Log(FI)	7.599	+ **	$3.80 \ 10^{-3}$ **				4	-18.5	42.9
Log(MPD)	5.207		$1.06 \ 10^{-3}$ *	$5.46 \ 10^{-3}$ **			4	-82.0	39.1
	5.359	+ *	$1.42 \ 10^{-3}$ **				4	-81.4	37.9
Log(MNTD)	4.246		$1.84 \ 10^{-3}$ *	$7.78 \ 10^{-3}$			4	-45.7	32.2
	4.425		$2.41 \ 10^{-3}$ **				3	-44.1	21.5
	4.218			$1.04 \ 10^{-2}$ *			3	-43.8	20.7
NRI	1.386	+ *	$-3.28 \ 10^{-2}$ **				4	104.1	
	4.656		$-2.53 \ 10^{-2}$ *	-0.116 *			4	104.6	39.1
NTI	1.229		$-1.85 \ 10^{-2}$ **				3	64.0	30.6

The FI, MPD and NRI derived from unresolved phylogeny correlated well with those derived from the resolved phylogenies; slopes lower than 0.95 or greater than 1.05 found for the MNTD and NTI showed that lacking phylogenetic resolution might over- or underestimate these indices slightly (Tab. 3). Nevertheless, correlation coefficients larger than 0.95 indicated that the indices were predicted with sufficient precision by the unresolved phylogeny.

Discussion

Calais shows higher FI and MPD than Lagoa Seca confirming findings for species richness and taxonomic diversity from previous studies (i.e., Gastauer *et al.* 2012). Although differences between study sites influence phylogenetic diversity measures, these increase furthermore with the percentage of rocky outcrops and/or fine soil content. Phylogenetic clustering decreases in the same direction.

Table 3. Slopes and R^2 values from the regression of the phylogenetic diversity and community structure from the unresolved phylogeny with that from randomly resolved phylogenies. The table entries are mean (minimum … maximum) values from randomly resolving the phylogenies 1000 times.

Variable	z	R^2
FI	1.046 (1.024 … 1.069)	0.996 (0.990 … 1.000)
MPD	1.005 (1.002 … 1.009)	1.000 (0.998 … 1.000)
MNTD	1.111 (1.066 … 1.163)	0.964 (0.913 … 0.990)
NRI	0.982 (0.965 … 1.001)	0.998 (0.995 … 0.999)
NTI	0.954 (0.870 … 1.061)	0.965 (0.926 … 0.991)

Strong correlations between outputs from the resolved and unresolved phylogenies indicate that the lack of phylogenetic resolution influences the results at most slightly.

While we are able to affirm that the lack of phylogenetic resolution has only small impact on the interpretation of our findings, we acknowledge that the size of the metacommunity (currently 156 species only) is inappropriate and might influence the outcomes of NRI and NTI computations. According to a recent census, 520 species from 13 well studied genera or families are already registered in Itacolomi State Park's *campos rupestres*; the overall richness of vascular plants is estimated to 1100 species, the majority of which are angiosperms (Gastauer & Meira-Neto 2013). However, a checklist of all angiosperms from the Itacolomi State Park is not available at present, although it would give further valuable insights in evolutionary aspects of *campo rupestre* community assembly. Increasing the metacommunity beyond *campos rupestres* would furthermore increase our knowledge about the environmental constraints limiting the *campo rupestre* species pool.

Phylogenetic diversity and community structure are related to the environmental variables percentage of rocky outcrops as well as the fine soil content. Within *campo rupestre* vegetation (see, for example, Fig. 2 in Supplementary Material), one might easily recognize that shrubs, small trees or treelets are restricted to rocky outcrops, while gaps between rocky outcrops are covered by gramineous communities (Caiafa & Silva 2005). This observation inspired Jacobi *et al.* (2007) to assume that cracks and cavities in the rocks and their surroundings provide access to deeper water and nutrients, thus reducing the severity of the environment.

The increased content of fine soil provides more nutrients and increases water retention (Saporetti Júnior *et al.* 2012), also alleviating environmental harshness of *campo rupestres.*

The observed relation of increasing phylogenetic diversity as well as decreasing phylogenetic clustering with percentage of rocky outcrops and fine soil content indicates that phylogenetic clustering increases with environmental severity. Where environmental filters are alleviated, we found less phylogenetic clustering, thus confirming our initial hypothesis. These observations are consistent with the stress-dominance hypothesis (Swenson & Enquist 2009; Coyle *et al.* 2014), when we assume ecological niches to be conserved within evolutionary lineages, so that phylogenetically more related species are ecologically more similar.

Many resource-related features in species pools from similar environments such as the Brazilian Cerrado show significant phylogenetic signal (Batalha *et al.* 2011; Baraloto *et al.* 2012; Cianciaruso *et al.* 2012), thus giving confidence to this interpretation. More severe environments select for ecologically more similar and phylogenetically more related species, while the importance of competition reduces, thus increasing phylogenetic clustering.

Although our data are consistent with the stress-dominance hypothesis, further processes may explain observed pattern as well (Johnson & Stinchcombe 2007). Mayfield & Levine (2010) postulated that competition may also lead to phylogenetic clustering, when competitive ability differences show strong phylogenetic signals, independent if niche differences are related to phylogenetic distances or not. In this scenario, superior competitors from Poaceae, Cyperaceae and Xyridaceae families may outcompete eudicot shrubs and treelets in gaps between rocky outcrops or in more sandy soils, thus increasing phylogenetic clustering in harsher environments (Godoy *et al.* 2014).

Therefore, more comprehensive approaches are necessary for more concluding evaluations about the stress-dominance hypothesis in *campo rupestre* vegetation. Future studies should critically challenge the assumption of ecological niche conservation within evolutionary lineages in *campo rupestre* species pool for a better understanding of community assembly processes within this endangered ecosystem.

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