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TREE DIVERSITY IN MINAS GERAIS, BRAZIL

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MARCELA DE CASTRO NUNES SANTOS TERRA

TREE DIVERSITY IN MINAS GERAIS, BRAZIL

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ciências Florestais, para a obtenção do título de Doutora.

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I dedicate this thesis to all Brazilians - the funders of public and high-quality education in Brazil.

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RESUMO

O Estado de Minas Gerais (MG), o quarto maior Estado da Federação, com tamanho comparável ao de países como França e Espanha, abriga grande heterogeneidade ambiental e, consequentemente, grande diversidade arbórea. A presente tese está organizada em três capítulos. O primeiro corresponde à apresentação geral e revisão de literatura sobre as principais questões ecológicas que embasam este trabalho. O segundo e o terceiro capítulos são artigos científicos que abordam a diversidade arbórea do Estado de MG, nos quais foram utilizadas 158 áreas amostrais de vegetação, incluindo diferentes fitofisionomias dos três diferentes domínios vegetacionais encontrados no Estado, a saber: Cerrado, Mata Atlântica e Caatinga. No primeiro artigo, intitulado "*Dominance and Diversity of Trees in the State of Minas Gerais, Brazil*", foram trabalhadas algumas questões básicas, porém negligenciadas, envolvendo diversidade arbórea no Estado de Minas Gerais: Quantas árvores e quantas espécies arbóreas existem no Estado de MG? Quanto foi perdido até agora? A resposta a estas questões foi obtida por meio do protocolo de estimativas baseado na criação de um grid de 6.634 células de 0,1 grau e os estimadores Fisher's alpha e Fisher's log-series. Foram estimados valores de 24,5 x 10^9 árvores e entre 3592 e 3743espécies arbóreas. Além disso, obteve-se que 68,54% e 4,03% foram perdidos, respectivamente, quando comparados à estimativa de número de árvores e espécies. Os resultados permitiram a obtenção de mapas de distribuição-abundância para as espécies. O segundo artigo, intitulado "*Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-Cerrado-Caatinga transition, Brazil*" aborda como gradientes, em características da vegetação como composição de espécies em diferentes níveis taxonômicos, diversidade de espécies, densidade, área basal, massa de sementes e densidade da madeira, respondem aos gradientes ambientais de clima e solo. Utilizou-se PCA para inferir sobre gradientes ambientais, onde foram detectados quatro gradientes principais, a saber: sazonalidade da precipitação, amplitude térmica, fertilidade do solo e umidade do solo. Os gradientes em vegetação, marcadamente gradientes de composição e diversidade responderam a sazonalidade de precipitação e umidade do solo. Concluiu-se que disponibilidade hídrica é o principal determinante das feições de vegetação considerada. Contudo, destaca-se a importância dos resultados apresentados para subsidiar iniciativas de conservação e para a compreensão ecológica de áreas transacionais de vegetação.

Palavras-chave: Macroecologia. Mata Atântica. Cerrado. Caatinga. Gradientes ambientais.

ABSTRACT

Minas Gerais State (MG), the fourth largest Brazilian State, with size comparable to countries such as France and Spain, harbors a great environmental heterogeneity and consequently tree diversity. The current thesis was structured into three chapters. The first one consists of an overall description and literature review on the main ecological points underlying this study. The second and third chapters are scientific papers on tree diversity in MG. We used 158 vegetation sample areas, including different phytophysiognomies of the following three vegetation domains found in MG: Cerrado, Atlantic Forest and Caatinga. The first paper, entitled "*Tree Dominance and Diversity in Minas Gerais, Brazil*", approaches some basic but neglected questions regarding MG tree diversity: how many trees and tree species are there in MG? How much of such diversity has been lost? We used a grid of 6,634 cells (0.1 degree) and Fisher's alpha and Fisher's log-series to run the estimates. We found that there are currently 24.5 x 10^9 trees and something between 3,592 and 3,743 tree species in MG. Besides, we've found 68.54% and 4.03% to be lost when compared to the estimate original numberss. These results enable us to create abundance-distributions maps and, for instance, find out the most abundant tree species in MG: *Qualea grandiflora*. The second paper, entitled "*Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-Cerrado-Caatinga transition, Brazil*", approaches how vegetation features such as species composition in different taxonomic levels, diversity, stem density, basal area, seed mass and wood density are correlated with environmental gradients in terms of soil and climate. PCA axes were used as proxies to infer about environmental gradients, and four major gradientes were detected as representatives of precipitation seasonality, temperature range, soil fertility and soil moisture. Regarding vegetation, the tree species composition and diversity, were closely related to precipitation seasonality and soil moisture. Thus, the availability of water was found to be the main determining factor for vegetation features under study. Therefore, these results may be important in the implementation of initiatives for vegetation conservation in the State, and for ecological comprehension of vegetation transitional areas.

Key-words: Macroecology. Atlantic Forest. Cerrado. Caatinga. Environmental gradients.

SUMÁRIO

FIRST PART

1 INTRODUCTION

Minas Gerais (MG) is an extensive and heterogeneous Brazilian State. Its extension (nearly 600,000 km²) comprises expressive abiotic gradients of climate, soil and land forms. Such gradients and their past fluctuations are reflected on vegetation, which varies in different scales according to these drivers. Therefore, a very complex vegetation mosaic was built, caracterized by both gradual and shaped transitions among its elements.

Several studies have focused on describing MG vegetation. Phytogeography studies on species occurence and distribution reveald solid patterns (EISENLHOR; OLIVEIRA-FILHO, 2015; OLIVEIRA-FILHO; FONTES, 2000) and carbon stocks have been recently studied (SCOLFORO et al., 2015). In smaller scales, several studies of composition, diversity and structure of local vegetation remnants are available (e.g. APGAUA et al., 2015; NAVES; BERG, 2012; POMPEU et al., 2014; PRADO-JUNIOR et al., 2012).

In this study, we tried to go a few steps further in the MG vegetation comprehension, mainly by including *species abundance* in the understanding of tree species distribution – previously adressed only in terms of occurence – among vegetation domains and vegetation types. This species counting data also allowed us to estimate the current and 'original' number of tree species and individuals in MG. Moreover, we adressed species abundance together with forest structure paramenters and functional traits over the climatic and edaphic gradients in MG territory.

Thanks to the effort and support of numerous persons who worked on data collection, this study enlisted a unique dataset, containg 158 high-quality vegetation inventories (summing up more than 350,000 trees) all over the State. These data come from three sources: Minas Gerais Forest Inventory (Secretaria de Estado de Meio Ambiente e Desenvolvimento Sustentável, Insituto Estadual de Florestas, and Universidade Federal de Lavras), the CONFLORA group (Universidade Federal de Lavras), and the Universidade Federal de Uberlândia.

The current thesis has been structured into three chapters. The first one corresponds to an overall presentation and a literature review on the main ecological issues underlying this study. The second and third ones are scientific papers on tree diversity in MG entitled “*Tree Dominance and Diversity in Minas Gerais, Brazil*” and “*Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-Cerrado-Caatinga transition, Brazil*”, prepared for the jounals Biodiversity and Conservation and Journal of Vegetation Science, respectively.

2 LITERATURE REVIEW

2.1 Minas Gerais vegetation

The transition between open vegetation and various types of forest has been described in several regions of the Neotropics (HIROTA et al., 2011; HOFFMANN et al., 2012; RATTER, 1992; STAVER; ARCHIBALD; LEVIN, 2011). In central-eastern South America, a remarkable transition is found between the vegetation belonging to the so called ‘open dry diagonal’ or simply ‘dry diagonal’ (PRADO; GIBBS, 1993; WERNECK et al., 2012), and the Atlantic Forest (OLIVEIRA-FILHO; FONTES, 2000; OLIVEIRA-FILHO; RATTER, 1995). The dry diagonal itself represents a very complex vegetation transition within its components, the Seasonally Dry Tropical Forests (SDTFs) – following Murphy and Lugo’s (1986) concept with the largest area in northeastern Brazil, Caatinga, but also present as patches of deciduous and semideciduous forests along the Paraguay-Paraná Basin and in Chaco in southwestern South America – and the Neotropical Savanna, “Cerrado”, in Central Brazil (PENNINGTON; LEWIS; RATTER, 2006; WERNECK, 2011). The components of the dry diagonal share basic ecological conditions, being seasonally stressed by drought (MURPHY; LUGO, 1995; PENNINGTON; LEWIS; RATTER, 2006) and having vegetation adapted to such climatic conditions (DALMAGRO et al., 2014). Besides, they all have unique biotas, complex mosaic-types distributions, and have received far less attention than tropical rainforest over past decades (SILVA; BATES, 2002; WERNECK, 2011).

Several controversial attempts have been made in order to understand the origin and evolution of this biogeographic picture (MAYLE, 2004; NEVES et al., 2015). Regarding the SDTFs, as an elder biome, the combined influences of Paleogene-Neogene geological processes and the Quaternary climatic-vegetation fluctuations are hypothesized to have generated the current range of Seasonally Dry Tropical Forest found in South America (PENNINGTON; LEWIS; RATTER, 2006). Therefore, the patches of SDTF in South America nowadays may represent a relic of a wider seasonally dry forest biota that reached its maximum expansion during the driest phases of the Pleistocene epoch covering the dry diagonal, the dry inter-Andean valleys in Peru and Ecuador (PRADO, 2000; PRADO; GIBBS, 1993), and even possibly covering tracts of the Amazon interior, in areas of fertile soil (PENNINGTON; PRADO; PENDRY, 2000). These authors interpret findings of repeated patterns of fragmented populations as evidence that the current dry forest nuclei constitute remnants (i.e. refugia) of such former single formation, the Pleistocene Dry Forest Arc, split by vicariance after the subsequent climate and geological changes (for alternative hypothesis see MAYLE, 2004). As in South America SDTFs grow under basically the same climatic conditions as Cerrado, recent adaptive shifts in the late Miocene (CERLING et al., 1997) driven by fire dynamics were identified as responsible for Cerrado current floristic and physiognomic distinction from SDTFs (DEXTER et al., 2015) remarkably by the key factors of C4 grass (OLIVEIRA-FILHO; RATTER, 2002; WERNECK et al., 2012).

The fact that the transition between Atlantic, Caatinga, and Cerrado Domains occurs specifically in MG, provide a general idea on how complex and heterogeneous is this region. Therefore, in Minas Gerais State, forest remnants comprehend from Atlantic rain formations near to the Serra da Mantiqueira and Zona da Mata (e.g. SANTOS, 2013) to seasonally dry tropical forest hinterland, forming enclaves of Atlantic forest in the Cerrado domain (e.g. WERNECK; FRACESCHINELLI; TAMEIRÃO-NETO, 2000), and northern, forming enclaves of Caatinga into the Cerrado domain (e.g. SANTOS et al., 2011). Such tropical forest display a conter-latitutinal pattern of tree species richness and diversity (PENNINGTON; LAVIN; OLIVEIRA-FILHO, 2009), where local environmental variables play an important role driving their structure and behavior (OLIVEIRA-FILHO; FLUMINHAN-FILHO, 1999). In MG State, we can also find forested formations typical of Cerrado Domain known as Cerradões (e.g. SOUZA et al., 2010) and savanic formations also in Cerrado domain (PRADO-JUNIOR et al., 2012; REYS et al., 2013) towards the western part of MG.

Vegetation complexity and diversity in MG is currently highly threatened, since it is inserted in Brazil's most populated areas (GALINDO-LEAL; CÂMARA, 2005; LEITÃO-FILHO, 1987; OLIVEIRA-FILHO et al., 1994) to the point that two out of the three vegetation domains found in MG territory are considered biodiversity "*hotspots*" (MYERS et al., 2000) and the third one (Caatinga) is considered a *Global Wildness Area* (GIL, 2002).

2.2 Patterns and process on tree species diversity and distribution

Lawton (1999, p. 178) defined patterns as regularities observed in nature, that is, "widely observable tendencies". According to this author, in order to discover general patterns, laws and rules in nature, ecology may need to pay less attention to the 'middle ground' of community ecology – where there is endless variety -, increasing research efforts into Macroecology. Lawton (1999, p. 179) also highlighted that "we should concentrate on trying to see where the woods are, and why, before worrying about individual trees".

Macroecology indeed seeks for a "bigger picture", searching for major, statistical patterns in the types, distributions, abundances, and richness of species, from local to global scales, and the development and testing of underlying theoretical explanations for such patterns (LAWTON, 1999). Nevertheless, Lawton warns that Macroecology is not a panacea in the search for patterns and rules in ecology. Instead, it is the certainty that avoiding delving into details will reveal far more general ecological patterns and rules than will the reductionist approach.

When it comes to species abundance and distribution in a macroecological approach, Gaston et al. (2000) paper about abundancy-occupancy relationshipsbrings the famous statement that 'distribution and abundance are obverse and reverse aspects of the same problem' (ANDREWARTHA; BIRCH, 1954). Brown (1984), on the relationship between abundance and distribution of species, compiles papers in which the pattern of the species abundance is greater in the center of their distribution and declines gradually toward the boundaries has been emphasized. Brown provides vegetation examples by citing out Whittaker's classical papers on patterns of vegetation (1956, 1960, 1965), in which he concludes that, although individual species attain maximum densities in different parts of the gradient, the abundance of most species decline relatively gradually and symmetrically with increasing distance in either direction from their peaks.

Another well stablished macroecological pattern for species diversity is the latitudinal gradient of species richness (GASTON, 2000), which is true for vegetation in great scales and may be not found in regional to smaller scales (GENTRY, 1995; PENNINGTON; LAVIN; OLIVEIRA-FILHO, 2009; and see Article 2 of this thesis). The latitudinal gradient of species richness is found to be a consequence of systematic variation in the balance of species speciation, immigration, extinction and emigration. More than 25 not mutually exclusive mechanisms have been suggested for generating systematic latitudinal variation in these processes (GASTON, 2000).

Regarding the patterns described for tree species abundance in the last decades, Pitman et al. (2001) found an "oligarchy" of common species that dominates large spatial scales in eastern Ecuador and southeastern Peru. Pitman et al. (2001) presented several hypotheses to explain the commonness of such species combining high reproductive investments and success, long-distance dispersal abilities, and a tolerance of a broad range of environmental conditions. The authors discussed that ‘perhaps the [tree] species abundance at local and large scales may be a simple function of its ability to recruit in close proximity with conspecific adults’, somehow running contraryto the Janzen–Connell hypothesis for intraspecific spatial distribution (CONNELL, 1970; JANZEN, 1970).

Pitman, Silman and Terborgh (2013) gave another dimension for the study of oligarchies by revisiting the 2001 paper. In 2013, these authors stated that wherever environmental heterogeneity is low, or perceived as low by tree species, the areas will be dominated by predictable oligarchies – a small proportion of taxa found to occur with high frequency and at high local abundances across the landscape. Such extrapolation is possible because, according to the authors, this pattern is closely related to one of the best-documented patterns in ecology: the abundance-occupancy relationship (GASTON, 1996; GASTON et al., 2000). This relationship refers to the observation that when biological communities are sampled via spatially scattered inventories, a species’ mean abundance in the network tends to be positively correlated with the number of inventory sites at which it is recorded.

The oligarchic pattern has been supported by other authors, such as Bridgewater, Ratter and Ribeiro (2004) (in Brazilian Cerrado) and ter Steege et al., 2013 in Amazon Basin. Pitman, Silman and Terborgh (2013) believe that papers that haven’t found the oligarchic pattern probably are based on datasets that cover much greater environmental heterogeneity than intended by the hypothesis (e.g. TUOMISTO et al., 2003).

In fragmented landscapes, another pattern has been observed: the replacement of late sucessional tree species and spreading of pioneers. Tabarelli et al. (2012) referred to this process as “the few winners and many losers paradigm" and reported this ongoing process in northeastern Atlantic forest in Brazil. Similar processes have been reported by Laurance et al. (2006), Magnago et al. (2014), Santo-Silva et al. (2016), and Steege and Hammond (2001).

Regardless, "pattern does not imply process". Laws and rules are the general principles that underpin and create the patterns (LAWTON, 1999). In this sense, mechanismsunderlying species composition (species distribution) and diversity are discussed mainly in terms of two nonexclusive hypothesis: (1) *ecological determinism* that stands up for the relationship between species distribution and abiotic conditions and (2) *neutral theory* that states that species are distributed by chance although there is spatial autocorrelation due to dispersal limitations (HUBBELL, 2001). Several methods in ecology are derived from these hypotheses and there is certainly much to come.

3 FINAL REMARKS

The theories and insights on species diversity described in the literature tested though a robust database may represent progress on elucidating ecological patterns and processes driving vegetation in Minas Gerais State.

The patterns presented here in this study, in terms of tree species abundance all over the State have the potential to better guide conservation and management initiatives. In a practical sense, this means that future laws, parks and managment thechniques can be thought and planned more accurately in MG.

Besides, the revelaled relationships between vegetation traits and environmental gradients may contribute to a better understanding of processes driving vegetation in transitional areas thoghout the tropics and also to predict vegetation future behavior in climate and land-use change scenarios.

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SECOND PART – SCIENTIFIC ARTICLES

MANUSCRIPT 1 - TREE DOMINANCE AND DIVERSITY IN MINAS GERAIS, BRAZIL

**prepared for *Biodiversity and Conservation*

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Abstract: Quantifying diversity is an old challenge for ecologists. It is also a social demand facing the increasing threatens that natural areas are going through. We sought to work on these issues by using data from 158 vegetation remnants (over 350,000 trees) in Southern Brazil (Minas Gerais State – MG, nearly 600,000 km^2). Specifically, we sought to answer the following questions (1) how many trees and tree species do exist currently in MG vegetation remnants? (2) how much of such biodiversity does belong to each vegetation domain (Atlantic forest, Cerrado and Caatinga) and vegetation type (Seasonally Dry tropical forest "semideciduous", Seasonally Dry tropical forest "deciduous", Rain Forest, Swamp, Cerrado and Cerradão) in MG? (3) how much has been lost in terms of trees and tree species? We built a 0.1 degree cells grid to estimate the number of trees via spatial regression and used Fisher' alpha and Fisher' log series to provide estimates on how many tree species there are and there were in MG. We found the number of trees in Minas Gerais to be around 24.5 x 10^9 and the number of tree species to be between 3592 and 3743. The distribution among the vegetation domains and vegetation types followed primarily the area of these classes. Consequently, the most abundant species in MG, *Qualea grandiflora*, belongs to Cerrado domain. The number of trees and tree species lost were respectively 68.54 and 4.03 percent of the original values. We believe our results may guide conservation initiatives and future ecological researches in Neotropical forests.

Key-words: Atlantic Forest; Caatinga; Cerrado; Fisher's log-series; Neotropical vegetation; species relative abundance.

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1. INTRODUCTION

One of the most important challenges facing ecologists and conservation biologists consists in providing reliable quantification of biodiversity. Tropical forests are responsible for numerous ecosystems services, and are crucial for mitigation of climate and land-use change impacts (Canadell and Raupach 2008; Harrison et al. 2014). They play a major role in the world's climate system by storing large stocks of carbon (Fauset et al. 2015) and by regulating energy and water fluxes (Ojea et al. 2012; Cabral et al. 2015). Quantitative studies in forest ecology are useful sources of information in planning the conservation of tropical forests (Condit and Costa 1987; ter Steege 1998; ter Steege et al. 2006). They provide not only information on the species occurrence, which is useful to study biogeography, but also species abundance data. Combining such data with the increasingly sophisticated statistical methods to provide estimates of species richness and abundance in broader scale, allow scientists to meet the demand for more accurate information on species diversity. However, still today, we face a scarcity of high-quality field data. Common problems regarding those data are the lack of a unified protocol (methodology conflicts) and, more importantly, problems involving species identity (Scott and Hallam 2002). This is so common that only recently an accurate estimate was given for the number of tree species in the Amazon, the largest tropical forest in the world (ter Steege et al. 2013). At the same time, slowing down tropical deforestation and forest degradation remains an enormous challenge with concomitant social, environmental, and economic implications (FAO 2010). In other words, our forests are disappearing before their structure and diversity are properly described.

Most of the available information about deforestation is based in area loss, especially coming from remote sensing sources (e.g. Achard et al. 2002; Soares-Filho et al. 2006; Beuchle et al. 2015). These data are very important for monitoring areas and to primarily access the impact of such losses in climate (e.g. Malhi et al. 2008). However, despite the notion given by the relation between area and species richness (Preston 1960), we know little about how much is lost in terms of biodiversity in such events of deforestation. This makes estimates of number of trees, population sizes and number of species an urgent matter for conservation (ter Steege et al. 2015), especially for human-threatened biomes (Crowther et al. 2015; Lima et al. 2015).

In the Neotropics, in spite of the rise in ecological studies in the last decades, highly-threatened non-Amazon domains have received relatively less attention from both scientists and society (Sobral and Stehmann 2009). The amount of biodiversity lost in those systems can be massive and the information we have available is negligible. For instance, Lima et al. (2015) found that the current knowledge on the structure of the Atlantic forest *hotspot* – considered the most studied neotropical biome, with remarkable biodiversity and endemism (Galindo-Leal and Camara 2003) – is based on only 0.01 percent of the 18.5 million ha of forest that are remaining. This is critical if we consider that rates of deforestation of the Atlantic forest are four orders of magnitude larger than rates of sampling (Lima et al. 2015).

Other vegetation domains are probably even less studied - the Cerrado global *hotstpot* andCaatinga *Global WildernessArea*, together accounting for about 30-35 percent of Brazilian total area have been called “the forgotten ecosystems” (Marris 2005; Santos et al. 2011). The Brazilian Cerrado, with the greatest plant diversity of all savannahs in the world, and the second-largest biome in South America, is one of the most threatened vegetation domains in the tropics (Marris 2005; Sano et al. 2010). Land-use change in the Cerrado, mainly due to expansion of agriculture over the last 20 to 30 years, has replaced natural areas with monocultures of soybean, sugar cane, corn, coffee and cotton (cash crops), as well as with flooded areas for energy plantations and pastures (Sano et al. 2010). Originally covering about 23 percent of Brazil, by the end of the 1990s the natural Cerrado retained only 50 percent of its original extent (Klink and Machado 2005) and now covers just 20 percent of the original area (Goulart et al. 2005; Cabral et al. 2015). The expectations about the Cerrado's future are not very optimistic. Based on recent trends in deforestation (Bianchi and Haig 2013), the Cerrado may effectively no longer exist in 25 years' time (Hunke et al. 2014; Cabral et al. 2015).

The Caatinga, the only exclusively Brazilian vegetation domain, also remains among the world's most threatened and least studied of the forested ecosystems, and, as such, may face greater threats than humid forests (Sunderland et al. 2015). Dry forests, one of the vegetation types found in Caatinga, have a smaller stature and lower basal area than tropical rainforests (Murphy and Lugo 1986), and thorny species are often prominent (see Pennington et al. 2000, for more). Although net primary productivity is lower than rainforests, Caatinga species are highly resistant to drought (Souza et al. 2015) which may become a key trait in climate change scenarios.

In Southeast Brazil, the State of Minas Gerais (hereafter MG), the fourth major Brazilian state, with a size comparable to countries such as Spain and France, harbours a very unique vegetation transition: between the Atlantic, Cerrado and Caatinga vegetation domains. The area represents a very intricate mosaic of vegetation types such as Seasonal Dry Tropical Forests (hereafter SDTFs), savannahs (Cerrado) and even Rain Forest in the very south of the state on the Mountain Ranges of Mantiqueira. At large scale this transition appears to be climate-driven, such as the transitions from the rain forest in the south towards the SDTFs in the north and western part of the state (Oliveira-Filho and

Fontes 2000). However, at smaller scales, patches of different biomes exist in each of these domains under similar conditions of climate, but different conditions of soil (e.g. galleries and enclaves) (Ratter 1992; Oliveira-Filho and Ratter 1995). Most authors pointed out that the boundaries between the forests and the open-formations in such local transitions are related to soil and topographical conditions, roughly with forest occurring on more fertile soils and open-formations (Cerrado) on dystrophic and well drained soils (Ratter 1992). Also, as it is usual for open vegetation-forest transitions, fire occurrence plays an important role in creating vegetation borders (Oliveira-Filho and Fluminhan-Filho 1999; Lehmann et al. 2014). Therefore, MG has a complex vegetation mosaic, with tree diversity increasing towards the south, that has been well studied in regards to phytogeography (Oliveira-Filho and Fontes 2000; Oliveira Filho and Ratter 2002; Eisenlhor and Oliveira-Filho 2015) and carbons stocks (Scolforo et al. 2015), but is still little explored in terms of biodiversity quantification.

Here we compiled stem density and species abundance data from 158 sites in MG (nearly 600,000 km^2), randomly distributed across the State and its vegetation domains and vegetation types. We sought to answer the following questions: (1) how many trees and trees species do exist currently in MG vegetation remnants? (2) how much of such biodiversity does belong to each vegetation domain (Atlantic Forest, Cerrado and Caatinga) and vegetation type (SDTF “semideciduous”, SDTF “deciduous”, Rain Forest, Swamp, Cerrado and Cerradão) in MG? (3) how much of the original vegetation has been lost in terms of trees and tree species?

2. METHODS

2.1 Data collection

Our dataset included 158 vegetation sites in MG (Fig. 1) gathered from three sources: the Minas Gerais Forest Inventory (Scolforo and Carvalho 2006), plot data from the CONFLORA group of the Universidade Federal de Lavras, and plot data from the Universidade Federal de Uberlândia. Inventory plots were established between 1990 and 2014 by several research groups. The area sampled in the inventories varied from 0.15 ha to 17.2 ha, with average 1.84 ha. The minimum diameter at breast height (DBH) of the trees recorded was 5 cm. Taxonomy was standardized to family, genus and species according to Taxonomic Name Resolution Service - TNRS (Boyle et al. 2013; http://tnrs.iplantcollaborative.org). Unidentified individuals accounted for 7.68 percent of the total trees sampled. The vegetation in our plots was classified as Atlantic Forest, Cerrado or Caatinga following the vegetation domain and also according to the vegetation type as SDTF "semideciduous" (SDTF_SD), SDTF "deciduous" (SDTF_D), Rain Forest (RF), Swamp (Brazilian "Vereda"; SW), Cerrado (CE) and Cerradão (a tallwoodland, CD).

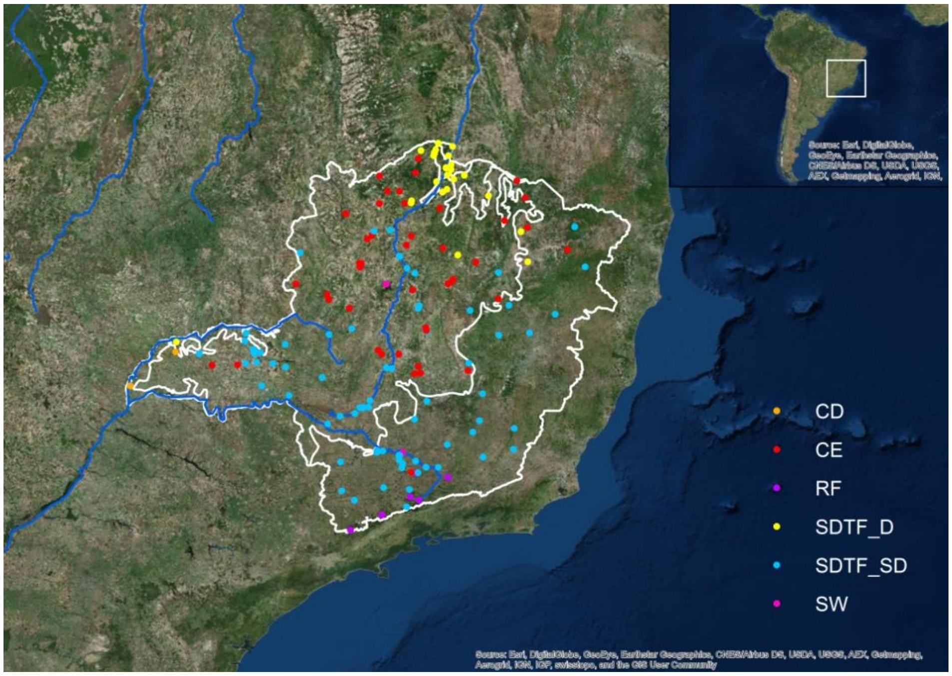

Fig. 1 Location of the 158 sites in Minas Gerais belonging to three vegetation domains (Atlantic Forest, Cerrado and Caatinga) and six vegetation types (Seasonally Dry tropical forest “semideciduous” (SDTF_SD), Seasonally Dry tropical forest “deciduous” (SDTF_D), Rain Forest (RF), Swamp (SW), Cerrado (CE) and Cerradão (CD).

2.2 Calculating species population sizes

Our procedure to calculate population sizes for individual species broadly follows ter Steege et al. (2013). Firstly, we divided MG into 6334 0.1-degree grid cells and calculate their areas using a correction for latitude. Then we calculated the area of vegetation remnants in our cells by merging our grid with the grid of vegetation remnants (10 × 10 km) up to 2009 (ICMBio 2013; Fig. 6 – Appendix 1). We fitted a spatial loess regression model (span = 0.5) for tree density (stems/ha) recorded in our plots against the longitude (x), latitude (y), and their interaction. We used the fitted model to predict the tree density in our grid cells by using their centroid coordinates. Finally, the total number of trees in each grid cell was then calculated by multiplying the density in each cell by the area of vegetation remnants in each cell.

The relative abundance of each tree species (Rabi) in each grid cell was also estimated via a spatial loess regression model (this time with span = 0.2) using the Rabi of our plot data against cells' longitude (x), latitude (y), and their interaction. By using the fitted model, we predicted the species' relative abundance in each grid cell. Occasional negative predicted abundances were replaced with 0. The final population size of each species was calculated by multiplying its relative abundance in each cell by the total number of trees in each cell and then summing up these products for all cells.

In order to reduce the impact of individual plots on the estimated relative abundance and quantify dispersion in the above procedure, we carried out a bootstrap exercise. This involved randomly drawing 158 plots from all plots (with replacement) and repeating (500 times) the procedure described above. Therefore, the final population sizes represent the mean of all those repetitions and their coefficient of variation (CV = 100*standard deviation/mean). We also present the proportion of the most abundant tree species in MG by both vegetation domains and vegetation types.

2.3 Estimating the number of species (Fisher's alpha and log-series)

Fisher's alpha, defined implicitly by the formula $S=\alpha*\ln(1+n/\alpha)$ where S is number of taxa, n is number of individuals and α is the Fisher's alpha (Fisher et al. 1943), was calculated by using the number of individuals and the number of species in our sample.

Fisher's alpha values can be used to extrapolate species richness of a defined region once the total number of individuals is known. Therefore, in order to estimate the number of species based on our sample, we estimated species richness in Minas Gerais using Fisher's alpha and the estimated total number of trees. However, to be considered acceptable, extrapolations using Fisher's alpha must meet the assumptions that (1) species abundances in the sample follow the log-series distribution, which was true for our dataset, and that (2) the community is homogeneous at the scale of sampling, which is clearly not the case of MG vegetation samples. We believe the intense sampling and the fact the data fitted a log-series very well may validate our estimates. Alternatively, we fitted Fisher's log-series to the estimated population sizes and we obtained a second estimate of species richness in MG by fitting a linear model to the central portion (50%) of the empirical relative abundance distribution(RAD) (ter Steege et al. 2013). The estimate of number of species in this case corresponds to the extrapolation of this model to the x axis.

2.4 Estimating total trees and species lost

We calculated the original population size by multiplying the predicted relative abundance of the species times the "original" total number of trees in our grid cells. The original total number of trees itself was calculated by multiplying the predicted densities in our grid cells times the total area of the grid cell (instead of the remnant area in our cells). Therefore, the total trees lost was calculated by subtracting the current number of trees from the original one. The number of individuals of each species lost was calculated by subtracting the number of individuals estimated from the original population size and the current population size. The number of original species was calculated similar as the current number: by both Fisher's alpha and the total original number of trees and by fitting log series to the RAD.

3. RESULTS

Our dataset encompassed 356,226 trees belonging to 1430 species in 448 genera and 97 families. The richest family was Fabaceae (220 species - 15.38% of all species), followed by Myrtaceae (147 - 10.35%), Rubiaceae (72 – 5.03%), and Lauraceae (67 – 4.7%). The richest genus was *Eugenia* (46 – 3.22% of all species), followed by *Miconia* (36 – 2.52%), *Myrcia* (35 – 2.44%) and *Ocotea* (30 – 2.1%). The most abundant species in our dataset was species was *Qualea parviflora* (10,581 – 3.0%), followed by *Qualeagrandiflora* (9408 – 2.6%), *Eugenia dysenterica* (6460 – 1.8%) and *Copaifera langsdoffii* (4245 – 1.2%). The most abundant genera were *Qualea* (22,863 individuals– 6.4%), *Eugenia* (9910 – 2.8%), *Machaerium* (9215 – 2.6%) and *Myrcia* (8263 – 2.3%). The most abundant family was Fabaceae (70,294 individuals – 19,7%), followed by Vochysiaceae (27,820 – 7.81%), Myrtaceae (26,128 – 7.33%), and Anacardiaceae (12,675 – 3.56%).

3.1 Estimating of the number of tree individuals and species in the vegetation remnants in MG

The sum of the area of our 6334 0.1-degree cells was 59,900,920 ha (599,009 km^2). According to our data in vegetation remnants, there was (in our grid cells) 19,774,428 ha of native vegetation (33.02% of the total area) left in MG. The estimated of number of trees >5 cm DBH in the vegetation remnants in grid cells in MG was 24,520,292,694 (24.5 billion or 24.5×10^9). Our model (Fig. 7 – Appendix 1) estimated the number of trees to be increasingly higher towards the north of MG. Fisher's alpha of our total sample was 192.039. Using this alpha and our total population size estimates for the tree species in MG we estimated the total number of tree species in Minas Gerais to be around 3592. The alternative estimate from the Fisher's log series fitted to the RAD provided an estimate of 3743 tree species for MG (Fig. 2). The 81 most abundant species (5.66% of the total nr of spp) in MG accounted for 50.1 percent of all individuals while the 580 (40.6%) rarest species account for only 1% of the individuals. The most abundant species in our estimates were savanna species such as thetwo species belonging to the genus *Qualea* – widely known as "pau-terra" (Table 1). We found a linear relation (R^2=85.43%) between the log of estimated population size and the maximum relative abundance recorded and a weaker quadratic relation (R^2=63.54%) between the log of estimated populations size and the frequency in our plots (Fig. 3). Surprisingly, we observed a suit of species among the most abundant species with very restricted ranges, as a consequence of extremely high local abundances. Therefore, locally highly successful species such as *Eremanthusincanus* and *Combretum duarteanum,* in spite of having narrower ranges, were estimated to be among the most abundant tree species in MG.

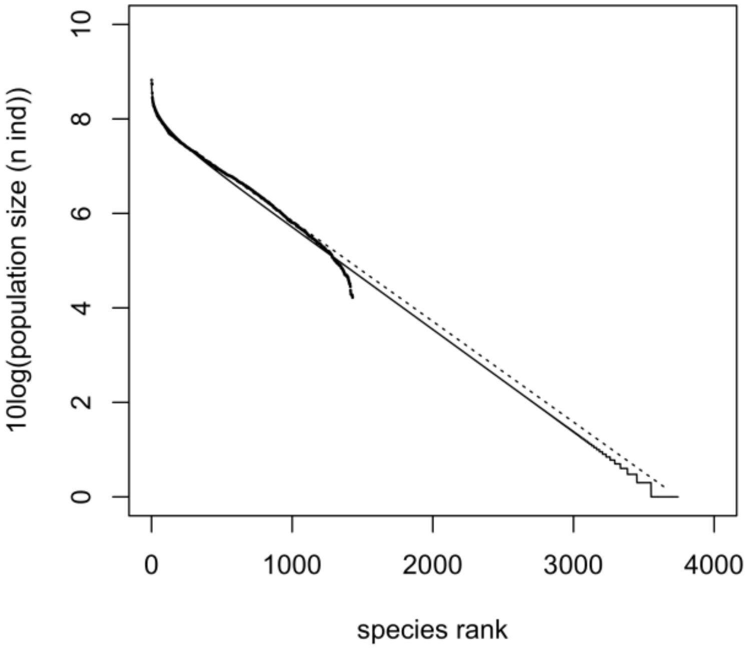

Fig. 2 Rank-abundance distribution of estimated population sizes of 1430 tree species and its extrapolation (dotted line) and hypothetical log-series extrapolation (dark black line) of all predicted species in MG vegetation remnants.

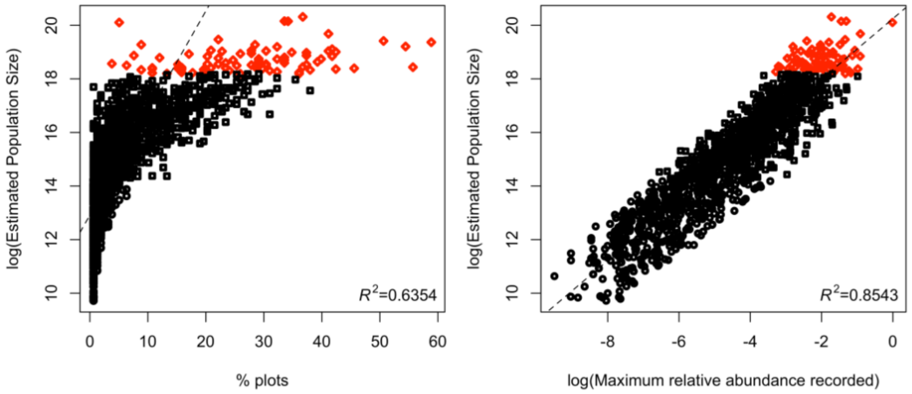

Fig. 3 Relation between estimated population size (log) and the maximum relative abundance recorded (log) and relation between the estimated population sizes and the frequency in forest inventory plots in Minas Gerais. Red dots represent the 81 most abundant species. Dashed lines represent respectively a linear and a second order polynomial regression between the variables considered.

3.2 Patterns in vegetation domains and vegetation types

The proportion of abundance by vegetation domain in MG (Fig. 4) reflected the area of those domains, with Cerrado having the majority of the most abundant species and Caatinga the majority of the rarest ones. The distribution by vegetation types also reflected the area sampled (sampling effort), showing a bigger proportion of rarest species in the poorly sampled “rain forest”.

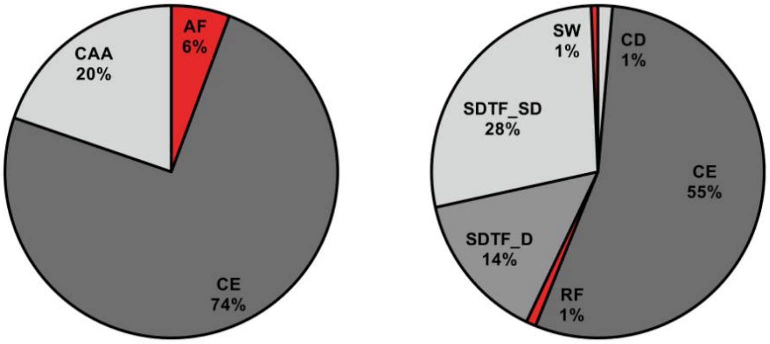

Fig. 4 Proportion of the 81 most abundant tree species in Minas Gerais per vegetation domain and vegetation type.

Although the majority of the most abundant species were savanna species, we found within the 20 most abundant species some generalist species such as *Copaifera langsdorffiii* (the most frequent species in our dataset), and *Tapirira guianesis* occurring all over the state in practically all vegetation types (Fig. 5).

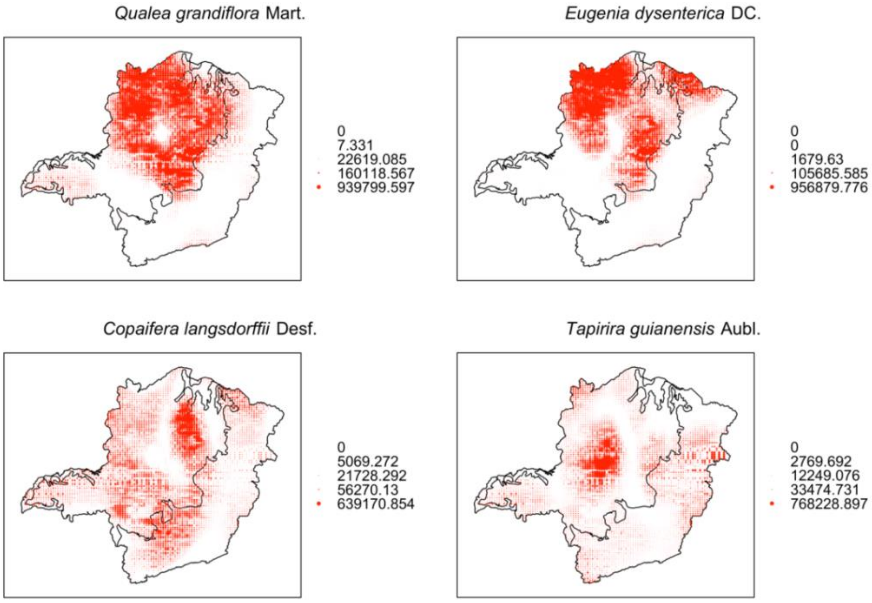

Fig. 5 Abundance-distribution maps of four of the most abundant species in MG illustrating the two main situations found for the most abundant species: the Cerrado species (*Qualea grandiflora* and *Eugenia dysenterica*) and generalist ones (*Copaifera langsdorffii* and *Tapirira guianensis*). (Distribution maps for the 20 most abundant species available in Appendix 2).

3.3 How much of the tree individuals and species were lost?

We estimated an original number of trees of 77.9 billion (77.9×10^9). Comparing this number with our estimated number of remaining trees (24.5×10^9), we estimate the number of tree lost in MG to be 53.4 billion, 68.54 percent of the original number of trees. Assuming Fisher's alpha to be a reasonable estimate and considering the original number of individuals, we estimate the original richness to be around 3819 species (alternatively, from the RAD =

4170), which suggests that MG may have lost between 4.03 and 8.42 percent of its original tree species, so far (Fig. 8 – Appendix 1).

4. DISCUSSION

The total number of trees estimated for the current remaining vegetation in MG is c. 24.5×10^9. This corresponds to about 6.29 percent of the total amount of trees (>10 cm DBH) in the Amazon Basin, estimated by ter Steege et al. (2013) and 0.81 percent of the estimated total amount of trees (>10cm DBH) in the world (Crowther et al. 2015). Considering the estimated human population in MG State in 2015 (IBGE 2015), there are, thus, about 1175 trees for each citizen in Minas Gerais. This is almost three times the global average of 422 trees per human earth-dweller estimated by Crowther et al. (2015). Our model estimated the number of trees per degree cell to be increasing towards the center/north of MG, more likely as an effect of the higher percentage of remnants in this region (see map of vegetation remnants in MG Fig. 6), than as consequence of differences in tree densities amongst vegetation types. After all, the historical deforestation process led indeed to more critical devastation in the southeast of MG, in the area originally cover by Atlantic SDTFs (Leitão-Filho and Morellato 1997; Oliveira Filho and Fontes 2000). This region belongs to the most populated area of Brazil and has some of the largest cities in Latin America and in the world, such as São Paulo and Rio de Janeiro. As the rest of Atlantic forest, this region has been ‘developed’ in the last five centuries – since the European colonization of the east coast of South America (Bueno 1998) – through an unplanned history of habitat loss and fragmentation (Myers et al. 2000; Tabarelli et al. 2005; Pereira et al. 2007; Joly et al. 2014; Pereira et al. 2015). Although the several remaining fragments in this region display various patterns of size and shape, they are usually smaller than those of MG’s north/center ones, and are still under severe anthropogenic pressure(Morellato and Haddad 2000; Higuchi et al. 2008; Ribeiro et al. 2009; Joly et al. 2014). In the Cerrado region, the occupation is more recent but has increased dramatically since. Thus, while the Cerrado vegetation remnants are bigger, they are currently severely threatened by land-use change (Sano et al. 2010).

The estimated species richness (by both methods) is higher than a previous non-empirical estimate for MG's woody flora (Oliveira-Filho 2006; 2500 species). The patterns of species abundance we describe here for MG arise in part from patterns of diversity at very narrow local scale in the different forest types (e.g. Felfili and Felfili 2001; Higuchi et al. 2008; Apgaua et al. 2014) combined with the distribution patterns described for vegetation domain scale (Oliveira-Filho and Fontes 2000; Ratter and Oliveira-Filho 2000). Therefore, basically we found two main situations when it comes to the most abundant species: the typical Cerrado species and the generalist ones.

As the majority of our most abundant species are typical Cerrado species and given the high correlation between abundance and frequency in our results, there is a clear overlap between our most abundant species and Ratter et al. (2003) Cerrado's most frequent species and Bridgewater et al. (2004) Cerrado "oligarchic" species. Ratter et al. (2003) pointed out a group of about 350 species which overwhelmingly dominates the woody vegetation throughout the Cerrado in Brazil. Some of those species (121) were confirmed to be widespread and frequent in Cerrado by Bridgewater et al. (2004), who called them "oligarchies", after the definition of Pitman et al. (1999) for 150 widespread generalists tree species in Amazon rain forest in Peru and Ecuador. Both Ratter et al. (2003) and Bridgewater et al. (2004) concluded that in despite of the heterogeneity and beta-diversity of Cerrado, a small suite of species dominates the biome. This pattern seems to hold here as well. For instance, *Qualea grandiflora*,our most abundant species, was reported by Ratter et al. (2003) as being present in 84 percent of the 356 sites studied by those authors, and is present in 94 percent of our Cerrado plots (36.7% of total). Ratter et al.'s list of species also includes other species found here as most dominant species such as *Eugenia dysenterica*, *Magonia pubecens* and *Caryocar brasiliese*.

Concerning the second group of abundant species (the generalist ones), we also observed an overlap between Oliveira-Filho and Fontes (2000) "*supertramp*" species in Atlantic Forest Southeast Brazil - species widespread in this domain - and some of our most abundant species, remarkably *Copaifera langsdorffii*and*Tapirira obtusa*. Both species were also pointed out by Oliveira Filho and Ratter (2000) to be frequent in gallery forest in Cerrado domain. These gallery forests work as a bridge throughout the Cerrado (in central Brazil) linking Atlantic forests and the Amazon and have boundaries with several vegetation types being influenced by them, which results in a remarkable species diversity. Many of the species often found in gallery forests are considered to be habitat generalists (*e.g.,Schefflera morototoni, Casearia sylvestris, Protium heptaphylllum, Tapirira guianensis, Virola sebifera, Copaifera langsdorffii* and *Hymenaea courbaril*) as they endure conditions not suitable for more "specialists" ones. Recently, Eisenlohr and Oliveira-Filho (2015) claimed that Atlantic Forest concept must encompass all of the types of forest east of the so-called "dry corridor" (Caatinga-Cerrado-Chaco) in South America, which lead us to conclude that the suit of species from the Atlantic that go through Cerrado (specially trough the galleries) might be the most non-Cerrado abundant species in MG

In general, two families stood out in terms of abundance (Fabaceae and Vochysiaceae). Fabaceae, the richest and most abundant family in the dataset, has 18 representatives amongst the 81 most abundant species in MG. The ability to form symbiotic associations with nitrogen-fixing bacteria is the most remarkable trait of Fabaceae, and its importance in the Neotropics has been widely explored (Pennington et al. 2006; ter Steege et al. 2006; Yahara et al.

2013), especially in dry forests (Pennington et al. 2000) where this family reaches high relative abundance. The importance of Vochysiace in Cerrado of MG was also stressed by Gooland (1970) and Goodland and Ferri (1979). Species of this family in the Cerrado are capable of regrowth after fire or have asexual reproduction and thus may have advantages over their competitors (e.g. Hoffmann et al. 2003). These traits make a species very successful locally in a savanna-like environment. Also, the success of *Qualea* both in frequency and abundance may arise from a suite of adaptations this genus has to cope with environmental odds. It is a deciduous genus in a seasonal environment, remaining leafless for one month at the end of the dry season, and is capable of aluminum accumulation when growing on acid soils – a typical condition of Cerrado soils (Haridasan 1982; Gonçalves-Alvim 2011). Additionally, *Q. parviflora*seems to be extraordinarily resistant to folivorus insects (Gonçalves-Alvim 2011) and the role played by extrafloral nectaries in *Q. grandiflora* in limiting herbivory (Costa et al. 1992) may boost the success of this species.

We observed a few species amongst the most abundant ones with a very low frequency, meaning they are locally very abundant. We believe this to be primarily a natural consequence of the environmental heterogeneity in MG, with different constraints that might favor different species in different locals. It's worth-noticing that most of these species seem to be specialists found usually in highly stressful environments. For instance, *Combretum duarteanum* is typical of northeastern deciduous forests (Lima et al. 2013), *Magonolia ovata*, "pinha-do-brejo", is found in Atlantic swampy sites (Kurtz et al. 2015) and *Sebastiania commersoniana* seems to be locally abundant in Atlantic alluvial forests (Silva et al. 2010).

We estimated the total amount of trees lost in MG to be 68.7 percent of the original number. This is primarily a function of the amount of area lost. However, it can also result from the late consequences of the fragmentation process (Morellato and Haddad 2000). We still know little about how much and in which way the edge effects impact tree community and structure in forest fragments as long as fragmentation is a transition process that drifts the fragments progressively apart from the original (often unknown) primary condition (Augusto et al. 2000; Paula et al. 2015; Santo-Silva et al. 2016). One of the widespread consequences of fragmentation and the resulting edge effect is the so called “replacement paradigm” (*sensu* Tabarelli et al. 2012), the proliferation of disturbance-adapted native organisms, such as pioneers tree species, over the later successional tree species. Similar processes have been reported by some authors (ter Steege and Hammond 2001; Laurance et al. 2006; Tabarelli et al. 2012; Magnago et al. 2014; Santo-Silva et al. 2016). In fact, some Atlantic pioneer tree species that we found among the most abundant species, such as *Cecropia pachystachya* and *Croton urucurana*, are apparently proliferating in many fragmented or edge-dominated landscapes (small fragments). This may result in locally impoverished and increasingly homogenized tree assemblages.

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Table 1 Mean estimated population sizes for the 81 most abundant tree species in Minas Gerais (Pop. Size); the coefficient of variation of this estimate (CV%); the number of trees of each species in our dataset (ntrees dataset); the percentage of all plot in which the species was recorded (%plots); the maximum relative abundance recorded (max Rab); and the number of individual recorded in each vegetation domain and vegetation type. (AF: Atlantic Forest; CE: Cerrado Domain; CAA: Caatinga; CD: Cerradão; CE: Cerrado; RF: Rain Forest; SDTF_D: Seasonally Dry Tropical Forest "deciduous"; SDTF_SD: Seasonally Dry Tropical Forest "semideciduous"; SW: Swamp).

Species	**Pop. Size**	**CV%**	**ntrees dataset**	**%plots**	**max Rab**	**Vegetation Domain**			**Vegetation Type**					
						CAA	**CE**	**AF**	**CD**	**CE**	**RF**	**SDTF_D**	**SDTF_SD**	**SW**
Qualea grandiflora	6.64E+08	140.03	9408	36.71	0.1783	15	9067	326	49	8779	0	223	357	0
Qualea parviflora	5.67E+08	188.64	10581	33.54	0.2701	1	10543	37	0	10134	0	295	152	0
Eugenia dysenterica	5.64E+08	170.08	6460	34.18	0.2346	176	6189	95	11	6170	0	204	75	0
Eremanthus incanus	5.39E+08	142.28	4050	5.06	0.9882	0	3597	453	0	3941	0	0	109	0
Myracrodruon urundeuva	3.53E+08	221.16	3771	41.14	0.4017	300	2844	627	3	567	0	2086	1115	0
Dalbergia miscolobium	2.85E+08	203.85	1850	22.15	0.2621	188	1058	604	1	1733	0	56	60	0
Myrcia splendens	2.70E+08	158.18	3403	50.63	0.0894	8	640	2755	0	395	425	1	2573	9
Copaifera langsdorffii	2.58E+08	175.11	4245	58.86	0.1663	2	2292	1951	95	1179	0	23	2882	66
Mabea fistulifera	2.35E+08	161.72	2084	8.86	0.2267	0	437	1647	207	192	0	0	1685	0
Eriotheca pubescens	2.35E+08	239.79	2891	28.48	0.1310	0	2879	12	2	2766	0	80	43	0
Astronium fraxinifolium	2.20E+08	139.59	2721	54.43	0.0607	0	1809	912	35	1315	0	78	1292	1
Pouteria torta	2.17E+08	149.03	1941	32.28	0.1325	1	1890	50	1	1692	0	44	204	0
Tapirira guianensis	1.99E+08	145.17	1736	41.77	0.1033	0	1128	608	14	514	46	1	976	185
Lithrea molleoides	1.90E+08	163.36	1278	20.89	0.3442	0	1156	122	0	150	0	0	1127	1

Table 1 Mean estimated population sizes for the 81 most abundant tree species in Minas Gerais (Pop. Size); the coefficient of variation of this estimate (CV%); the number of trees of each species in our dataset (ntrees dataset); the percentage of all plot in which the species was recorded (%plots); the maximum relative abundance recorded (max Rab); and the number of individual recorded in each vegetation domain and vegetation type. (AF: Atlantic Forest; CE: Cerrado Domain; CAA: Caatinga; CD: Cerradão; CE: Cerrado; RF: Rain Forest; SDTF_D: Seasonally Dry Tropical Forest "deciduous"; SDTF_SD: Seasonally Dry Tropical Forest "semideciduous"; SW: Swamp).

Species	Pop. Size	CV%	ntrees dataset	%plots	max Rab	Vegetation Domain			Vegetation Type					
						CAA	CE	AF	CD	CE	RF	SDTF_D	SDTF_SD	SW
Caryocar brasiliense	1.89E+08	182.77	1870	27.85	0.0636	20	1713	137	3	1814	0	0	53	0
Kielmeyera coriacea	1.86E+08	199.91	2494	30.38	0.1162	11	2370	113	2	2396	0	0	96	0
Bowdichia virgilioides	1.86E+08	125.83	2394	41.14	0.0758	45	2059	290	7	2093	0	39	255	0
Magonia pubescens	1.83E+08	180.65	2883	22.78	0.1539	0	2881	2	14	2636	0	21	212	0
Plathymenia reticulata	1.80E+08	138.31	2254	42.41	0.1863	56	1732	466	13	1640	0	360	241	0
Hymenaea stigonocarpa	1.77E+08	155.79	2746	34.81	0.1323	58	2599	89	15	2396	0	106	229	0
Tapirira obtusa	1.74E+08	171.37	2045	37.34	0.0980	0	837	1208	1	41	71	0	1912	20
Byrsonima coccolobifolia	1.70E+08	189.29	1968	27.85	0.0931	21	1825	122	26	1915	0	18	9	0
Xylopia aromatica	1.68E+08	234.03	2148	25.95	0.1714	0	1791	357	53	1629	0	0	413	53
Byrsonima pachyphylla	1.66E+08	290.48	467	17.09	0.1852	0	295	172	2	227	1	15	222	0
Combretum leprosum	1.57E+08	210.85	1387	7.59	0.3210	3	443	941	0	24	0	1363	0	0
Machaerium acutifolium	1.57E+08	240.37	2401	37.34	0.1281	552	1589	260	152	249	35	1742	223	0
Handroanthus ochraceus	1.53E+08	779.93	2799	41.77	0.4000	1120	1585	94	4	870	0	1804	121	0

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Species	**Pop. Size**	**CV%**	**ntrees dataset**	**%plots**	**max Rab**	**Vegetation Domain**			**Vegetation Type**					
						CAA	**CE**	**AF**	**CD**	**CE**	**RF**	**SDTF_D**	**SDTF_SD**	**SW**
Pouteria ramiflora	1.51E+08	236.42	3092	20.25	0.1452	0	3042	50	5	2990	0	1	96	0
Machaerium opacum	1.46E+08	152.79	2496	33.54	0.0589	28	1849	619	4	1698	0	102	692	0
Poincianella pluviosa	1.44E+08	705.00	3863	12.03	0.2151	2144	1719	0	0	0	0	3863	0	0
Casearia arborea	1.42E+08	188.87	1703	22.15	0.0517	10	531	1162	0	12	95	4	1592	0
Stryphnodendron adstringens	1.39E+08	314.41	1343	29.11	0.1093	5	1051	287	0	1132	0	6	205	0
Platypodium elegans	1.38E+08	141.17	2109	39.87	0.2562	6	610	1493	884	401	0	43	777	4
Leptolobium dasycarpum	1.38E+08	236.30	2021	32.28	0.0677	16	1890	115	9	1953	0	0	59	0
Terminalia argentea	1.36E+08	240.47	2103	29.11	0.2434	0	2083	20	29	1751	0	22	301	0
Anadenanthera colubrina	1.33E+08	523.88	3358	33.54	0.1307	694	2226	438	1	23	0	2430	904	0
Vochysia rufa	1.32E+08	296.81	1854	24.68	0.1508	0	1852	2	0	1769	0	55	30	0
Lafoensia pacari	1.26E+08	185.04	2017	29.11	0.0717	32	1917	68	0	1867	16	21	111	2
Qualea multiflora	1.24E+08	204.68	2534	39.24	0.0787	0	2485	49	73	2264	0	27	169	1
Myrcia guianensis	1.19E+08	243.06	1079	23.42	0.0816	23	561	495	2	515	92	3	467	0
Siparuna	1.19E+08	246.19	1343	33.54	0.1145	0	791	552	1	94	0	1	1245	2

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Species	**Pop. Size**	**CV%**	**ntrees dataset**	**%plots**	**max Rab**	**Vegetation Domain**			**Vegetation Type**					
						CAA	**CE**	**AF**	**CD**	**CE**	**RF**	**SDTF_D**	**SDTF_SD**	**SW**
guianensis														
Protium brasiliense	1.16E+08	154.97	418	3.80	0.2089	0	415	3	0	35	0	0	21	362
Terminalia fagifolia	1.14E+08	207.02	2838	20.25	0.0863	719	2114	5	1	1878	3	917	39	0
Albizia polycephala	1.14E+08	294.68	851	30.38	0.0704	0	492	359	0	242	15	77	510	7
Handroanthus impetiginosus	1.14E+08	270.43	530	22.15	0.1628	130	334	66	13	79	0	333	105	0
Triplaris gardneriana	1.13E+08	365.83	1011	15.19	0.1761	17	992	2	0	31	0	692	288	0
Diospyros hispida	1.12E+08	256.88	1405	37.34	0.0593	0	1316	89	1	744	1	0	659	0
Protium spruceanum	1.10E+08	217.87	1312	27.85	0.1286	0	561	751	2	59	0	0	1178	73
Cecropia pachystachya	1.08E+08	365.38	720	30.38	0.1439	0	549	171	0	189	28	1	415	87
Aparisthmium cordatum	1.08E+08	206.72	685	6.33	0.1222	0	345	340	0	0	0	0	685	0
Guazuma ulmifolia	1.08E+08	185.24	532	25.32	0.2482	0	415	117	5	26	0	42	450	9
Aspidosperma tomentosum	1.05E+08	165.98	1510	29.11	0.0403	5	1434	71	0	1459	0	31	20	0
Ixora brevifolia	1.03E+08	267.89	1087	28.48	0.0854	1	469	617	5	50	10	3	997	22
Ocotea	1.03E+08	232.05	1179	36.71	0.0650	0	673	506	1	15	95	0	1060	8

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Species	Pop. Size	CV%	ntrees dataset	%plots	max Rab	Vegetation Domain			Vegetation Type					
						CAA	CE	AF	CD	CE	RF	SDTF_D	SDTF_SD	SW
corymbosa														
Roupala montana	1.01E+08	147.79	1790	55.70	0.0424	0	1297	493	63	1148	77	12	484	6
Myrsine guianensis	1.00E+08	152.76	760	15.82	0.1319	0	721	39	0	73	9	0	678	0
Duguetia lanceolata	9.89E+07	265.88	770	20.89	0.1311	0	673	97	0	1	0	0	766	3
Combretum duarteanum	9.89E+07	649.39	3400	10.76	0.1854	1485	1915	0	0	12	0	3388	0	0
Machaerium brasiliense	9.84E+07	167.58	1327	23.42	0.0977	0	285	1042	9	12	6	55	1245	0
Croton urucurana	9.74E+07	435.36	522	15.19	0.2099	0	275	247	0	4	1	0	517	0
Casearia sylvestris	9.74E+07	315.25	1216	45.57	0.1374	0	380	836	25	69	23	6	1092	1
Byrsonima verbascifolia	9.56E+07	212.01	1282	29.75	0.0531	10	1241	31	0	1226	0	13	43	0
Anadenanthera peregrina	9.55E+07	503.03	700	10.76	0.3745	218	291	191	92	33	0	527	48	0
Eugenia florida	9.45E+07	484.48	799	42.41	0.2024	29	427	343	13	17	35	33	699	2
Styrax camporum	9.42E+07	176.65	569	15.82	0.2465	0	546	23	0	12	2	0	555	0
Buchenavia tomentosa	9.40E+07	198.83	906	15.82	0.0832	0	728	178	103	550	0	0	253	0
Xylopia sericea	9.28E+07	202.89	1060	19.62	0.0909	0	475	585	0	196	0	0	864	0

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Species	Pop. Size	CV%	ntrees dataset	%plots	max Rab	Vegetation Domain			Vegetation Type					
						CAA	CE	AF	CD	CE	RF	SDTF_D	SDTF_SD	SW
Kielmeyera speciosa	9.19E+07	382.14	1104	8.86	0.1175	1	1090	13	1	1089	0	1	13	0
Guapira opposita	9.16E+07	178.61	1661	37.97	0.1156	7	575	1079	2	293	115	7	1244	0
Curatella americana	8.93E+07	219.35	1157	24.05	0.1064	0	1157	0	0	1031	0	24	102	0
Inga vera	8.90E+07	329.35	986	31.01	0.2916	1	696	289	1	13	11	72	886	3
Piptadenia gonoacantha	8.75E+07	206.89	973	20.25	0.1900	0	104	869	0	20	83	185	685	0
Dimorphandra mollis	8.58E+07	159.92	1361	32.28	0.0374	1	1334	26	32	1244	0	11	74	0
Virola sebifera	8.38E+07	180.13	640	15.82	0.0548	0	636	4	0	63	0	0	482	95
Senegalia polyphylla	8.33E+07	599.14	1764	36.08	0.1534	809	756	199	18	25	1	1317	398	5
Guettarda viburnoides	8.28E+07	164.07	505	19.62	0.1887	0	470	35	14	21	8	2	460	0
Ocotea aciphylla	8.23E+07	540.12	755	17.72	0.3084	0	255	500	0	0	23	0	732	0
Galipea jasminiflora	8.16E+07	291.85	969	10.76	0.1831	0	244	725	0	1	0	0	958	10
Emmotum nitens	8.00E+07	242.68	849	13.29	0.0595	0	849	0	0	665	0	0	184	0
Talisia esculenta	7.96E+07	380.05	574	25.95	0.2632	3	563	8	114	67	0	66	327	0
Cabralea canjerana	7.95E+07	198.43	784	36.08	0.0508	12	248	524	1	69	183	24	501	6

APPENDIX 1

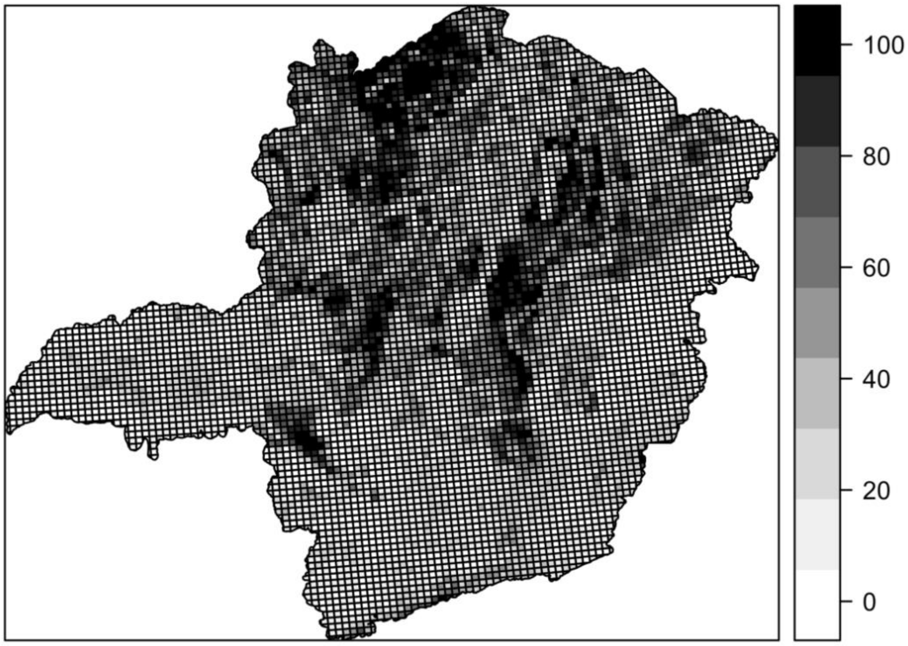


Fig. 6 Minas Gerais vegetation until 2009 **-** 10 X 10 km grid containing data of natural vegetation in km^2 and percentage for each cell. Source: ICMBio, 2013.

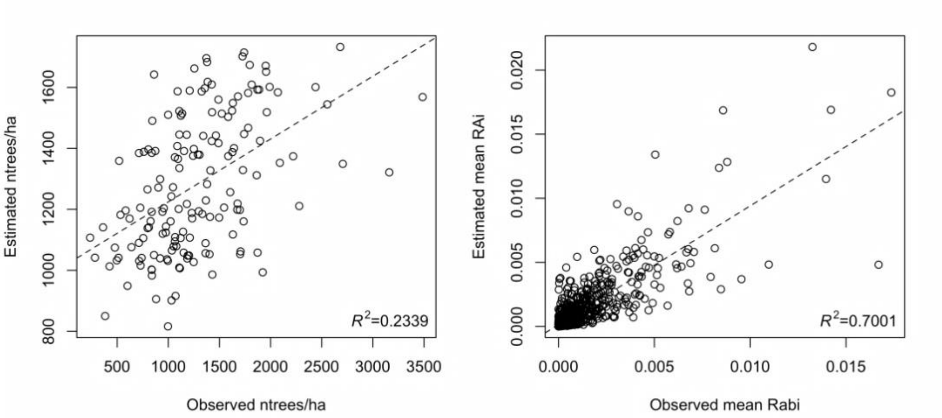


Fig. 7 Estimated ntrees/ha against observed ntrees/ha and estimated relative abundance against observed ntrees/ha for the 158 sites in Minas Gerais.

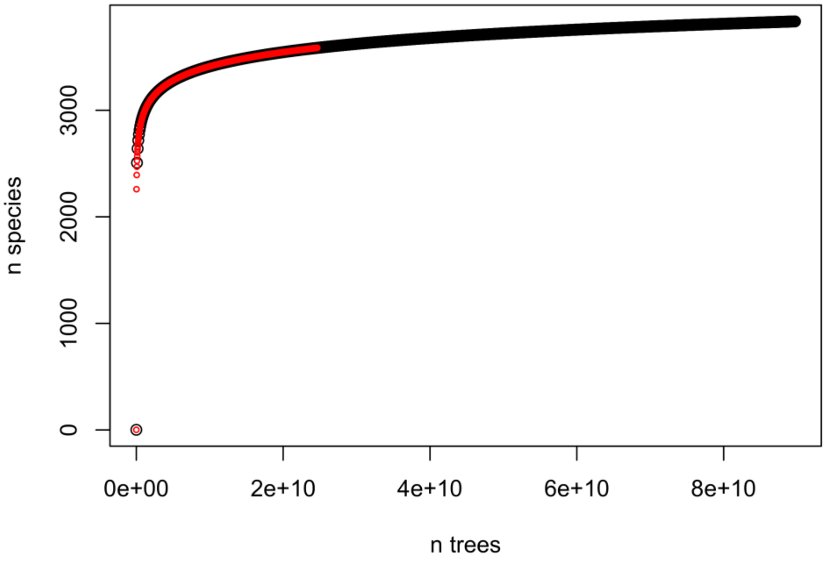


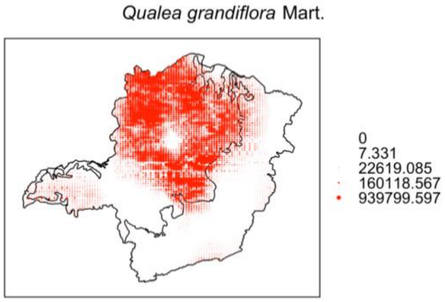
Fig. 8 Species-individuals curve for the estimated original number of trees and tree species (black) and the same curve for the estimated current number of trees and tree species in Minas Gerais.

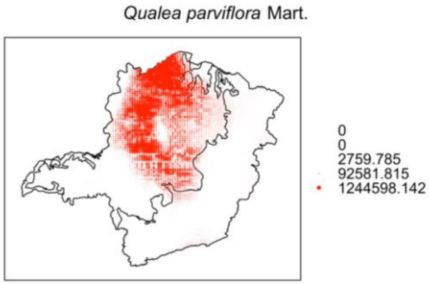
APPENDIX 2
Tree Dominance and Diversity in Minas Gerais, Brazil

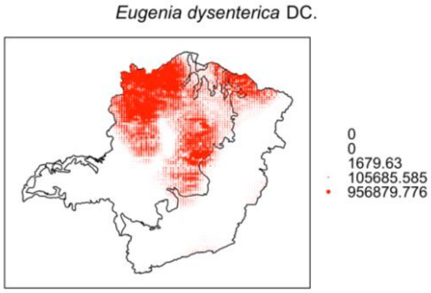
Biodiversity and Conservation

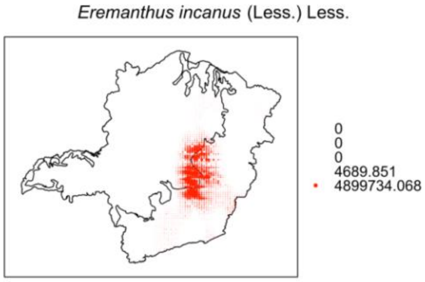
Marcela de Castro Nunes Santos Terra, Rubens Manoel dos Santos, Marco Aurélio Leite Fontes, José Marcio de Mello, José Roberto Soares Scolforo, Lucas Rezende Gomide, Jamir Afonso do Prado Júnior, Ivan Schiavini, Hans ter Steege

Abundance-distribution maps for the 20 most abundant species in Minas Gerais, Brazil.

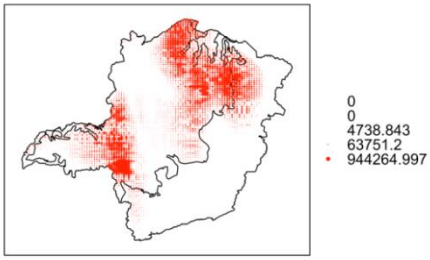

Qualea grandiflora Mart.


Qualea parviflora Mart.

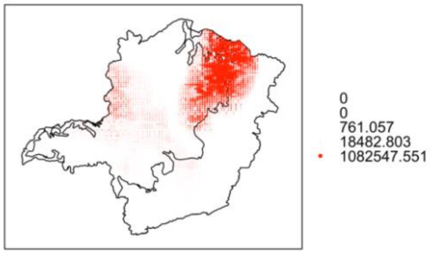

Eugenia dysenterica DC.


Eremanthus incanus (Less.) Less.

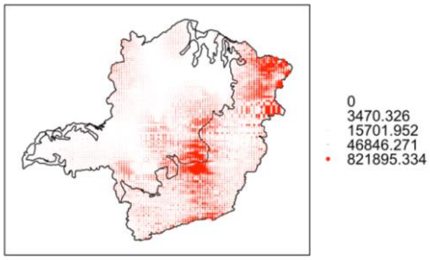
Myracrodruon urundeuva Allemão



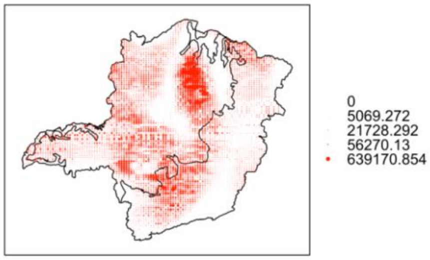
Dalbergia miscolobium Benth.



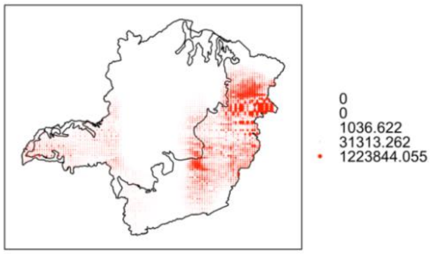
Myrcia splendens (Sw.) DC.



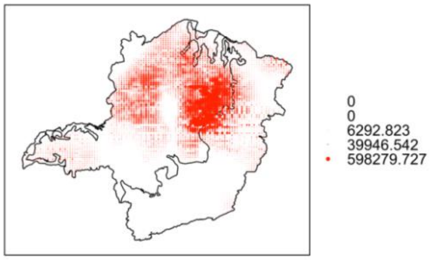
Copaifera langsdorffii Desf.



Mabea fistulifera Mart.



Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.



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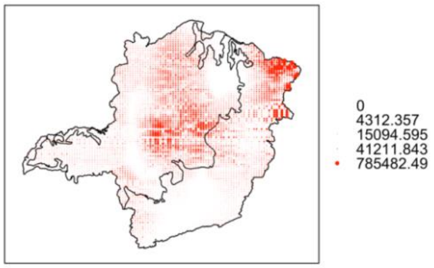

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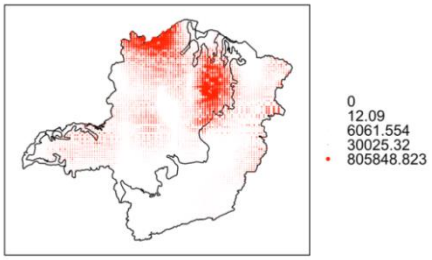

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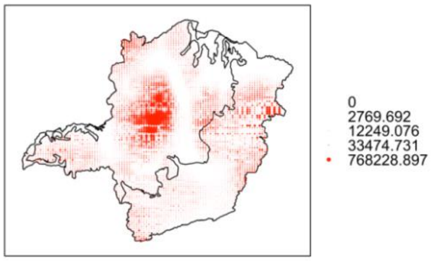

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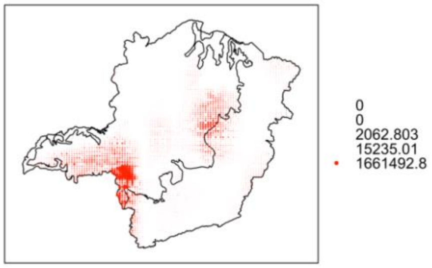
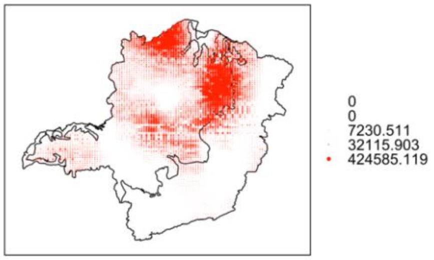


Caryocar brasiliense A.St.-Hil.



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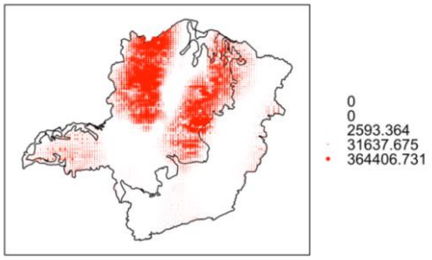

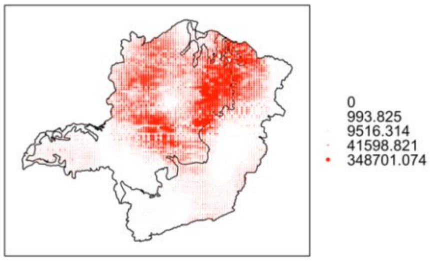
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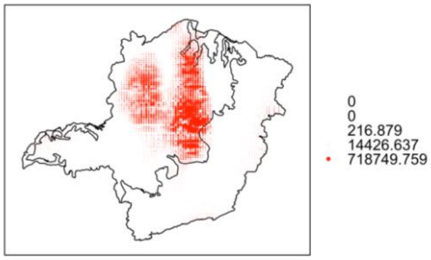
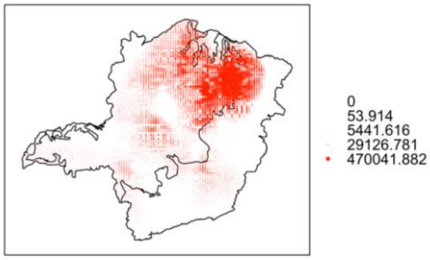

Magonia pubecens A. St.-Hil.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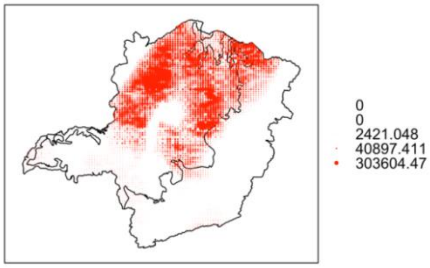
Hymenaea stigonocarpa Hayne

MANUSCRIPT 2 - WATER AVAILABILITY DRIVES GRADIENTS OF TREE DIVERSITY, STRUCTURE AND FUNCTIONAL TRAITS IN THE ATLANTIC-CERRADO-CAATINGA TRANSITION, BRAZIL

**prepared for*Journal of Vegetation Science*

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Abstract: Climate and soil are among the most important factors determining variation in vegetation features, but the comprehension of their independent effects is less clear. Here we evaluate how climate and soil gradients independently affect gradients of vegetation composition, species diversity and dominance, structure, and functional traits (seed mass and wood density) using over 327,000 trees in158 sites distributed along environmental gradients in the transition among Atlantic Forest, Cerrado and Caatinga in Minas Gerais state (MG), Brazil (nearly 600,000 Km²). Gradients in species abundance, genus abundance and family abundance,in addition to basal area, stem density, Fisher's alpha, dominance percentage, seed mass and wood density were correlated with environmental variables, summarized in four PCA axes (two climatic – precipitation seasonality and temperature range – and two edaphic – soil fertility and soil moisture). Multiple regressions models indicate that all variables but dominance percentage were affected by one or more of the environmental gradients, but the average R² was low (26.25%). Ordinary Kriging maps reinforced the patterns found in the regression models. Precipitation seasonality and soil moisture gradients were the most important gradients affecting vegetation features. This suggests that water availability is an important determinant of vegetation features in MG.

Key words: climate, soil, environmental gradient, vegetation, Southeast Brazil.

INTRODUCTION

One of the most important challenges facing plant ecology is to understand and predict the variation of plant communities across environmental gradients. By examining how species abundance, structure and functional traits vary across spatial abiotic shifts, especially in broader scales, we can begin to unravel the processes driving such ecological transitions and meet the demand for more realist scenarios in response to climate change and land-cover change.

The transition between open vegetation physiognomies and different forests types has been described in several regions of the Neotropics (Ratter 1992; Hirota et al. 2011; Staver et al. 2011; Hoffmann et al. 2012a,b). In central-eastern South America, a remarkable transition is found between vegetation belonging to the so called ‘open dry diagonal’ or simply ‘dry diagonal’ (Prado & Gibbs 1993; Werneck et al. 2012) and the Atlantic Forest (Oliveira-Filho & Ratter 1995; Oliveira-Filho & Fontes 2000). The dry diagonal represents a complex vegetation transition among its two main components: 1) the Seasonally Dry Tropical Forests (SDTFs, following the concept of Murphy and Lugo (1986)), present in Caatinga in northeastern Brazil and in Chaco in southwestern South America, and also as patches of deciduous and semideciduous Atlantic forests along Paraguay-Paraná Basin (Pennington et al. 2006; Werneck 2011); and 2) the Neotropical Savanna (Cerrado) in Central Brazil. The vegetation components of the “dry diagonal” share basic ecological conditions, being seasonally stressed by up to ten months of drought (Murphy & Lugo 1995; Pennington et al. 2006; Dalmagro et al. 2014).Although these vegetation types are among the most fragmented and threatened ecosystems in the world (Miles et al. 2006), presenting a complex mosaic-types distributions with high species endemism, they have received far less attention than tropical rainforest over past decades (Silva & Bates 2002; Werneck 2011).

Several controversial attempts to understand the origin and evolution of this biogeographic picture were made (Mayle 2004; Neves et al. 2015). The combined influences of Paleogene-Neogene geological processes and the Quaternary climatic-vegetation fluctuations are hypothesized to have generated the current range of Seasonally Dry Tropical Forest found in South America (Pennington et al. 2006). Therefore, the current patches of SDTF in South America may represent a relic of a wider seasonally dry forest biome that reached its maximum expansion during the driest phases of the Pleistocene covering the dry diagonal, the dry inter-Andean valleys in Peru and Ecuador (Prado & Gibbs 1993; Prado 2000), and even possibly covering lands in the Amazon interior, in areas of fertile soil (Pennington et al. 2000). These authors interpret findings of repeated patterns of fragmented populations as evidence that the current dry forest nuclei constitute remnants (i.e. refugia) of such former single formation, the Pleistocene Dry Forest Arc, split by vicariance after the subsequent climate and geological changes (for alternative hypothesis see Mayle 2004). As in South America, SDTFs grow under basically the same climatic conditions as Cerrado, recent adaptive shifts in the late Miocene (Cerling et al. 1997) driven by fire dynamics were identified as responsible by Cerrado current floristic and physiognomic distinction from SDTFs (Oliveira-Filho & Rattter 2002; Werneck et al. 2012; Dexter et al. 2015).

In Southeast Brazil, Minas Gerais state harbors the transition amongst the Atlantic, Cerrado and Caatinga Brazilian Domains. This transition represents a very intricate mosaic of SDTFs, savanna and even rain forest in the very south of the state. At a large scale, this transition seems to be climate-driven, taking for instance the transition from the rain forest in the south towards the SDTFs in the center, north and west (Oliveira-Filho & Fontes 2000). However, at a smaller scale, the edaphic influence is conspicuous, as patches of different biomes exist in each of these domains under similar climate conditions, but different soil conditions (e.g. galleries and enclaves) (Ratter 1992; Oliveira-Filho & Ratter 1995). Therefore, local boundaries between the forests and the open-formations (Cerrado) in such transitions are related to soil conditions, roughly with forest occurring on more fertile soils and open-formation on dystrophic and well drained soils (Ratter 1992; Coelho et al. 2016), and more frequent fire (Hoffmann et al. 2012). These different drivers, acting simultaneously, result in a complex vegetation gradient that has been well studied in terms of occurrence of tree species but poorly explored using abundance data.

Among several structural parameters used to describe tree community patterns, stem density and basal area seem to be strongly climate-soil-driven (Toledo et al. 2011; Arellano et al. 2014; Magnago et al. 2015). In tropical forests, they tend to be higher with a shorter dry season (Murphy & Lugo 1986; Toledo et al. 2011) and richer soils (Wright et al. 2011; Quesada et al. 2012). Therefore, in addition to providing a sense of the biomass and ecosystem productivity (Vieira et al. 2004), those parameters are also important to elucidate processes structuring a wide range of vegetation communities, and the main environmental drivers of such patterns (Toledo et al. 2011).

In addition to the composition and structural parameters, species functional traits allows us to understand the underlying determinants of species performance in a given environment and to demonstrate the importance of environmental filtering in determining the assembly of tropical forests (Poorter et al. 2008). Traits such as seed mass and wood density seem to respond to environmental conditions and have been called ‘functional response traits’ (Lavorel & Garnier, 2002; Prado-Junior et al. 2016). Sources differ on how seed size should be affected by stress gradients because seed mass is thought to reflect a tradeoff between viability and dispersal (Kitajima 2007). For instance, seeds are larger in the wetter areas or less dynamic forest in the Amazon (ter Steege et al. 2006) while larger seeds are also expected in stressful nutrient-limited environments (Lee & Fenner 1989; Mustard & Cowling 1992), such as Cerrado. For wood density, there is a consensus on the increasing density with environmental stress (Santiago et al. 2004; King et al. 2006; Poorter et al. 2008; Reich 2014). Here we hypothesize that two main abiotic gradients (climate and soil) drive current vegetation transition patterns in Minas Gerais, Brazil (approximately 600,000 Km^2): 1) one related to climate seasonality, which increases towards the north, and 2) one relative to soil fertility, which decreases towards the northwestern of the state. We address the implications of these gradients in tree taxa relative abundance (species, genus and family), diversity, species dominance, structure (basal area and stem density) and community weighted mean (CWM) functional traits of seed mass and wood density. We expect patterns of composition, diversity, structure and functional traits in tree communities in Minas Gerais to be consistent with the shifts in soil and climate. More specifically, we expect species diversity, basal area and density to increase towards the south of the state mainly due to climatic conditions; and seed mass and wood density to be higher in the north related to both climate and soil conditions.

METHODS

Data gathering. Our dataset included 158 vegetation sites in Minas Gerais State, Brazil (Figure 1; Appendix S1), from three main sources: the Minas Gerais Forest Inventory (Scolforo et al., available online), the Federal University of Lavras (CONFLORA group) and the Federal University of Uberlândia. Our dataset covered three Brazilian vegetation domains (Atlantic Forest, Cerrado and Caatinga) and six vegetation types (Rain Forest - RF, Seasonally Dry Tropical Forest semideciduous - SDTF_SD, Seasonally Dry Tropical Forest deciduous - SDTF_D, Cerrado sensu stricto - CE, Cerradão - CD and Swamp - SW). The sample area in those inventories varied from 0.12 to 17.2 ha (average 1.9 ha). The minimum diameter at breast height (DBH) of trees recorded was 5 cm. Taxonomy was standardized to family, genus and species according to TNRS (Boyle et al. 2013; http://tnrs.iplantcollaborative.org). The total number of trees recorded was 354,956, but we worked with a final number of 327,606 by not including unidentified trees.

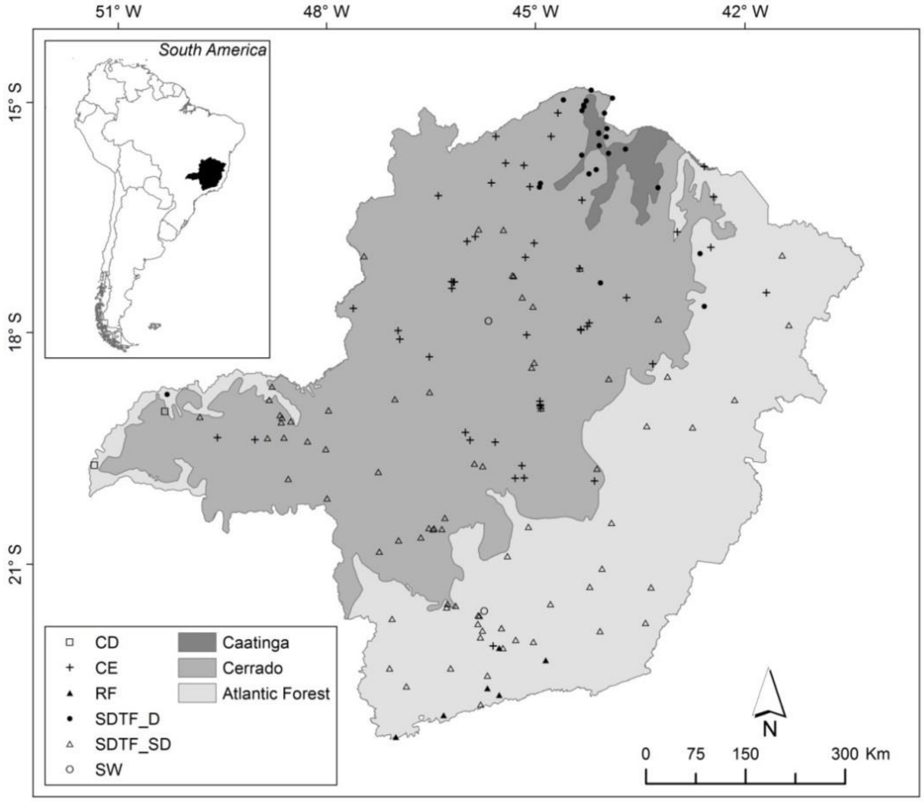


Figure 1. Location of the 158 sites in Minas Gerais state and their vegetation type classification. (Rain Forest - RF, Seasonally Dry Tropical Forest semideciduous - SDTF_SD, Seasonally Dry Tropical Forest deciduous - SDTF_D, Cerrado *sensu stricto* - CE, Cerradão - CD and Swamp - SW)

Environmental gradients. Based on the coordinates of each site, we obtained 19 WorldClim bioclimatic variables and site altitude (Hijmans et al. 2005; http://www.worldclim.org/bioclim). Two depths (0-5 cm and 5-15 cm) soil data – cation exchange capacity (CEC), Sand content (Sand), Clay content (Clay), Silt content (Silt), pH, Organic Carbon (ocarbon) – were extracted from ISRIC - World Soil Information (Hengl et al., 2016). In order to confirm the existence of the environmental gradients we ran principal component analysis (PCA) for both climate and altitude (PCA Climate) and soil (PCA Soil) variables. We considered the first two axes of each PCA as summaries of the variation in these abiotic components.

Composition, diversity and structure variables. To access the turnover in species relative abundance we carried out a detrended correspondence analysis (DCA) in different taxonomic resolutions (species, genera and family). We calculated Fisher's alpha (Fisher et al. 1943) as a diversity index for each site and a dominance index (%Dom) as the number of individuals of the most abundant species in a site divided by the total number of individuals in this site. Structure was addressed in terms basal area per hectare and the stem density (individuals per hectare).

Community-weighted mean traits We evaluated two functional traits that are important for responses to environmental conditions: community-weighted mean seed mass (CWM seed mass) and community-weighted mean wood density (CWM wood density). When calculating site scores for the functional tree traits, we followed ter Steege et al. (2006) and all individuals were counted. For seed mass, individuals were scored by genus and the traits values were obtained from SID-Kew (SID, 2015). Eighteen genera (4.04% of the genera) were not found in this database. For Wood density (oven-dried weight divided by green volume) was also scored by genus and the data were obtained from a global wood density database (Zanne et al. 2009; Global Wood Density Database, available online) which provided data for all genera recorded in the area.

Multiple regression and Ordinary kriging. To investigate the effects of the environmental gradients on vegetation composition gradients, species diversity and dominance, structural and functional variables we used linear multiple regression, with the four main environmental gradients as independent variables (tested by t-test) and each vegetation parameter as a dependent variable.

Finally, to better illustrate the variation in the vegetation variables we mapped all variables using geostatistical interpolation (ordinary kriging). We checked for spatial dependency via empirical semivariogram and fitted the Gaussian, Exponential and Sphericalspatial models (Journel & Huijbregts 1978) using weighted least squares. Thus, the selection of the best spatial model was based on the cross-validation measurements (mean standardized error and root-mean-square standardized error) (Vieira 2000). The set of parameters of the best model for each variable were then used to proceed with the ordinary kriging.

We used R vegan package (Oksanen et al. 2016) for diversity and ordination analysis and geoR package (Ribeiro-Júnior & Diggle 2015) and ArcGis 10.1 (Esri 2010) for geostatistical analysis.

RESULTS

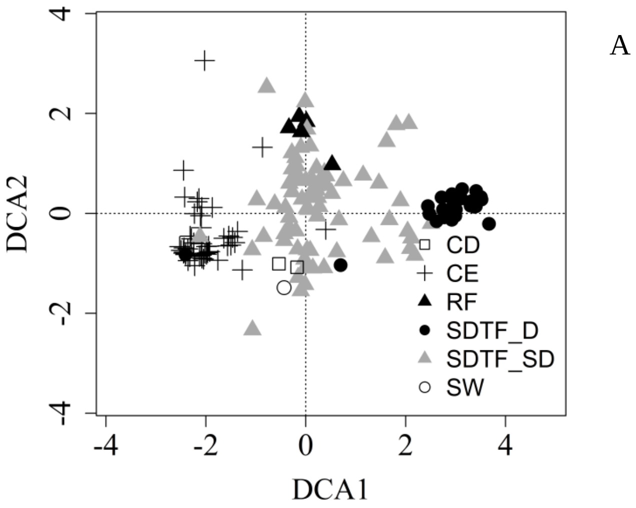
Environmental gradients

The firstaxis of the PCA Climate explained 67.83% of the total variation and was regarded as a proxy for precipitation seasonality and total precipitation, separating the sites in rain forest and deciduous forest (Figure S1). The second axis explained far less variation (12.12%) and was determined mainly by temperature (annual and diurnal) range, separating, for instance, semideciduous sites in the south from semideciduous sites in Jequitinhonha region (northwestern). The first axis of PCA Soil explained 43.85% of the total variation in the soil data and it is related to soil fertility and the second one explained 28.68% (Figure S2). . The second component was taken as a proxy of soil moisture, as it is related to soil texture and separated the deciduous sites from those of the rain forests in our dataset. Therefore, the four main axes of the

PCAs will, hereafter, be referred as Precipitation seasonality, Temperature Annual Range, Soil Fertility and Soil Moisture, respectively.

Composition gradients

The first axis of the DCA species level analysis was long (eigenvalue = 0.7809) and represented the turnover of species over a gradient between Cerrado and deciduous forest of Caatinga. The second axis of the DCA (0.5175) reflected the variation within Deciduous and Semideciduous Forests in Atlantic and Caatinga Domains. The genus level DCA (eigenvalues: 0.6017 and 0.5503) displayed an approximation between Cerrado and SDTF_D and at family level (0.3391 and 0.3295) we observed that the three main groups (Cerrado, Deciduous and Semideciduous) were closer along the first axis. Atlantic forest was the most heterogeneous group in all scenarios and Cerrado the most homogeneous. The two main axes of the three DCAs will, hereafter, be referred as species gradient (1 and 2), genus gradient (1 and 2), and family gradient (1 and 2), respectively (Figure 2).


A
DCA2
DCA1
4
2
0
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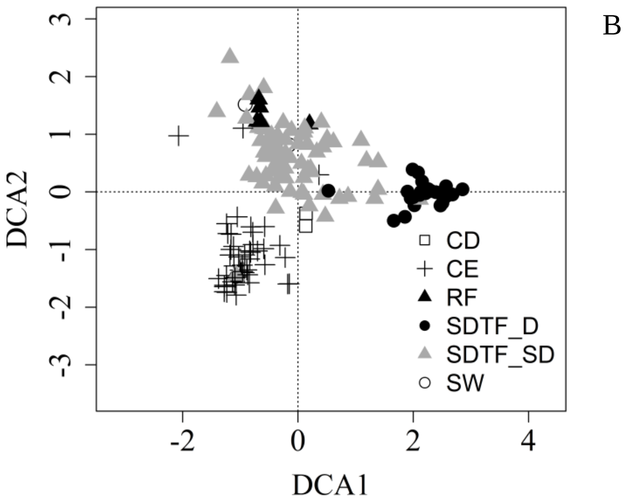
B
DCA2
DCA1
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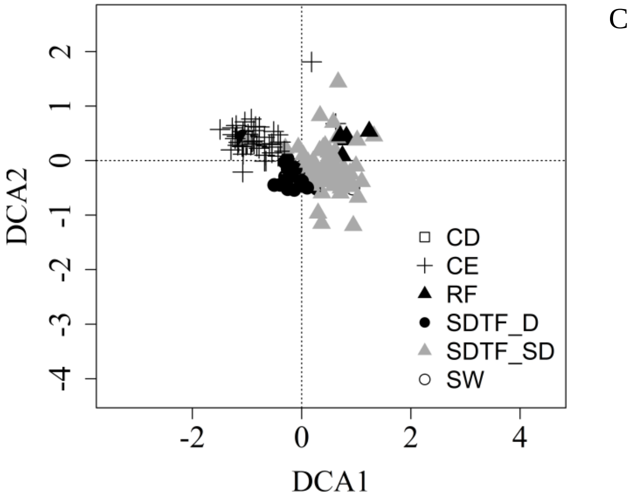

Figure 2: Detrended correspondence analysis (DCA) ordination plots of tree species (A), genus (B) and family (C) relative abundance of 158 sites in southeast Brazil. (Rain Forest - RF, Seasonally Dry Tropical Forest semideciduous - SDTF_SD, Seasonally Dry Tropical Forest deciduous - SDTF_D, Cerrado *sensu stricto* - CE, Cerradão - CD and Swamp - SW)

Regression and Ordinary Kriging

All the regressions between vegetation and environmental gradients were significant (F-test; p-value<0.05), except for the %Dom (Table 1). The average coefficient of determination (R²) was 26.25%, with the compositions gradients (DCA axes) and Fisher's alpha having the highest values and the structural and functional traits variables the lowest ones. Precipitation seasonality and Soil moisture were more important for vegetation than Temperature Annual Range and Soil fertility, according to t-test.

Table 1. Linear multiple regression analysis of vegetation composition gradients, species diversity and dominance, structure, functional traits variables on environmental variables (climatic and soil axes and their quadratic terms, as indicated by the squares) for 158 sites in Southeast Brazil. (Variables shaded in gray were significant according to t-test).

	(Int.)	**Precip. seasonality**	**Temp. Range**	**Soil fertility**	**Soil Moisture**	**R^2**	**p-value (F-test)**
Spp. grad. 1	-1.56E-10	0.888	-0.008	0.406	0.486	15.45	3.393E-05
p-value	1.000	2.11E-06	0.953	0.010	0.017		
Spp. grad. 2	-3.50E-11	1.037	-0.220	-0.011	0.441	35.20	1.077E-13
p-value	1.000	2.51E-13	0.023	0.924	0.003		
Genus grad. 1	0.019	1.414	-0.070	0.381	0.398	42.71	< 2.2e-16
p-value	0.777	< 2e-16	0.540	0.005	0.021		
Genus grad. 2	-0.013	0.581	-0.029	-0.354	-0.637	39.27	8.386E-16
p-value	0.844	2.38E-04	0.803	0.009	3.09E-04		
Family grad. 1	0.005	0.695	-0.048	0.045	0.141	57.21	< 2.2e-16
p-value	0.849	<2e-16	0.275	0.382	0.035		
Family grad. 2	-0.012	0.010	-0.042	-0.351	-0.452	22.71	5.059E-08
p-value	0.784	0.920	0.591	1.53E-04	1.63E-04		
Basal area	19.586	3.469	-0.787	1.263	-7.811	14.72	6.290E-05
p-value	2.00E-16	0.179	0.680	0.571	0.007		
Tree density	1.28E+03	243.800	18.950	-123.760	-123.450	16.39	1.530E-05
p-value	2.00E-16	0.008	0.777	0.115	0.222		
Fisher's alpha	2.37E+01	6.412	-1.000	-1.151	-10.421	29.32	6.930E-11
p-value	2.00E-16	0.011	0.589	0.594	2.57E-04		
%Dom	1.61E-01	-0.013	-0.017	-0.016	0.025	4.03	0.176
p-value	<2e-16	0.512	0.247	0.346	0.256		
Seed mass	4.51E+00	-0.153	-4.00E-04	0.140	-0.178	9.97	0.003
p-value	<2e-16	0.021	0.994	0.015	0.016		
Wood density	6.67E-01	-0.023	0.015	0.017	0.004	17.23	7.370E-06
p-value	2.00E-16	0.007	0.016	0.019	0.638		

All the variables displayed spatial dependency fitted by different spatial models (see semivariograms inAppendix 2). The range of the spatial models fitted varied from 70 to 900 Km. Longer ranges were found for differentiation in species abundance (composition gradients) and diversity. In the other hand, Basal Area, Stem density, seed mass and wood density displayed more variance in shorter distances (shorter ranges) but kept a pattern in longer distances. Especially for the functional traits, the maps displayed a bit of a specs effect due to the shorter ranges of the spatial dependency. Overall, the kriging maps (Figure 3) reinforced the results of the regressions.

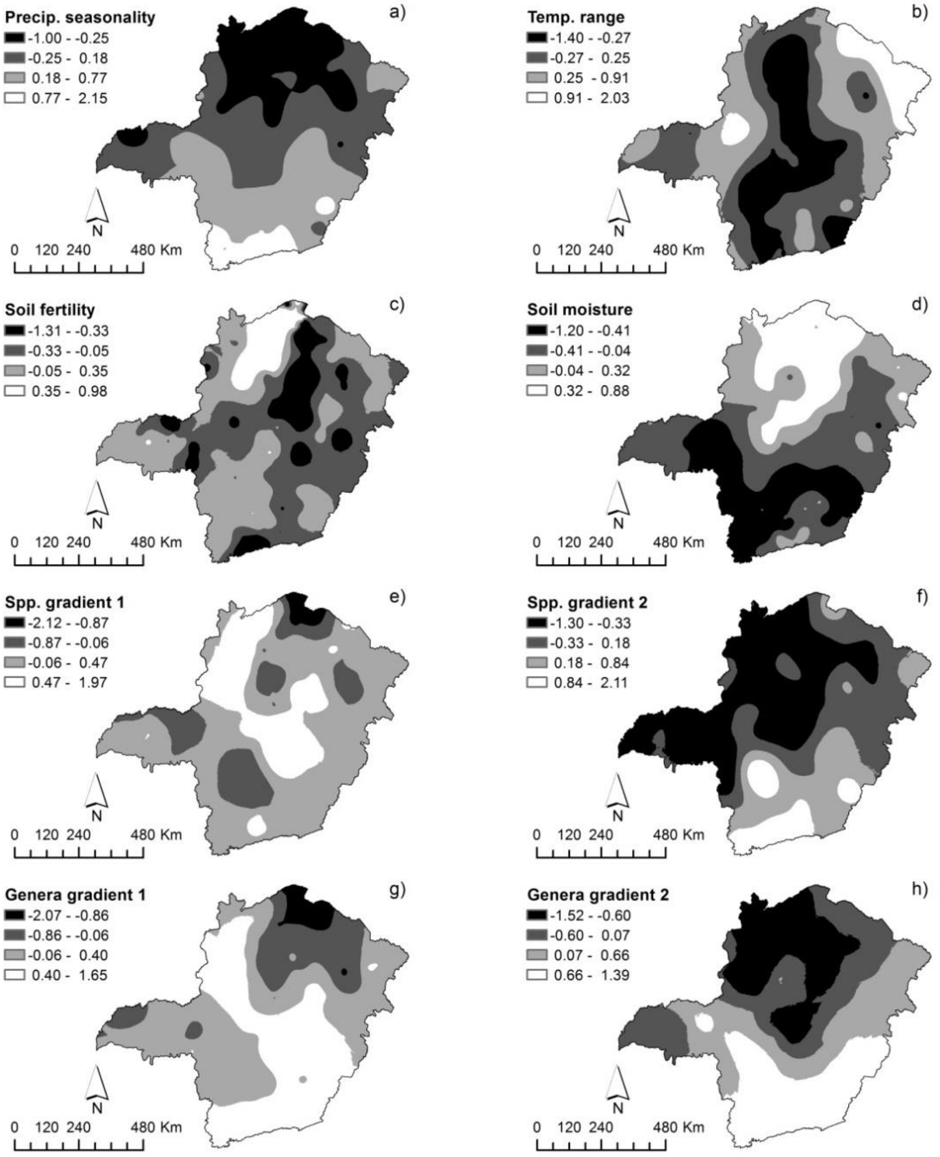

Figure 3. Interpolation by Ordinary Kriging maps of the variables considered in this study and the intervals values for each class in the maps. (The classes' values of climate, soil and composition gradients represent site scores in PCA and DCA analyses).

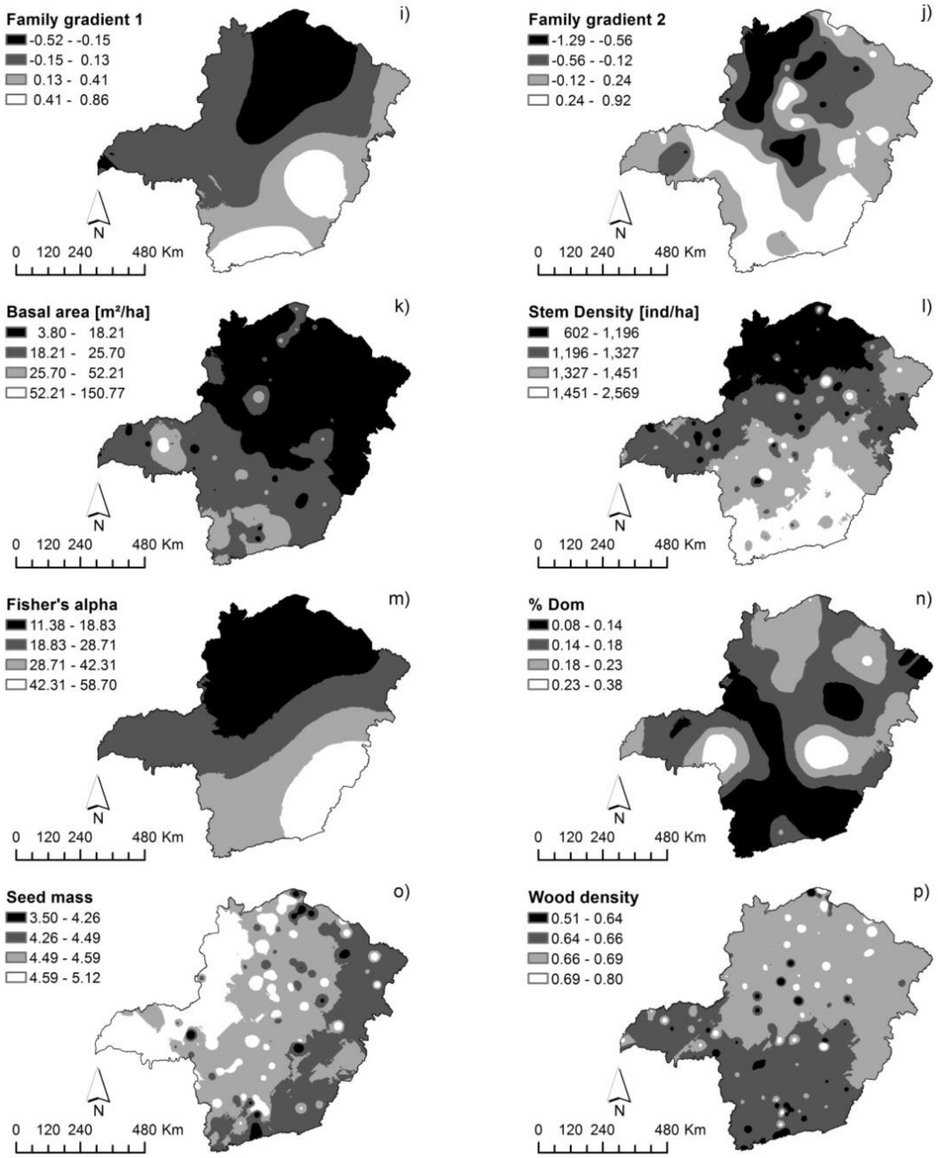

Figure 3. Interpolation by Ordinary Kriging maps of the variables considered in this study and the intervals values for each class in the maps. (The classes' values of climate, soil and composition gradients represent site scores in PCA and DCA analyses).

A combination between the regressions and maps lead to the scheme presented in Figure 4.

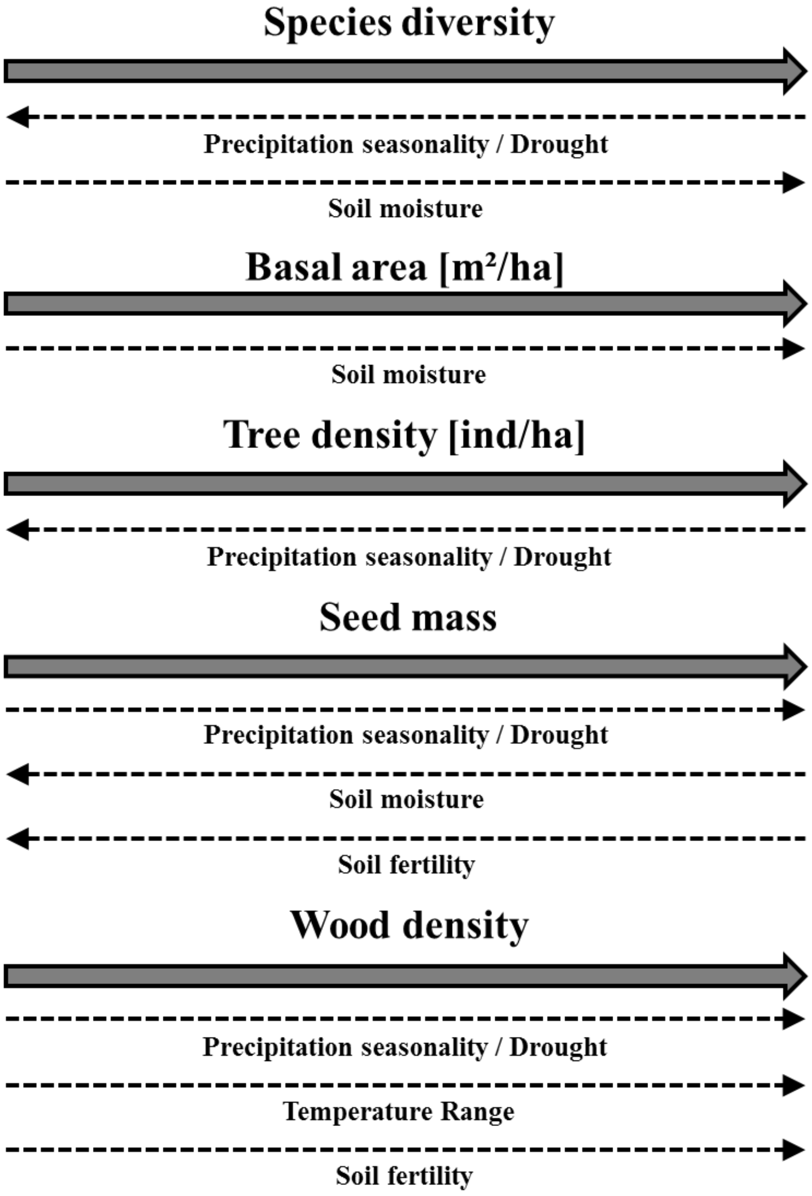

Figure 4. Schematic diagram illustrating relations between vegetation parameters and environmental gradients in Southeast Brazil.

DISCUSSION

This paper aimed to evaluate to what extent patterns in vegetation attributes are driven by climate and soil in Southeastern Brazil by correlating attributes of diversity, structure and functional traits of tree communities in different vegetation types with abiotic environmental gradients (climate and soil). Our results showed the different roles played by the environmental drivers in each feature of the vegetation in Minas Gerais displaying very complex patterns.

Environmental gradients

Precipitation seasonality clearly displayed a gradient of sites of Rain forests, semi-deciduous forests, Cerrado and deciduous forests and its map illustrates this gradient, which has a north-south pattern (stronger seasonality in north). Secondarily, temperature annual and diurnal range seemed responsible for variation along longitude, as one can see in the kriging map. The lower class in the temperature range map (the black one), coincided with the Espinhaço Range (altitude up to 1,700 m) (Fernandes et al. 2014), suggesting the impact of this mountain range on the regional climate, especially on the temperature ranges which are higher in this region. In addition, the general pattern of temperature range map roughly coincided with Koppen climate classification for MG, with the two “Tropical Zones” (Koppen’s ‘A’) separated by a “Humid Subtropical Zone” (Koppen’s ‘C’) (Alvares et al. 2013). Soil fertility caused major differentiation between deciduous forest and Cerrado. Soil moisture was responsible for differentiating the extremes of rain and deciduous forest.

Composition and diversity gradients

Gradients in taxa composition (relative abundance) had different patterns for different taxonomic resolution (species, genus and family). At the species level, we found a major differentiation between Cerrado and Deciduous forests, and the rain and semideciduous forests interleaved between them. The values of the DCA first axis scores at species level varied according to the precipitation seasonality and soil moisture. As the major differences were between Cerrado and dry forest, and they share some basic climatic conditions, subtle differences in the length of dry season (slightly greater at deciduous forest) might contribute to differentiate them. Rain distribution act as a selective force influencing the reproductive behavior of the plants and causing differential birth and mortality in the plant populations, especially in deciduous forest, with the predominant period of germination occurring during the rainy season (Araújo et al. 2007; Santos et al. 2007; Albuquerque et al. 2012). Regarding the soil, Cerrado is known as a soil climax vegetation (Pinheiro & Monteiro 2010), occurring mainly in well-drained soil, with high Al levels (Ratter & Dargie 1992). Conversely, we have deciduous forest occurring in dry but highly fertile soils in northern MG (Apgaua et al. 2014). Those soil differences certainly filter species. For instance, many widespread dominant Cerrado genera, such as *Qualea* and *Eugenia* (Terra et al., in review) are Al accumulators (Jansen et al. 2002; Haridasan 2008). Besides, the plant phylogenies presented by Simon et al. (2009) showed that Cerrado lineages are strongly associated with recent (4 Mya or less) adaptations to fire. Therefore, the synergic interaction of all these factors (especially soil and fire) might be causing the differences observed here at species level by selecting the species adapted to local conditions (Silva & Batalha 2008).

The variation within deciduous and semideciduous forests and between semideciduous and rain forest at species level (species gradient 2) are related to temperature range and also to soil moisture. These forests present more idiosyncrasies related to altitude variation – especially semideciduous and rain forest (Oliveira-Filho & Fontes 2000; Eisenlohr & Oliveira-Filho 2015) – and punctual soil and geology variation – mainly dry forest (Santos et al. 2012; Apgaua et al. 2014) – harboring a great species turnover. These “internal” differences seem not to reach Cerrado, which presents less species turnover, behaving in a more stable way when it comes to climate and soil moisture leading to a minor beta-diversity when compared to forests in our dataset. Having less beta-diversity does not mean having little beta-diversity, as all three systems are reported to hold great beta-diversity (Bridgewater et al. 2004; Françoso et al. 2016; Apgaua et al. 2014).

Despite all the differences showed at species levels, the mutual influence between forest and savanna throughout evolutionary history in our study region has been reported in the literature, as occasional occurrence of species from a certain formation in another, to which the species is less tolerant is not rare, especially in the edges and transitions (Forni-Martins & Martins 2000; Silva & Batalha 2008; Simon et al. 2009; Albuquerque et al. 2012). At genus and family level, the three main vegetation types (Cerrado, semideciduous and deciduous) are closer, and we observed an approximation between Cerrado and Deciduous Forest in the DCA’s fist axis. Simon et al. (2009) reported the existence of sister groups between Cerrado and largely fire-free nearby wet forest, seasonally dry forest, subtropical grassland, or wetland vegetation. For instance, the semideciduous forests are known for having strong links with Cerrado at genus and family levels sharing important families such as Rubiaceae and Melastomataceae (Oliveira-Filho & Fontes, 2000). On the other hand, the relative importance of families such as Myrtaceae and Fabaceae approximates Cerrado and Deciduous forest at these taxonomic levels (Mendonça et al. 1998; Ratter et al. 2003; Pennington et al. 2006). Mytaceae and Fabaceae families are also important in semideciduous forests, especially in low altitudes (Fabaceae) (Oliveira-Filho & Fontes 2000).

A review of studies across environmental gradients found that the most common pattern is increasing species richness with gradients of water availability (Cornwell & Grubb 2003). We corroborate with this pattern as the gradient in diversity (Fisher's alpha) was highly correlated to the gradients of water availability in terms of both climate (the lower the precipitation seasonality the higher the tree diversity) and soil (the higher the soil moisture the higher the diversity). Therefore, in MG we observed a "counter-latitudinal" pattern of tree species diversity. In the north of MG, drought can be interpreted as a strong environmental filter selecting species, as it has been shown for other regions within the Neotropics (Esquivel-Muelbert et al. 2016). In the south, in less seasonal and more "favorable" environments, more species can establish leading to higher diversity. Besides, the internal variation in the south caused mainly by the topography may create more local niche opportunities (Leigh Jr et al. 2004), increasing the diversity. Such patterns have an evolutionary influence, since Atlantic forest, although retracted, remained forested throughout dry glacial times (Werneck et al. 2011), and this has potentially increased its relative diversity.

Percentage of dominance has not followed any environmental gradient, but their interpolations clearly showtwo regions of major dominance (white class in the interpolation map). The western one represents the effect of *Myracrodruon urundeuva* in patches of deciduous forest and the eastern one is a*Eremanthus incanus*occuringregion. Both of these species are among the most abundant tree species in the regions (Terra et al., in review). In addition, it is possible to see a background trend of local dominance increasing towards the north, following the diversity pattern.

Structure gradients

We found vegetation structure patterns consistent with the literature. We found, in general, more basal area per hectare in the humid south and less in the dry north. The increasing of basal area towards the west in the region better known as “triângulo mineiro” is due to the existence in such region of the Cerradão, a forest-like face of Cerrado (Oliveira & Marquis 2002). Cerradão is physionomically a forest but its species composition is related to Cerrado. Also, Cerradão is one of the reasons we found basal area significantly related to soil conditions, as this vegetation type has more basal area than Cerrado *sensu stricto* and occurs typically at dystrophic to mesotrophic soils (Oliveira & Marquis 2002; Neri et al. 2013). Another reason for the pattern presented is that deciduous forest up north, which have lower basal area per hectare, mainly as an effect of climate limitation (precipitation seasonality), occur in fertile soils (Apgaua et al. 2014).

In which comes to density, we found punctual differences within a general pattern of decreasing towards the deciduous in the north. We found this pattern to be correlated to precipitation seasonality. Seasonally Dry forests usually have fewer individuals per area than humid ones (Murphy & Lugo 1986), mainly because the period of recruitment of seedlings is strongly restricted to the rainy period (Albuquerque et al. 2012). The occurrence of a region of higher density in the northeast of MG is due to effect of the transition from the Atlantic forest of coastal Bahia from evergreen to semi-deciduous, and then to deciduous forests up to a distance of 200–250 km inland (Thomas et al. 2008; Saiter et al. 2015). The occurrence of areas of lower density in the south is possibly due to anthropogenic interference. Human interference certainly produces long-lasting and complex effects on natural vegetation. Fragmentation (Santo-Silva et al. 2016), and human impacts (Pereira et al. 2015) might have masked some natural differences, especially in the Atlantic semideciduous and rain forest. For instance, Pereira et al. (2015) studying 20 areas in Southeastern Brazil reported that forest structural parameters (basal area and tree density) are affected by cattle and outer roads. The presence of cattle in the forest fragments studied by Pereira et al. has direct relationship with the trees that had larger diameters, suggesting that recruitment was affected by trampling by livestock causing damage to smaller plants. In addition, outer roads lead to landscape changes and had a significant impact on basal area and densities of less high trees.

Functional traits gradients

We expected the CWM seed mass to increase towards the sites with lower precipitation seasonality, but instead, apparently, in semideciduous and rain forests where the environmental filter is weaker we have a mix of seed sizes. Our results pointed out differences in the seed ecology between Cerrado and forest (semideciduous, deciduous and rain), with the CWM increasing towards the Cerrado. Additionally, we found that CWM seed mass was related to both climate and soil conditions with higher CWM seed mass in more seasonal sites and with lower soil fertility and soil moisture.

In a broader scale, our results seem to support experimental evidence (Lee & Fenner 1989; Mustart & Cowling 1992) that larger seeds enhance species fitness in nutrient limited soil (Cerrado). Dainese & Sitzia (2013) also documented, regarding the relationship of seed mass with soil fertility that seed mass decreases from low – fertility grasslands to high – fertility grasslands, which roughly explains the lower average in Atlantic forests and the higher values in the region of Cerrado. Species with higher seed mass have the larger seed reserves, which allows them to make large, robust seedlings that face fewer problems caused by defoliation and drought (ter Steege 1994; Leishman et al. 2000; Paz et al. 2005) enhancing their fitness in stressful environments.

The interpolation map showed some areas occurring in the extremes (rain and deciduous forest) sharing the same class, the one with smaller seeds, and a major tendency to increase to towards the west. Both small and large seed can be advantageous in stressful environments, whereas large seeds are advantageous under strong competition (Leishman 2001; Moles & Westoby 2004; Coyle et al. 2014). Again, the lower seed mass in the south can be a consequence of the fragmentation that lead to proliferation of fast-growing pioneer species (Santo-Silva et al. 2016) which have in general lighter seeds. Hanley et al. (2007) recommend caution in attempts to link traits like seed size to wider patterns of plant community ecology. The authors advert that habitat-specific differences in regeneration conditions and/or evolutionary history may influence the role that seed size plays in dictating how seedlings of different species respond to nutrient shortage. Functional groups may be filtered by different traits, implying that process of community assembly operate differently depending on the functional group (Hoffmann et al. 2004) which might explain the convergence between deciduous and rain forest in which regards to this trait.

We found that CWM wood density was also related to both climate gradients and soil fertility (higher CWM wood density in sites with higher precipitation seasonality, temperature range and soil fertility). The interpolation map showed a broader north-south variation, but also a great variation in smaller scales. Low-water and nutrient availability in stressful environment favors high resource use efficiency and resistance to embolism leading to high wood density (Barajas-Morales 1987; Hacke et al. 2001; Martínez-Cabrera et al. 2009; Markesteijn et al. 2011; Coyle et al. 2014), as we could see in our dry forests in the north. On the other hand, competition favors fast growth and consequently low wood density species (Hacke et al. 2001; Martínez-Cabrera et al. 2009; Coyle et al. 2014) so we found lighter wood average in the rain forest in the south. This might be boosted by the increase in short-lived pioneer species in these forests (Santo-Silva et al. 2016). Chave et al. (2006) also found higher mean wood density for dry forest (Cerrado, deciduous, and semideciduous) in South America when compared with other Neotropical vegetation and attributed this pattern to the fact that higher wood density is better to resist to drought-induced embolism.

FINAL REMARKS

Finally, here we reinforce a pattern that at a regional scale, variation in tree communities in tropical region are related mainly to water and energy availability, and energy–water balance (Oliveira-Filho & Fontes 2000; Pausas & Austin 2001; Toledo et al. 2011; Qian 2013). Precipitation seasonality and soil moisture were the most important drivers of vegetation parameters. Precipitation seasonality and soil moisture together determine tree water availability, which seems to be the key factor in vegetation ecology in MG. As climate-change scenarios predict an increase of summer precipitation over southeastern South America and reduction of winter precipitation over most of the continent (Vera et al. 2006), we may expect potentially large changes in the structure, diversity and functioning of these and other tropical forests.

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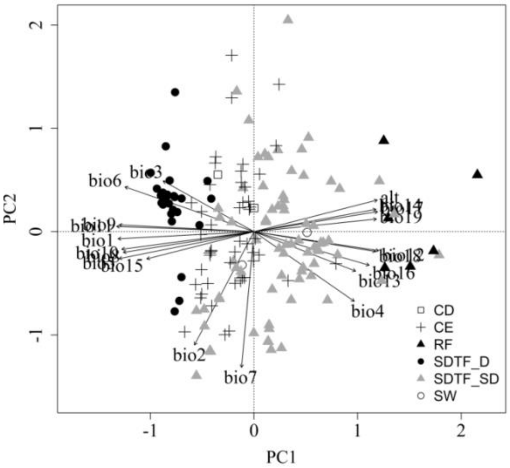
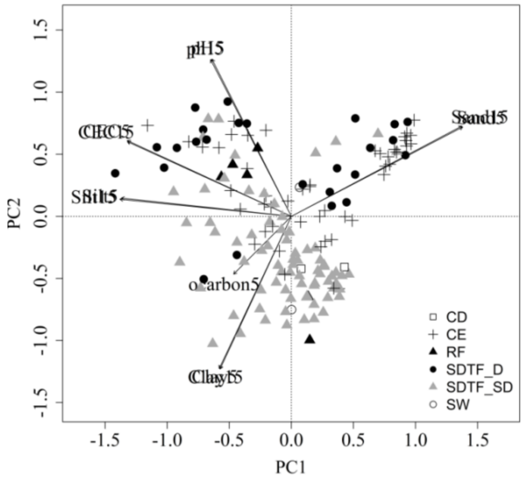
Supporting information
Terra, M.C.N.S. et al. Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-Cerrado-Caatinga transition, Brazil.

Appendix S1. Principal Component Analysis for (a) the 19 climatic variables and altitude and (b) the five soil variables (in two different depths).

a)



b)



Supporting information to the paper
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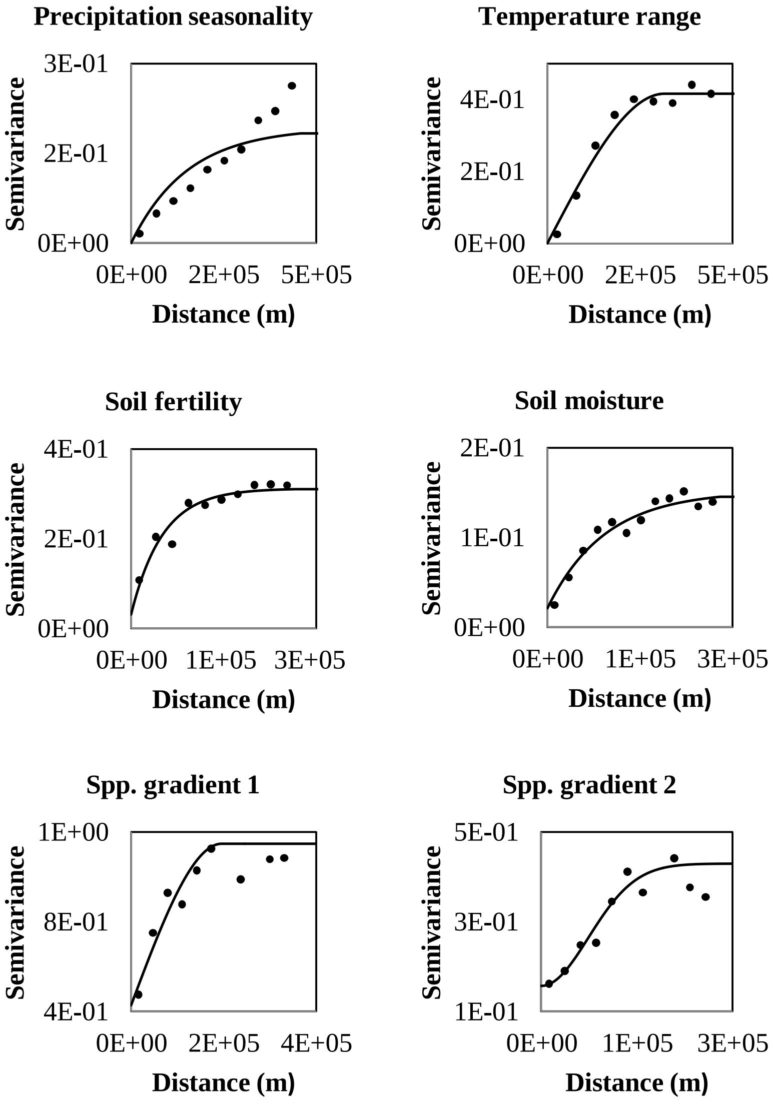
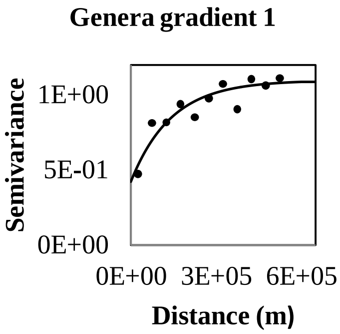
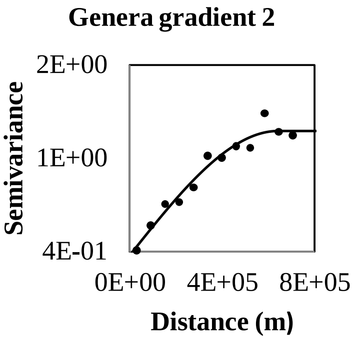
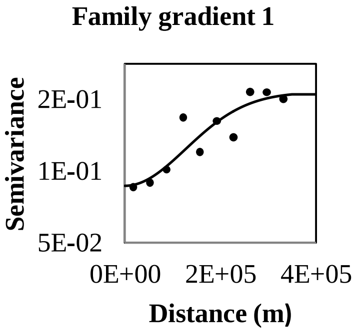
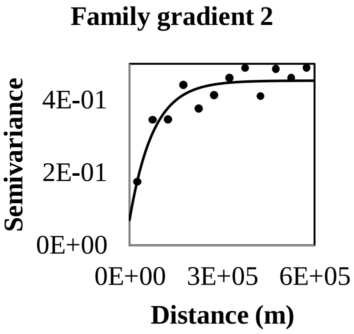
Appendix S2. Experimental semivariograms for the 16 variables used in the modelling presented presented in Table 1.


Precipitation seasonality
Temperature range
Soil fertility
Soil moisture
Spp. gradient 1
Spp. gradient 2


Genera gradient 1


Genera gradient 2


Family gradient 1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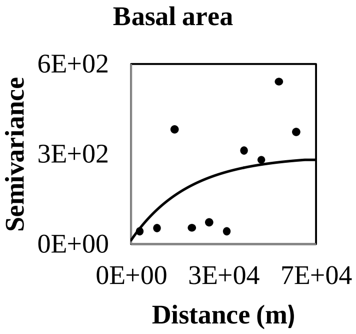
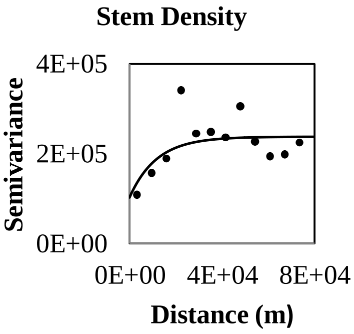
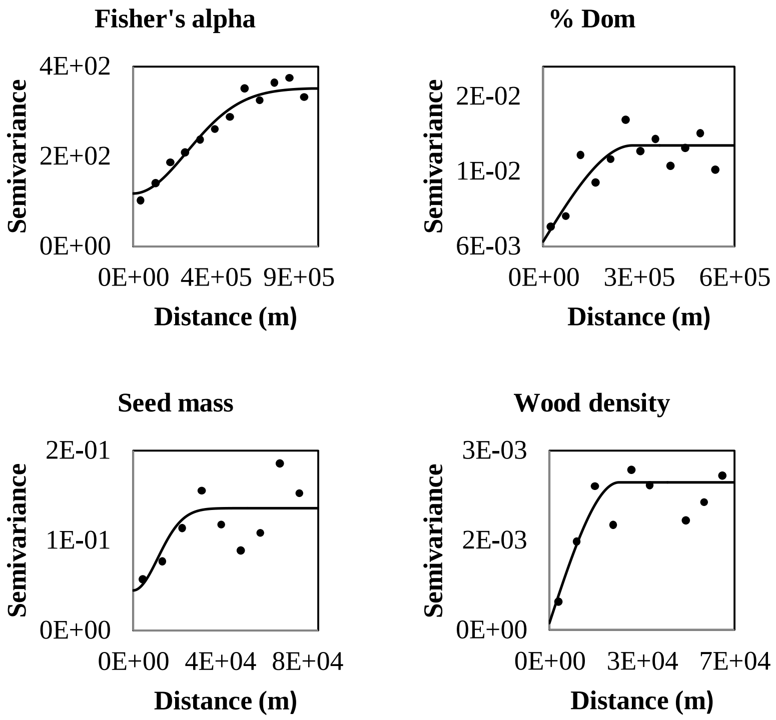

Basal area


Stem Density


Fisher's alpha
Semivariance
4E+02
2E+02
0E+00
0E+00
4E+05
9E+05
Distance (m)
% Dom
Semivariance
2E-02
1E-02
6E-03
0E+00
3E+05
6E+05
Distance (m)
Seed mass
Semivariance
2E-01
1E-01
0E+00
0E+00
4E+04
8E+04
Distance (m)
Wood density
Semivariance
3E-03
2E-03
0E+00
0E+00
3E+04
7E+04
Distance (m)