POLYANNE APARECIDA COELHO

SPECIES OR ENVIRONMENT: WHAT DRIVES ECOSYSTEMS
PROCESSES IN TROPICAL FORESTS?

LAVRAS – MG
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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.

Prof. Dr. Rubens Manoel dos Santos
Orientador

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SPECIES OR ENVIRONMENT: WHAT DRIVES ECOSYSTEMS PROCESSES IN TROPICAL FORESTS?

ESPÉCIES OU AMBIENTE: O QUE GUIA OS PROCESSOS ECOSSISTÊMICOS NAS FLORESTAS TROPICAIS?

> 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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GENERAL ABSTRACT

The ecosystem processes provided by tropical forests are of central importance to life on Earth. Brazil is a country with extensive vegetation coverage and great environmental heterogeneity, thus harbouring great biodiversity within its phytogeographical domains. To better understand the ecosystem processes along the time, the Long Lasting Ecological Projects are a very important tool, where an area is periodically revisited with biological information updated. Linking these data with climate, soil and biodiversity characteristics provides a set of important information about ecosystem functionality, which helps to understand and predict vegetation changes along the time. The present work sought to understand the role of climate, soil and biodiversity (taxonomic and phylogenetic) in the explanation of four ecosystem processes: aboveground biomass (AGB) storage, aboveground wood productivity (AGWP), mortality and recruitment of tree communities, along a seasonal gradient in the southeast of Brazil. Two work scales were considered: one at the fragment level (Site) and another at the plot level, being that in a Site there are several Plots. There was a tendency for higher values of AGB and AGWP in Evergreen Moist Forest, higher recruitment in Deciduous Tropical Forest and higher mortality in the Semideciduous Tropical Forest. The different scales showed different importance among the factors studied. On the larger scale, in addition to the environmental variables, floristic composition variables were also explanatory for AGB and mortality, while on the smaller scale, both taxonomic and phylogenetic biodiversity variables were important. We considered that the use of smaller scales, especially in more heterogeneous environments, can capture greater fineness of interactions, being able to provide more detailed explanation for the studied processes. Generally, in our study, environmental variables were more explicative of ecosystem process than biodiversity and we believe that it occurs because we worked in a seasonality gradient, where the difference in environmental characteristics among the forest types already define the presence of the species found in each of them. Even so, especially on a smaller scale, biodiversity variables can account for some of the variation in ecosystem processes.

Key-words: Forest dynamics. Atlantic Forest. Caatinga.

RESUMO GERAL

Os processos ecossistêmicos fornecidos pelas florestas tropicais são de grande relevância para a vida na Terra. O Brazil é um país com extensa cobertura vegetal e grande heterogeneidade ambiental, abrigando assim grande biodiversidade dentro de seus domínios fitogeográficos. Para melhor entender os processos ecossistêmicos ao longo do tempo, os Projetos Ecológicos de Longa Duração são uma importante ferramenta, onde uma área é periodicamente revisitada e tem suas informações biológicas atualizadas. Vinculando tais informações com características climáticas, edáficas e de biodiversidade, produz-se uma série de importantes informações sobre a funcionalidade dos ecossistemas, ajudando a entender e prever mudanças da vegetação ao longo do tempo. O presente trabalho buscou entender o papel do clima, solo e biodiversidade (taxonômica e filogenética) na explicação de quatro processos ecossistêmicos: estoque de biomassa acima do solo (AGB), produtividade lenhosa acima do solo (AGWP), mortalidade e recrutamento da comunidade arbórea, ao longo de um gradiente de estacionalidade climática no sudeste do país. Considerou-se duas escalas de trabalho: uma a nível de fragmento e outro a nível de parcela, onde em um mesmo fragmento existem várias parcelas. Houve uma tendência de os maiores valores de AGB e AGWP serem encontrados na Floresta Ombrófila, o maior recrutamento na Floresta Estacional Decidual e maior mortalidade na Floresta Estacional Semidecidual. As diferentes escalas mostraram importância distinta entre os fatores estudados. Na escala maior, além das variáveis ambientais, variáveis de composição florística também se mostraram explicativas para AGB e mortalidade, enquanto que na escala menor, tanto as variáveis de biodiversidade taxonômica quanto filogenética foram importantes. Considera-se que o uso de escalas menores, principalmente em ambientes mais heterogêneos, consegue captar maior fineza de interações, podendo fornecer explicação mais detalhada para os processos estudados. De forma geral, em nosso estudo, as variáveis ambientais foram mais explicativas que as variáveis ligadas a biodiversidade e nós acreditamos que isso aconteça porque, trabalhando em um gradiente de estacionalidade, onde as diferenças nas características ambientais entre os tipos florestais já definem a ocorrência das espécies encontradas em cada um deles. Mesmo assim, especialmente na escala menor, as variáveis de biodiversidade ajudam na explicação de parte dos processos ecossistêmicos.

Palavras–chave: Dinâmica florestal. Mata Atlântica. Caatinga.

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CHAPTER 1 – GENERAL INTRODUCTION

ABSTRACT

Tropical forests have high biodiversity and provide important ecosystem services. Long-term ecological studies provide key information for increasing knowledge about these environments. In particular, long-term monitories allows estimation of biomass storage, productivity and demography of plant communities. All these vital functions and processes are associated with a wide range of variables that should be considered. Climatic aspects such as precipitation and temperature, soil fertility and texture characteristics are of recognized importance in the elucidation of ecosystem processes. In addition to climatic and edaphic variables the importance of the species themselves and their associated functional characteristics, has also been perceived as playing a key role for determining these functions. In hyper diverse forests there is still no exact knowledge of which traits are most important and it is of great logistic and financial difficulty to measure a large number of traits. In this sense, the knowledge about the phylogenetic relationships among species is of great importance, since related species tend to share a large number of functional traits, thus optimizing the information about them. The knowledge of biotic and environmental characteristics helps in the elucidation of the ecosystem functionality, being of special importance in very heterogeneous environments, such as Brazilian Tropical Forests.

Keywords: Biomass storage. Productivity. Climate. Soil. Phylogenetic diversity.

RESUMO

 As florestas tropicais possuem elevada biodiversidade e fornecem importantes serviços ecossistêmicos. Os estudos ecológicos de longa duração, onde uma área estudada é revisitada periodicamente para remensuração e observação de indivíduos mortos e recrutas, fornecem informações-chave para o aumento do conhecimento sobre esses ambientes. Através de tais estudos, é possível realizar estimativas sobre o estoque de biomassa, a produtividade e os processos demográficos da comunidade vegetal. Para a explicação de tais processos, uma ampla gama de aspectos deve ser considerada. Os aspectos climáticos de precipitação e temperatura e as características de fertilidade e textura do solo são de reconhecida importância na elucidação dos processos ecossistêmicos. Mais recentemente, tem-se percebido a importância das próprias espécies nesse processo, através de suas características funcionais. Porém, em florestas hiperdiversas não se tem ainda um conhecimento exato de quais traços são mais importantes e é de grande dificuldade logística e financeira a medição de um grande número de traços. Nesse sentido, o conhecimento sobre as características filogenéticas das espécies é de grande importância, já que espécies aparentadas tendem a compartilhar grande número de características, otimizando assim a informação sobre elas. O conhecimento do máximo possível de características bióticas e ambientais ajuda na elucidação da funcionalidade dos ecossistemas, sendo de especial importância em ambientes muito heterogêneos, como as florestas tropicais brasileiras.

Palavras-chave: Estoque de biomassa. Produtividade. Clima. Solo. Diversidade filogenética.

1 INTRODUCTION

Tropical forests have always been a man's best interest. In particular, Brazilian forests have aroused naturalists and botanists curiosity who visited Brazil in order to describe, through drawings, paintings and texts, the great diversity of life forms found. These documents mark the beginning of the knowledge evolution about Brazilian biodiversity, with the pioneering contribution of the naturalist Georg Marcgrave, who arrived in Brazil in 1638 and wrote one of the volumes of "Natural History of Brazil", which describes 245 vertebrate species, introducing the nomenclature in Tupi and Portuguese, with description and numerous illustrations.

Today, a considerable part of such biodiversity is known, although much still needs to be discovered. From the growing knowledge about which species populate the forests and how they are distributed today, new questions about forest functionality are taking place. To answer such questions, Long-Lasting Ecological Projects are a tool of great relevance. By monitoring forests for long time intervals, many of the questions about community temporal behaviour can be answered. From such studies, it can be seen that not all forests behave in a similar way. An important advance of science today is to understand what factors modulate the ecosystem and demographic processes of such communities. Factors such as climate in macroscale and soil characteristics in mesoscale, are widely described as important in determining the establishment of different species in a given location. The species tolerances to such factors, as well as their requirements, act as filters that allow or not such species to survive.

Another point, which importance has been recognized in recent times, is about the specific characteristic of each species, or it's functional traits. However, measuring a big number of functional characteristics is a difficult and expensive task, especially in hyper diverse ecosystems, where we don't really know which traits may be important. Because closely related species tend to share a considerable number of characteristics, the phylogenetic diversity may be a good proxy for functional traits, enriching the discussion about the role of species in the functionality of ecosystems. However, this is a tool that should be used with caution, as over the evolutionary scale other processes have been acting and can drive to completely different patterns.

In this sense, the Laboratory of Evolutionary Ecology of the Federal University of Lavras has been conducting long-term studies in different Brazilian Phytogeographic Domains in recent decades. Overall, across the different domains both climate and soil play a

major role for determining vital ecosystem functions and key demographic processes. Given the diversity of environments studied and the huge tree diversity associated with these ecosystems, this thesis aims to investigate the role of different facets of diversity on key functions: aboveground biomass, wood productivity, mortality and recruitment rates. I will focus on taxonomic and phylogenetic diversity and composition metrics. Because all these functions are associated with both soil and climate, I will also consider their effect on these variables.

2 THEORETICAL REFERENCE

2.1 Brazilian Forests

Brazil is the fifth biggest country in the planet, with an area of 8.514.876 km^2. Of this extent, 43.7% (3.719.801 km^2) is occupied by forests (IBGE, 2018). For this purpose, it was considered "Forest" as an area with tree formations higher than 5 meters tall, including physiognomies of Evergreen Moist Forest, Seasonally Dry Tropical Forest, Forested Savanna, Forested Campinarana, Mangroves and Buritizais, distributed in a heterogeneous way across the country among Amazonian, Cerrado, Caatinga and Atlantic Domain (IBGE, 2012).

In Southeast Brazil, the Minas Gerais state is the fourth largest of the country, with a heterogeneity of climate conditions mediate by its longitudinal and altitudinal variations, giving conditions for the existence of a diverse set of vegetations (OLIVEIRA-FILHO; FONTES, 2000). In this single region, three Domains are represented: Atlantic Forest, Caatinga and Cerrado, comprising physiognomies of Seasonally Tropical Dry Forest (Deciduous Forest, Semideciduous Forest) and Evergreen Moist Forest.

Evergreen Moist Forest belongs to the Atlantic Domain and comprises the coastal rain forests up to 300 km inland (OLIVEIRA-FILHO; FONTES, 2000). Those forests are located in an unseasonal climate, with precipitation well distributed along the whole year and characterized by the presence of tree species that do not lose their leaves. Semideciduous Tropical Forest also occur in the Atlantic Domain, is found until 700 km inward from the coast (FERNANDES; BEZERRA, 1990) characterized by a seasonal climate and roughly 20 to 50% of tree species that lose their leaves during the dry season. Both Evergreen Moist Forest and Semideciduous Tropical can occur in the Cerrado Domain along the watercourses, where they are named gallery forests (RATTER et al., 1996). Whereas, Deciduous Tropical Forest occur both in the Atlantic Forest and in the Caatinga Domain (named Arboreal Caatinga when found in Caatinga Domain) (SANTOS et al., 2012) and are characterized for flushing more than 50% of its leaves during the dry season.

Evergreen Moist Forest, Semideciduous and Deciduous forests share a number of common species as they are located along a gradient and there is no sharp boundaries among them, however they all have their particular and characteristic species composition (EISENLOHR; OLIVEIRA-FILHO, 2015; OLIVEIRA-FILHO; FONTES, 2000; SANTOS et al., 2012). Biomass stocks and wood productivity vary widely among these vegetation types

and because they have different species composition, are under different climate and include distinct soils, it's expected divergent functionality patterns along these gradient.

2.2 Forest dynamics

Tropical forests comprise a vast array of life forms and its interaction in time and space is still poorly understood. Understanding the mechanisms responsible for present day patterns of species abundance, distribution, their coexistence and the maintenance of diversity over time is crucial, not only for the advancement of tropical forest ecology but for understanding basic ecology in any natural system (CARSON; SCHNITZER, 2008).

Forest dynamics studies that include periodic remeasurement of permanent plots offer a unique opportunity to understand the temporal behaviour of tropical forests (KORNING; BASLEY, 1994). These studies include delimited areas where all individual trees that meet the inclusion criteria (e.g. individual trees with diameter at breast height greater than 5 cm) are marked, measured and identified. Forest plots are revisited periodically, individual tress that died and recruited are recorded and surviving trees remeasured. These forest monitoraments provide information on mortality and recruitment rates and allows the estimation of loss and gain in basal area, biomass storage and productivity (SHEIL et al., 1995).

Observations in permanent plots underlies the construction of hypotheses about the causes and mechanisms of species substitution over time, biomass accumulation and the factors associated with ecosystem functionality (BAKKER et al., 1996). Mortality and recruitment estimates are fundamental descriptors of populations of tropical tree species (LEWIS et al., 2004) and the understanding on biomass storage and accumulation is of growing interest because of carbon increase in atmosphere and its potential effect in Global Climatic Change (KEENAN; WILLIANS, 2018; IPCC, 2014). At the practical level, such information is of great importance for the sustainable management and forest conservation, mitigation of climatic change by the retention of carbon as aboveground wood biomass, as well as for the understanding of anthropic and natural changes that are occurring in the tropics (FAUSET et al., 2019; LEWIS et al., 2004).

Several factors, both external and internal to the community, may influence their temporal behaviour. In addition to temperature and precipitation conditions, as well as natural or anthropogenic disturbances, soil properties are widely described as important driver of vegetation patterns and the combination of these and other different factors can lead to a large

multiplicity of vegetation responses (ALI; YAN, 2017; KORNING; BASLEY, 1994; LIEBERMAM; LIEBERMAM, 1987; LEWIS et al., 2004; PHILLIPS et al., 2004).

2.3 Drivers of ecosystem processes

Different vegetation types present distinctions in their ecosystem processes. Ecosystem processes such as biomass storage, productivity, recruitment and mortality rates are all conditioned by spatial and temporal variations in environmental conditions and resource availability, which modulate the survival, establishment and productivity of organisms (ALI et al., 2019; MITCHARD, 2018; POORTER et al., 2017).

The main climatic variables that control ecosystem processes at a large spatial scales are total annual rainfall, mean annual temperature and seasonality, variables that directly influence the physiological mechanisms associated with carbon flow (ALI et al., 2019; MITCHARD, 2018; PAN et al., 2011). Even in a short gradient, seasonal differences in precipitation have strong influence on vital ecosystem functions and species distribution due to their importance in physiological and reproductive processes, such as seed and seedling tolerance, growing and survival (ALI; YAN, 2017; ENGELBRECHT et al., 2007; ENQUIST; ENQUIST, 2011). In some places, the total amount of rainfall occurring in the wet season is the most important variable determining floristic composition (TAYLOR; HAMILTON, 1994), while in others, rainfall seasonality determines the patterns of species diversity (COWLING; PROCHES, 2005). Soil attributes and geographical relief conditions, such as texture, fertility, depth, presence of flooding or freezing and altitude also influence ecosystem process by enhancing or harming plant life cycles (BOHLMAN et al., 2008; PAN et al., 2013). Studies in different forest types, associating the greatest possible range of edaphic and climatic factors to vegetation dynamics, are thus essential to understand how communities change over time, as well as for possible predictions of vegetation response to events caused by anthropic alterations and global climatic changes.

Different tree species have its own structural and demographic traits such as intrinsic growth rates, lifetimes and maximum heights (BAKER et al., 2009; KEELING et al., 2008), thus functional characteristics can be a proxy to understand ecosystem processes. As closely related species tend to have more similar functional aspects than distantly related ones (CADOTTE et al., 2008, 2009; FELSENSTEIN, 1985), the various metrics of phylogenetic diversity are usually used as a proxy for accessing functional diversity.

The presence of a species in a community depends on its existence in a regional pool where the community is located, its dispersal ability (allowing it to reach the community) and, once in the community, its ability to tolerate local biotic and abiotic conditions (WILLIS et al., 2010). Studies on phylogenetic diversity help to understand the multiplicity of factors that structure a community, demonstrating the importance of evolution in this process (CAVENDER-BARES et al., 2009). The evolutionary history and genealogical relationships of species allow to relate small-scale local processes to continental and even global processes that occur along the evolutionary scale (ACKERLY, 2003; EMERSON; GILLESPIE, 2008; GRAHAM; FINE, 2008).

The structure of a community has been characterized based on the processes of adapting species to local conditions and colonization of species in different environments (CAVENDER-BARES et al., 2009). Evidence that relevant ecological features are phylogenetically conserved over time has supported the hypothesis that it is easier for organisms to move to environments where those characteristics are relevant to their survival than to adapt to existing local characteristics (CAVENDER-BARES et al., 2009).

Thus, the understanding of phylogenetic diversity in a community can be of great importance to understand and predict long-lived dynamic processes, ecosystem processes and even the possible responses of these ecosystems to global changes (ALI et al., 2019; CAVENDER-BARES et al., 2009; FAUSET et al., 2019). Also, the evolutive background and genealogical relationships among species have been recognized as of great importance to the understanding of community structure and ecosystem processes (CAVENDER-BARES et al., 2004; FAUSET et al., 2019; PHILLIPS et al., 2019; WEBB et al., 2002). The association of phylogenetic information with soil-climatic factors can be an important tool in the advancement of the understanding of forest dynamics, helping to elucidate issues still not clarified.

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CHAPTER 2 – SPECIES OR ENVIRONEMNT: WHAT DRIVES THE ECOSYSTEM PROCESSES ALONG A SEASONAL GRADIENT OF TROPICAL FOREST?

ABSTRACT

The ecosystem processes provided by tropical forests are of central importance to life on Earth. Brazil is a country with extensive vegetation coverage and great environmental heterogeneity, thus harbouring great biodiversity within its phytogeographical domains. The present work sought to understand the role of climate, soil and biodiversity (taxonomic and phylogenetic) in the explanation of four ecosystem processes: aboveground biomass (AGB), aboveground wood productivity (AGWP), mortality and recruitment rates, along a seasonality gradient from Evergreen Moist Forest to Semideciduous Tropical Forest to Deciduous Tropical Forest, in the southeast of the country. Two work scales were considered: one at the fragment level (Site) and at the plot level, while in a Site there are several Plots. There is a tendency to find higher AGB and AGWP values in Evergreen Moist Forest, highest recruitment in the Deciduous Tropical Forest and higher mortality in the Semideciduous Tropical Forest. Different scales showed different importance among the factors studied. At large scales, environmental variables and floristic composition were associated with both AGB and mortality. Whereas at smaller scales taxonomic diversity was more strongly associated with AGB and AGWP and phylogenetic diversity with mortality and recruitment rates. Generally, in our study, environmental variables were more explicative of ecosystem process than biodiversity and we believe that it occurs because we worked in a seasonality gradient, where the difference in environmental characteristics among the forest types already define the presence of the species found in each of them. Even so, especially on a smaller scale, biodiversity variables can account for some more variation in ecosystem processes.

Key-words: Evolutionary diversity, forest dynamics, vegetation ecology.

RESUMO

Os processos ecossistêmicos fornecidos pelas florestas tropicais são de grande relevância para a vida na Terra. O Brazil é um país com extensa cobertura vegetal e grande heterogeneidade ambiental, abrigando assim grande biodiversidade dentro de seus domínios fitogeográficos. O presente trabalho buscou entender o papel do clima, solo e biodiversidade (taxonômica e filogenética) na explicação de quatro processos ecossistêmicos: estoque de biomass acima do solo (AGB), produtividade lenhosa acima do solo (AGWP), mortalidade e recrutamento, ao longo de um gradiente de estacionalidade climática no sudeste do país. Considerou-se duas escalas de trabalho: uma a nível de fragmento e outro a nível de parcela, onde em um mesmo fragmento existem várias parcelas. Os maiores valores de AGB e AGWP foram encontrados em Floresta Ombrófila , o maior recrutamento na Floresta Estacional Decidual e maior mortalidade na Foresta Estacional Semidecidual. As diferentes escalas mostraram importância distinta entre os fatores estudados. Na escala maior, além das variáveis ambientais, variáveis de composição florística também se mostraram explicativas para AGB e mortalidade, enquanto que na escala menor, a diversidade taxonômica foi importante da explicação de AGB e AGWP, enquanto a diversidade filogenética foi relevante para mortalidade e recrutamento. De forma geral, em nosso estudo, as variáveis ambientais foram mais explicativas que as variáveis ligadas a biodiversidade e nós acreditamos que isso aconteça porque, trabalhando em um gradiente de estacionalidade, onde as diferenças nas características ambientais entre os tipos florestais já definem a ocorrência das espécies encontradas em cada um deles. Mesmo assim, especialmente na escala menor, as variáveis de biodiversidade ajudam um pouco mais na explicação de parte dos processos ecossistêmicos.

Palavras-chave: Diversidade evolutiva, dinâmica florestal, ecologia vegetal.

1 INTRODUCTION

Covering just 7–10% of the Earth's land surface (BONAN et al., 2008), tropical forests hold 96% of world's tree species (FINE et al., 2008). Specifically, the Neotropical flora comprises more flowering plants (ca. 90 000) than tropical Africa (ca. 35 000 species) and tropical Asia (ca. 40 000 species) combined (FORERO; MORI, 1995; PRANCE, 1977; THOMAZ, 1999). Brazil is the country in Neotropics which encompass the most diverse flora, with an estimative of 33,161 vascular plant, being 55.2 % (18,316 species) endemic to the Brazilian region (ULLOA et al., 2017).

All this biodiversity hold many ecosystem processes that are essential for the equilibrium of the life on Earth. Tropical forests are considered the main sink for atmospheric carbon, having highest biomass accumulation compared to other forests around the world and accounting for two-thirds of all terrestrial biomass (PAN et al., 2013). The amount of carbon stored as Aboveground Biomass is of special interest due to recent increase of this element in the atmosphere and its potential effect in Global Climatic Change (IPCC, 2014; KEENAN; WILLIANS, 2018). Because tropical forests are particularly important to mitigate the impact of current and predicted climate change (PAN et al., 2011, 2013) a number of studies are trying to figure out which are the main drivers of biomass and productivity (ALI et al., 2019; ALI; YAN, 2017; BECKNELL; POWERS, 2014; CADOTTE et al., 2008, 2009; CAVANAUGH et al., 2014; CHISHOLM et al., 2013; FAUSET et al., 2019; FRIDLEY, 2001; LIANG et al., 2016; PHILLIPS et al., 2019; POORTER et al., 2015; SULLIVAN et al., 2017).

A number of different factors are associated with carbon storage and forest productivity: climate-related variables such as temperature and water availability (eg. BECKWELL et al., 2012; FAUSET et al., 2019; QUESADA et al., 2012), edaphic characteristics, linked to soil fertility and texture (eg. BECKNELL; POWERS, 2014; QUESADA et al., 2012), species richness, composition (eg. ALI; YAN, 2017; LIANG et al., 2016; POORTER et al., 2015) and also their associated traits. However, understanding which species characteristics are more important to understand these processes is still a challenge. Moreover, the enormous species diversity and their respective high number functional traits (BARALOTO et al., 2010) make the functional approach very difficult in these hyper diverse ecosystems. In order to try to summarize as many functional traits as possible, the use of phylogenetic diversity can be of great relevance, since depending on the position of a species in a phylogenetic tree, an expressive amount of characteristics is expected, when the

characteristics have phylogenetic signal (CADOTTE et al., 2008, 2009; FELSENSTEIN, 1985).

Demographic processes such as mortality and recruitment also influence forest dynamics. Johnson et al. (2016) found that mortality rates are the main controlling factor of biomass because they directly affect forest structure. Recruitment is another key demographic process, whereby new individuals replace those lost via mortality. So, understanding how climate, soil, and biodiversity influence the processes of biomass storage, productivity, mortality, and recruitment can improve our understanding about forest functionality.

Another important point is the role of the study scale. Changing the scale can broadly change the importance of both climate, soil and biodiversity, being generally climate more important at a macroscale, soil at mesoscale and biodiversity at small scales (CHISHOLM et al., 2013; SIEFERT et al., 2012). The study scale is also important to understand the patterns involved in community assembly as the processes that influence species diversity can shift with spatial scale (CAVENDER; BARES, 2009). So, studies that seek to point out how ecosystem process are affected by those cited factor probably needs to have since smaller to larger scales.

In Brazil, recent studies were conducted to help unravel the role of environment and diversity for determining present day patters of ecosystems processes, however, these are mainly focused in the Amazon region (eg. COELHO DE SOUZA, in press; FAUSET et al., 2019; JOHNSON et al., 2016; QUESADA et al., 2012; PHILLIPS et al., 2019). However, there is a gap of knowledge on the subject in other phytogeographic domains, such as Cerrado, Atlantic Forest and Caatinga. These domains shelter forests that change their physiognomy according to the seasonality gradient, ranging from Evergreen Moist Forest in the Atlantic Forest, with perennial leaves all over the year, through the Semideciduous Tropical Forests that extend into the Cerrado gallery forests (along the rivers) and in the Atlantic Forest, presenting the characteristic of losing between 20 and 50% of leaves in the dry season, and the Deciduous Tropical Forests, present in the Atlantic Forest and Caatinga, with deciduousness of at least 50% of leaves in the dry season (IBGE, 2012; SANTOS et al., 2012). This forest gradient, found in the southeast of the country, house a great biodiversity encompassing two hotspots (Cerrado and Atlantic Forest) which ecosystem processes are still poorly known. Along the gradient, it is found different soil conditions and great diversity of species (IBGE, 2012). Understand better how the environmental heterogeneity existing in the tropical region sets the functioning of diverse ecosystems, such as within the climate seasonality gradient, is an important contribution to understand the role of such variables in

tropical forests all over the world, since the climate seasonality gradient gives rise to a wide range of environmental and biological conditions.

The aims of the paper are to assess (i) the differences in ecosystems process across three forest types along a seasonal gradient; (ii) the importance of climate and soil in explaining these processes (iii); after take climate and soil into account, how taxonomic and phylogenetic aspects contributes to elucidate these processes; (iv) the role of the scale of study to determine these patterns. We hypothesize that, as subject to different biotic and abiotic conditions, the studied forest types will not present the same pattern for the ecosystem processes. In agree to the reported before, we also expect a major importance of climate and soil at the larger scale, with increasing important of biodiversity (taxonomic and phylogenetic aspects) at the smaller scale.

2 METHODS

2.1 Tree Community Data

We conducted our research in the state of Minas Gerais, in south-eastern Brazil. Minas Gerais is the fourth largest Brazilian state, with an area of 586,528 square km^2 and includes three vegetation domains: Atlantic Forest, Caatinga and Cerrado. In these domains, we can find different forest types, such as Seasonally Dry Tropical Forest (SDTF), represented by Deciduous and Semideciduous Forest; and Evergreen Moist Forest. The existence of this complex vegetation mosaic seems to be mediated at a larger scale by climate factors, and the existence of different physiognomies and biomes under the same climate is possible due to different, local soil conditions (FERNANDES, 2007; SILVA DE MIRANDA et al., 2018). Also, Semideciduous Tropical Forest and Evergreen Moist Forest are closed located and the existence of both forest types are possible due to different elevation between then (Supplementary material, TABLE S1).

We used a dataset from 24 forest fragments gathered from the Evolutionary Ecology Laboratory of the Federal University of Lavras (Brazil), which comprise seven areas of Deciduous Tropical Forest (DTF), 13 of Semideciduous Tropical Forests and four of Evergreen Moist Forests (FIGURE 1). These forests are in an advanced stage of ecological succession and the authors are not aware of any anthropic disturbance during the study period. In each fragment from 10 to 64 plots were present, according to the fragment size, with areas from 200 m^2 to 400 m^2, comprising a total of 694 plots with a total area of 25.145 ha (Supplementary material, TABLE S1). Plots were established between 1989 to 2007, with at least one re-census. In each plot, all trees with a minimum of 5 cm diameter at breast high (DBH) were included. Trees were identified at the species level and standardized using Taxonomic Name Resolution Service (BOYLE et al., 2013). In those plots, we surveyed 53709 individuals, belonging to 95 families, 331 genus and 864 species.

Figure 1 − Location of the fragments studied in Minas Gerais state, Brazil. Sites with both Semideciduous Tropical Forest and Evergreen Moist Forest have different elevation, which allows the existence of both forest types.
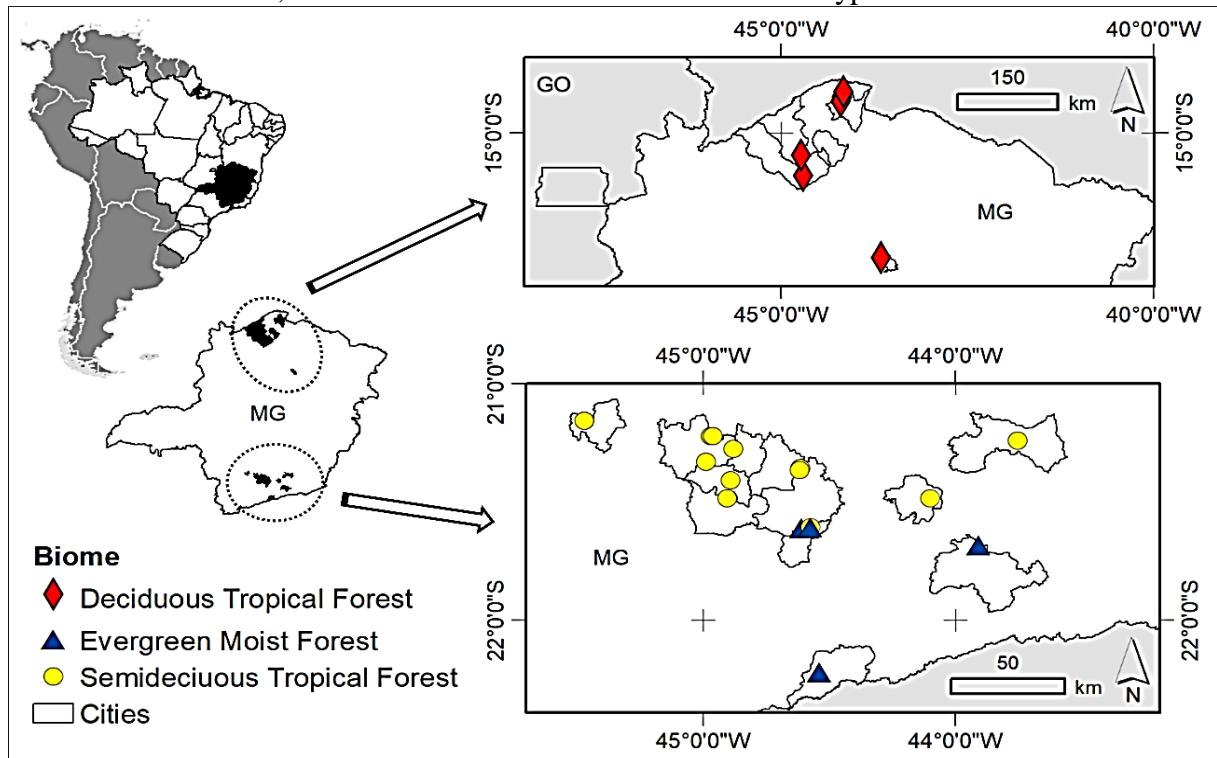
Fonte: Do autor (2019).

2.2 Ecosystems processes

We analysed four major ecosystems processes: annual mortality and recruitment rates, aboveground wood biomass (hereafter AGB) and aboveground wood productivity (hereafter AGWP). Annual rates of mortality and recruitment were calculated following Sheil and May (1996). Mortality was calculated using the initial number of individuals and the number of confirmed dead individuals in each plot after each re-census; recruitment was calculated using the final number of individuals in each plot after a re-census and the number of observed recruits (individuals that achieved 5 cm of DBH).

AGB per individual was estimated using the Global Equation proposed by Chave et al. (2014), based on the diameter, measured in the field, wood density, extracted from the Global Wood Density database (CHAVE et al., 2009; ZANNE et al., 2009) and E, which is a measure of environmental stress based on temperature seasonality, precipitation seasonality and maximum climatological water deficit (CHAVE et al., 2014). For each plot, we calculated the mean AGB across all censuses.

AGWP was estimated as the rate of gain in aboveground biomass during each census interval, following the corrections proposed by Talbot et al., 2014. Such corrections seek to minimize the undetected growth and mortality effects on AGWP across the census interval, especially significant at longer intervals. Plots that we had more than one census interval, we calculated the weighted mean AGWP based on the number of years of each interval.

2.3 Environmental variables

To investigate the effect of environmental factors, we used soil and climate data. To access edaphic variables in each fragment, chemical-textural analyses were done after the first measurement, from composed samples of soil collected in each permanent plot analysed, accessing pH (extracted with KCl), total phosphorous (P, mg/dm^3), effective cation exchange capacity (eCEC, cmolc/dm^3) (all variables less correlated than 0.7) and the percentage of sand, silt and clay.

For climate data, to avoid collinearity among explanatory variables, we selected Annual Temperature Range, available in WorldClim dataset at 30' ($\approx$ 1km) resolution (HIJMANS et al., 2005) and CWD (Climatological Water Deficit) per year (CHAVE et al., 2014). Because of the resolution of the dataset, all plots in the same site had the same values for these climatic variables.

2.4 Biodiversity metrics

To better represent the different aspects of biodiversity, we used two overarching approaches to quantify plot biodiversity: taxonomic and phylogenetic metrics of diversity. Taxonomic characteristics was divided into measures of richness (species richness) and measures of composition (axes from a detrended correspondence analysis, DCA).

To quantify the phylogenetic diversity of plots, we used a genus-level phylogeny developed by Coelho de Souza et al. (in press) that covers 96.9% of genera in our plots, 98.1% of species and 99.3% of individuals. To represent phylogenetic diversity, we used the total lineage diversity, represented by the standardized effect size of phylogenetic diversity (sesPD), as PD is strongly correlated with species richness and these do not vary independently; basal lineage diversity, represented by the standardized effect size of mean pairwise distance (sesMPD) and neighbour lineage diversity, represented by the standardized effect size of mean nearest taxon distance (sesMNTD).

To account for phylogenetic composition, we performed an evolutionary correspondence analysis (evoCA), which is an adaption of a correspondence analysis (CA) to analyse the distributions of lineages among sites, using its axes as explanatory variables, (PAVOINE, 2016). We are not aware of any methods developed to conduct detrended correspondence analysis based on phylogenetic composition.

2.5 Statistical analysis

Our statistical framework consisted primarily of analysing drivers of variation in ecosystem at the level of individual plots using generalized linear mixed effects models (GLMM) with site as a random effect, given that plots were grouped into sites. Climatic data were only available at the site level, while soil data were available for all individual plots, and therefore our model is essentially hierarchical.

We also constructed null models, with just site (random effect) as explanatory variable and simpler models with major vegetation type as an explanatory variable, to compare to results with quantified environmental variables. At both scales, the final model was selected based on Akaike information criterion (AIC; AKAIKE, 1973), with the model with lowest AIC selected. As a means of data exploration, we conducted principal component analyses of measures of ecosystem function.

We first assessed the role of the environment (climate and soil) and then evaluated whether biodiversity has additional explanation. To that end, we first constructed the best environmental model in terms of variation explained, for each ecosystem process. We then added measures of taxonomic and phylogenetic diversity and composition as additional predictors in the best environmental model to determine if any additional variation in ecosystem function could be explained. We considered the models where the variables gave a variance inflation factor (VIF) less than 4.

Once 'final' models were obtained, we tested for spatial autocorrelation using semi variograms (ZUUR et al., 2009). No spatial autocorrelation was observed for any ecosystem functions studied (Supplementary Material, FIGURE S1). To account for heteroscedasticity and obtain residuals that were normally distributed, mortality, recruitment, AGWP and AGB were all log-transformed prior to analyses. In other to compare the chosen variables in results, we standardized explanatory variables prior to analyses too. Plots with zero values for mortality or recruitment were excluded.

We also estimate ecosystem function at the site level (all plots considered together, n = 24) using generalized linear models (GLM). As did before, we determined the best environmental model and then assessed if any measure of taxonomy or phylogenetic diversity or composition improved the model. For this purpose, climate data was already at site level and soil characteristics values were used as means of all plots in each site. The final model was selected based on lowest AIC value.

Analyses were performed in the R Statistical software v3.1.1 (R CORE TEAM, 2018) using the vegan (OKSANEN, 2016), lme4 (BATES et al., 2015), ape (PARADIS et al., 2004), picante (KEMBEL et al., 2010) and MuMIn (BARTON, 2018) packages.

3 RESULTS

The ecosystem processes differed between forest types, but with distinct patterns for each process. Evergreen Moist Forests has a tendency to present higher AGB and AGWP than Deciduous, while Semideciduous Forests show a high variation for these measures of ecosystem function, overlapping with the values for Deciduous and Evergreen Forests (FIGURE 2A). Differences among forest types for recruitment and mortality rates are not as pronounced as observed for AGB and AGWP (TABLE 1), but are evident when analysing components 1 and 3 of the PCA (FIGURE 2B). Deciduous forests show a tendency to has, on average, higher recruitment and semideciduous, higher mortality rates.

Figure 2 − Principal component analysis for Mortality, Recruitment, Biomass and Aboveground Wood Productivity in three different forest types (Deciduous Tropical Forest (DTF), Semideciduous Tropical Forest (STF) and Evergreen Moist Forest (EMF),) in Minas Gerais, Brazil.
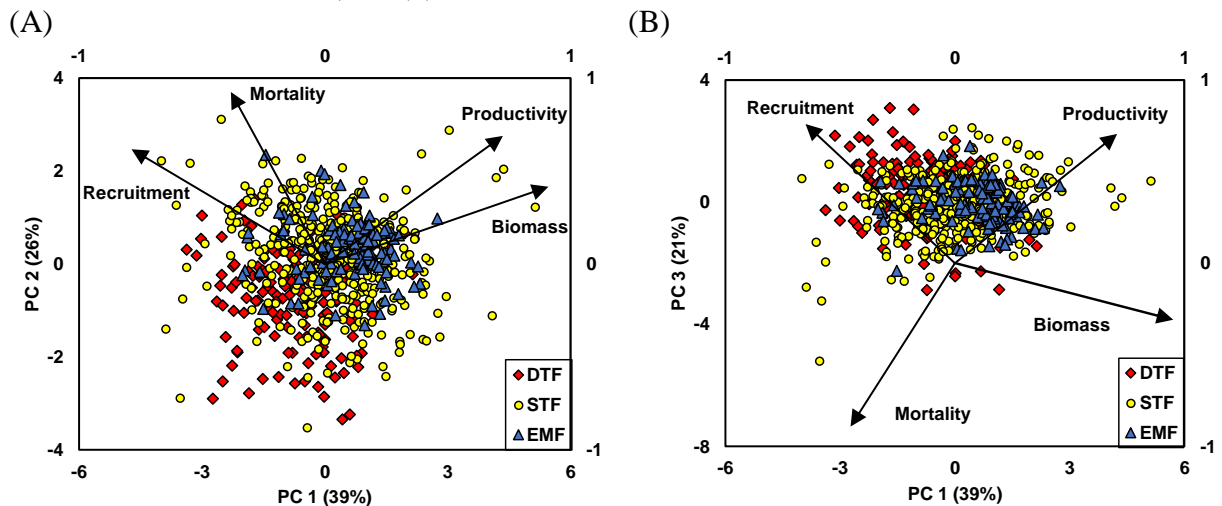
Fonte: Do autor (2019).

Taxonomic composition varies substantially across the forest types, which is evident in the DCA (FIGURE 3A). Evergreen Moist Forest and Semideciduous Tropical Forest have some overlap, while Deciduous Tropical Forest is at the opposite extreme of the main floristic gradient. A similar pattern can be observed regarding phylogenetic composition (evoCA, FIGURE 3B), where the forest types occupying distinct portions of compositional space, although with Deciduous Tropical Forest not as differentiated evolutionarily as it is taxonomically. Meanwhile, some plots of Semideciduous Tropical Forest are distributed separately from the rest, likely because of the abundance of basal clades.

Figure 3 − Ordering diagram of the first two axes of: (A) detrended correspondence analysis (DCA) and (B) evolutionary correspondence analysis (evoCA) of 694 plots of Decidual Tropical Forest (DFT), Semidecidual Tropical Forest (STF) and Evergreen Moist Forest (EMF) across Minas Gerais state, Brazil. Axis 1 and 2 inform the proportion of total variation explained by that specific axis.

(A)　　　　　　　　　　　　　　　　　　(B)
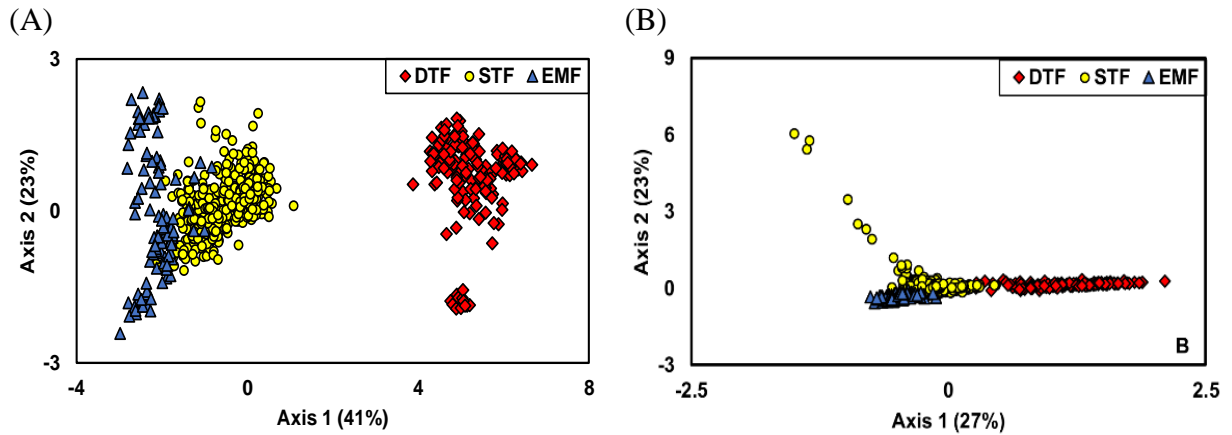
Fonte: Do autor (2019).

The overall results regarding the models are summarized in Tables 1 (results by plot) and 2 (results by site). For AGB, almost half of the explanation is due to site and, a notable part of it, is attributed to forest type, that is, for biomass, the forest type per se can explain a part of the variation at both scales. Mortality also presented a high explanation due to site, but without forest type contribution (again, at both scales). Productivity had a good explanation due to forest type just at the larger scale. Recruitment is poorly related to forest type at both scales.

At plot level, we found that AGB is explained by soil (eCEC, estimate=0.039), climate (CWD, estimate = 0.416; the positive effect arise because CWD is represented here by negative values, so as more negative, greater CWD) and species composition (DCA axe 2, estimate = 0.203) and, at site level, just climate (CWD, estimate = 0.387) and species composition (DCA axe 2, estimate = 0.170). AGWP, instead, was explained by soil (pH, estimate = -0.144 and eCEC, estimate = 0.047) and species richness (estimate = 0.107) at plot level, while soil (eCEC, estimate = 0.065) and climate (CWD, estimate = 0.267) were selected at site level.

Mortality rates were explicated by both soil (lowest content of P (estimate = -0.025), lowest eCEC (estimate = -0.036), higher Clay content (estimate = 0.066)), climate (higher temperature annual range, estimate = 0.095) and phylogenetic diversity (sesMNTD, estimate = 0.051) at plot level. At site level, climate (CWD (estimate = 0.132), temperature annual range (estimate = 0.228)) was a good environmental predictor, together with species composition (DCA axe 2, estimate = 0.153). Recruitment rates were explained in the plot

level by the edaphic characteristics (higher soil pH (estimate = 0.039) and lower sand content (estimate = -0.042) and phylogenetic diversity (sesMPD, estimate = -0.034). In the other hand, at larger scale, just soil (Silt, estimate = 0.083) was a good predictor.

Table 1 − Comparison among mixed linear models (model using forest type as the fixed effect, best environmental model and best overall model) using Akaike criterion (AIC), marginal R^2 (R^2m) and conditional R^2 (R^2c) values, for each ecosystem process analysed.

Biomass	Model	AIC	R^2m	R^2c
Null		978.4	0	0.45
Forest type		958.8	0.26	0.42
Environment	eCEC, CWD	951.4	0.29	0.43
Best model	Environment + DCA axe 2	907.45	0.37	0.47
Wood Productivity				
Null		1481.1	0	0.18
Forest type		1471.3	0.08	0.17
Environment	pH, eCEC	1468.5	0.10	0.17
Best model	Environment + species richness	1467.0	0.10	0.18
Mortality				
Null		516.5	0	0.39
Forest type		517.4	0.04	0.38
Environment	P, eCEC, Clay, Temperature Annual Range	505.6	0.12	0.40
Best model	Environment + phylogenetic diversity (sesMNTD)	498.06	0.13	0.41
Recruitment				
Null		607.8	0	0.2
Forest type		610.5	0.01	0.2
Forest type	pH, Sand	603.9	0.03	0.21
Best model	Environment + phylogenetic diversity (sesMPD)	601.9	0.04	0.21

Fonte: Do autor (2019).

Table 2 − Selected generalized linear models (GLM) using Akaike criterion (AIC) and adjusted R^2 (R^2) values, for each ecosystem process analysed.

Biomass	Model	R^2m	R^2c
Null		35.56	
Forest type		19.26	0.53
Environment	CWD	18.42	0.56
Best model	CWD + DCA axe 2	10.39	0.67
Wood Productivity			
Null		22.26	
Forest type		7.16	0.51
Environment	eCEC, CWD	0.11	0.63
Best model	Environment	0.11	0.63
Mortality			
Null		23.89	
Forest type		24.91	0.03
Environment	CWD, temperature annual range	19.62	0.22
Best model	Env. + DCA axe 2	16.06	0.35
Recruitment			
Null		-1.69	
Forest type		1.67	-0.07
Environment	Silt	-3.42	0.11
Best model	Environmental	-3.42	0.11

Fonte: Do autor (2019).

4 DISCUSSION

The ecosystem processes varied along the gradient and different from our initial hypothesis, climate and soil were not always more important at the larger scale and the species at smaller scale. In fact, each process presented its own peculiarities about it.

Deciduous Tropical Forests presented greater recruitment rates. This result is explained at the plot level by the edaphic characteristics (pH, sand percentage) and phylogenetic diversity (sesMPD). Local edaphic characteristics are relatively constant in time, being expected to influence plant communities and the biochemical processes occurring in the soil, influencing therefore on plant community features what give rise to relatively stable and predictable patterns in the vegetation (TUOMISTO et al., 2003). Soil acidity (measured by its pH) influence nutrient accessibility (BAGAYOKO et al., 2000; GALE et al., 2001) because H+ and OH- ion balance controls the availability and depletion of some nutrients (LEMIEUX, 1997), which can influence the ability of species to achieve the size inclusion criterion of the study. Sandy soils can be favourable for acidic conditions (AMANI et al., 2013), limiting nutrients availability. So, the presence of a high pH, together with less sand content, as we find in this study, can benefit recruitment rates by providing better conditions for the use of nutrients necessary for the full growth of trees.

Besides the soil properties, phylogenetic diversity is another important predictor of recruitment rates: areas with lower basal lineage diversity (sesMPD) show greater recruitment. Basal lineage diversity is very sensitive to the presence of basal clades in the phylogeny (i.e. Magnoliids and Monocots) (HONORIO CORONADO et al., 2015). In Deciduous Forest, Fabaceae is the most representative family, both in number of species and individuals, followed by Myrtaceae, Rubiaceae and Bignoniaceae, representing together, 41.5% of all species presented in Deciduous Tropical Forest in this study. Those families are all whithin Eudicot, a more recently evolved clade. Communities with a greater proportion of Magnoliids and Monocots have a more even species distribution across the three major angiosperm clades and a totally equal distribution of species in each of the three clades would give the highest value for MPD (HONORIO CONORADO et al., 2015). Using a large scale (1ha plot), subdivided into 20x20m plots, Fauset et al. (2019) found that species functional traits (i.e. specifically the total leaf area index - LAI), rather than climate, is a better predictor for recruitment, rates. As more closely related species tend to have more similar functional characteristics (CADOTTE et al., 2008, 2009; FELSENSTEIN, 1985), the various phylogenetic diversity metrics are usually used as a proxy for accessing functional diversity.

Indeed, in many studies phylogenetic diversity was a better predictor of ecosystem functions than the functional traits analysed (CADOTTE et al., 2009), perhaps because it carries more information than just a few isolated and non-measured features. In this sense, our result goes directly to the one found by Fauset et al. (2019), since, according to the authors, the size of the crown determines LAI. Greater LAI is associated with wider crowns and higher recruitment rates (FAUSET et al., 2019). So, lower sesMPD, which is associated with the presence of more basal clades and thus, the presence of species with smaller crowns (and then smaller LAI) could lead to a lower recruitment. In our case, the selected phylogenetic variable (sesMPD) may be acting as a proxy for the crown size functional characteristic.

In the other hand, at larger scale, just soil (Silt) was a good predictor for recruitment, but not a strong one (TABLE 2). Some plots in our study have portions subject to greater water influence in the soil. Thus, the silt content may be acting as a proxy for water availability and saturation, factors that may influence the recruitment of trees. The weak explanation of the only selected variable shows that others factors, rather than the measures in this study, actuate influencing recruitment on larger scale. Based on Fauset et al. (2019), functional characteristics are more relevant to predict recruitment and, although in a smaller scale the phylogenetic diversity can incorporate these characteristics, it's no longer enough in the larger scale (to note the differences in phylogenetic diversity between the studied scales, see Figures S2 for small scale and S3 for larger scale (Supplementary material)).

We found highest mortality rates at the Semideciduous Tropical Forest and it was explicated by both soil (lowest content of P, lowest eCEC, higher Clay content), climate (higher temperature annual range) and phylogenetic diversity (sesMNTD). Lowest content of P and lowest eCEC are characteristics of a less fertile soil, thus more restrictive to plant survival, while increasing soil clay content can increase the resistance to penetration, considered critical to root growth (GERARD et al., 1982). Therefore, in more clayey soils, increasing soil density and soil resistance to penetration may be more restrictive to roots than in sandy soil, leading to less effective use of nutrients and water, what could increase mortality (GERARD et al., 1982). About climatic effects on mortality, we found higher temperature annual range leading to higher mortality rates. Allen et al. (2010), in a broad review about tree mortality around the world, found that the rise in temperature is a major factor driving mortality in all ecosystems studied, from monsoonal savannas with mean precipitation lower than 400 mm per year, to subalpine conifer forests with a Mediterranean climate, to tropical rainforests with mean precipitation higher than 3000 mm per year. These cases reveal a complex set of mortality patterns in response to drought and heat stress,

extending from modest and short-lived local increases in background mortality rates to episodes of acute, regional-scale forest die-off (ALLEN et al., 2010).

The full model also included the phylogenetic diversity, where higher neighbour lineage diversity (sesMNTD) is found where mortality rates are higher. High sesMNTD would be explained by the presence of long phylogenetic branches separating the nearest taxa (HONORIO CONORADO et al., 2015). Being Semideciduous Tropical Forest colonized by both Deciduous Tropical Forest and Evergreen Moist Forest species, it's expect the presence of multiple lineages with diverse evolutionary backgrounds, increasing sesMNTD by the repeated establishment of plant lineages on communities over evolutionary time-scales (HONORIO CONORADO et al., 2015). However, such species tolerate the conditions but possibly are not in their optimal environment, which could favour higher mortality rates, either for competition with characteristic species of the environment, or because of a lack of any important characteristic for its development. At larger spatial scale, just climate (CWD, temperature annual range) and species composition were good predictors of mortality rates. For the vegetation characteristics such as biomes and species distribution, the role of climate driving patterns at the larger scales and soil at medium and small spatial scales have been previously reported (FERNANDES, 2007; SILVA DE MIRANDA et al., 2018). Now, our study shows that the role of climate and soils at large and small spatial scales respectively may also be valid for demographic features. Another major difference, at larger scale the taxonomic composition is associated with mortality rates while at smaller scales phylogenetic diversity was associated with mortality. As different tree species have its own proper structural and demographic traits such as intrinsic growth rates, lifetimes and maximum heights (BAKER et al., 2009; KEELING et al., 2008). Quesada et al. (2012) consider that both local and large-scale patterns in dynamics might be related to differences in species composition because its own characteristics. Our results show, however, that a smaller scale can capture deeper the relationships among the species, being the phylogenetic proximity a proxy for a better understanding of the mortality processes.

Higher AGB was explained by higher effective cation exchange capacity and lower water stress (CWD), together with species composition in the smaller scale, and just CWD and species composition were selected at larger scale. The positive relationship between biomass, fertility and water availability, as we found here, is also present in other studies (BECKNELL; POWERS, 2014; BECKNELL et al., 2012). Although the positive effect of eCEC is low (estimate = 0.03928), it is expected that sites with higher amounts of essential nutrients have superior growth and thus higher AGB (BAKER et al., 2009; BECKNELL;

POWERS, 2014) and studies in tropical forests have found positive relationships between soil fertility and AGB (GOURLET-FLEURY et al., 2011). At both scales, climate (CWD) is an important predictor of AGB. CWD has the higher effect in biomass in our results, being rainfall and seasonal water stress been broadly reported as major factors controlling AGB (POORTER et al., 2015, 2017).

In our results, species composition had also effect on AGB, at both scales. Although at larger scale the estimate is negative, it's about the species composition, or how the species change along the studied gradient, not just the species number (species richness). There is a major discussion about the species control in AGB in different ecosystems, usually with positive response (but not always; see SULLIVAN et al., 2017) (ALI; YAN, 2017; ALI et al., 2019; CASPERSEN; PACALA, 2001; CAVANAUGH et al., 2014; GILLMAN; WRIGHT, 2006; HECTOR et al., 1999; TILMAN et al., 1997a). Theoretical and practical models shows that, regarding of AGB, at small scales sampling effects, facilitation and niche complementarity dominate, while environmental gradients drive patterns at large scales (CHISHOLM et al., 2013; FRIDLEY, 2001). Sampling effects or selection effects arises because species richness varies across the sampling area, and a place with more species can have by chance, higher probability to contain more productive species (HUSTON, 1997; TILMAN et al., 1997b). Similarly, facilitation occurs in an area with high biodiversity because one species can collaborate to others performance, by creating better conditions for their survival (HOOPER, 1997). The niche complementarity occurs as a place with higher biodiversity has more chance to contain species with different functional and structural characteristics, thus optimizing the use of available resources (POORTER et al., 2015; SULLIVAN et al., 2017; TILMAN, 1999; TILMAN et al., 2001, 2014; VAN DER SANDE et al., 2017).

Contributing to this discussion, Chisholm et al. (2013) notice that a proportion of the positive effect of species richness in biomass at small spatial grains may be attributable to local variation in stem density, being both biomass and species richness positively related to stem density, which varies locally within a forest plot. It was being already reported a major influence of mortality rate on biomass (JOHNSON et al., 2016), what could obscure the effect on species richness on AGB (COELHO DE SOUZA et al., in press). In our study, the species richness do not explicate AGB, but species composition. Our largest scale also showed the effect of species composition on biomass and it could be due to great difference of species composition along the studied gradient (FIGURE 1A), where this difference encompass characteristics that could lead to a high or low biomass. Phillips et al. (2019) attributed this

influence of species composition on AGB, at both scales, due to differences in the wood density of species, which varies at all scales and even vertically within a stand.

For AGWP, soil is important at both grades (pH and eCEC at smaller scale, eCEC at larger scale) but climate is only important at the larger scale. This has been notice by Siefert et al. (2012), who found change of major importance of soil at smaller scales to a primarily climatic influence on plant community composition with increasing scale. In our study, this is also true for the AGWP. Being AGWP usually correlated with species richness (CADOTTE et al., 2008), this scale-dependence could arise because of the specific characteristics of the present species at local scale. Indeed, species richness was selected to explain AGWP in our models just at the smaller scale (see FIGURE S4 (Supplementary material) to note the differences in species richness at both scales).

However, much of the variation at the studied ecosystem processes remained unexplained (TABLES 1 and 2). As we worked on a very heterogeneous gradient, even inside the forest types, local characteristics, not measured here, could be driving the ecosystem process together with climate, soil and species. Obtaining as much information as possible in each plot (see Morel et al., 2015) can be useful for a better explanation of ecosystem processes. In our studied gradient, we can observe a great heterogeneity within the same fragment, for example, plots that suffer water saturation and that do not suffer, within a same site. A detailed description of such peculiarities may assist in minimizing the noise caused in the analyses by unmeasured heterogeneity.

5 CONCLUSION

Along the seasonal gradient, forest types presented differences in ecosystem processes. The scale played a major role in the selection of the explanatory variables, and, contrary to hypothesized, for Biomass and Mortality, species taxonomy are important at the larger scale too. Overall, environmental variables were more explicative than biodiversity and we believe that it occurs because we worked in a seasonality gradient, where the difference in environmental characteristics among the forest types already define the presence of the species found in each of them. Even so, especially on a smaller scale, biodiversity variables can account for some more variation in ecosystem processes. We concluded that, in a heterogeneous environment as the studied one, ecosystem processes are driven by a multiplicity of factors and the differences found changing the spatial scale shows that smaller scales can possibly capture a fine range of important variables necessary to proper elucidate each process.

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APPENDIX − Suplementary material

Table S1 − Studied sites in Minas Gerais (Brazil), with respective altitude and geographic location (latitude and longitude in decimal degrees).

Forest type	Sites	Altitude	Latitude	Longitude
DTF	1	507	-15.5502	-44.7010
DTF	2	500	-15.3116	-44.7349
DTF	3	820	-21.1552	-45.4711
DTF	4	530	-14.4919	-44.1841
DTF	5	650	-14.4704	-44.1884
DTF	6	630	-14.5447	-44.2105
DTF	7	513	-14.4138	-44.1627
STF	1	1100	-21.2397	-43.7534
STF	2	850	-21.0946	-45.3482
STF	3	950	-21.3556	-44.6155
STF	4	930	-21.2737	-44.8820
STF	5	824	-21.1553	-45.4714
STF	6	883	-21.4098	-44.8929
STF	7	940	-21.3525	-44.6089
STF	8	870	-21.2166	-44.9802
STF	9	928	-21.4977	-44.9134
STF	10	1200	-21.6069	-44.5569
STF	11	1023	-21.3292	-44.9717
STF	12	1136	-21.4884	-44.1006
STF	13	950	-21.2214	-44.9631
EMF	1	1151	-22.1617	-44.4658
EMF	2	1491	-21.6121	-44.6120
EMF	3	1403	-21.7103	-43.8855
EMF	4	1450	-21.3300	-44.9883

Figure S1 − Geostatistical semi variogram of the spatially autocorrelated model residuals for the analysed ecosystem processes.

Biomass

Aboveground Wood Productivity
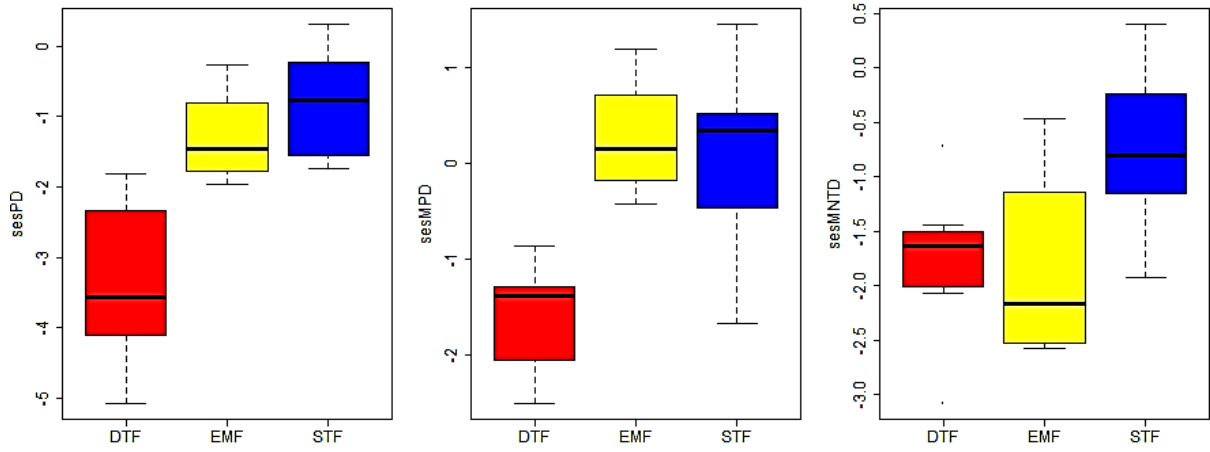

Mortality

Recruitment
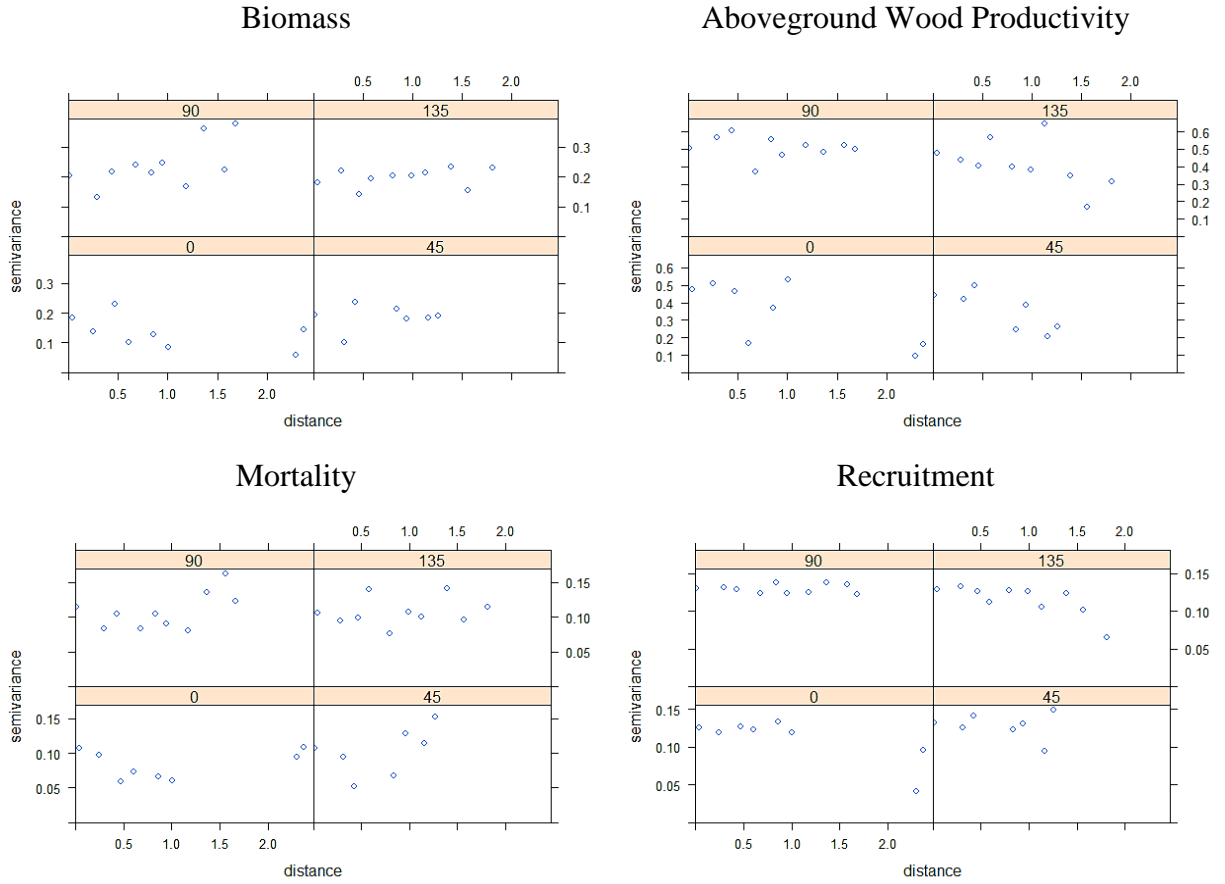
Fonte: Do autor (2019).

Figure S2 − Phylogenetic diversity calculated by plot (small scale) for three forest types: DTF (Deciduous Tropical Forest), EMF (Evergreen Moist Forest) and STF (Semideciduous Tropical Forest) located in Minas Gerais, Brazil.
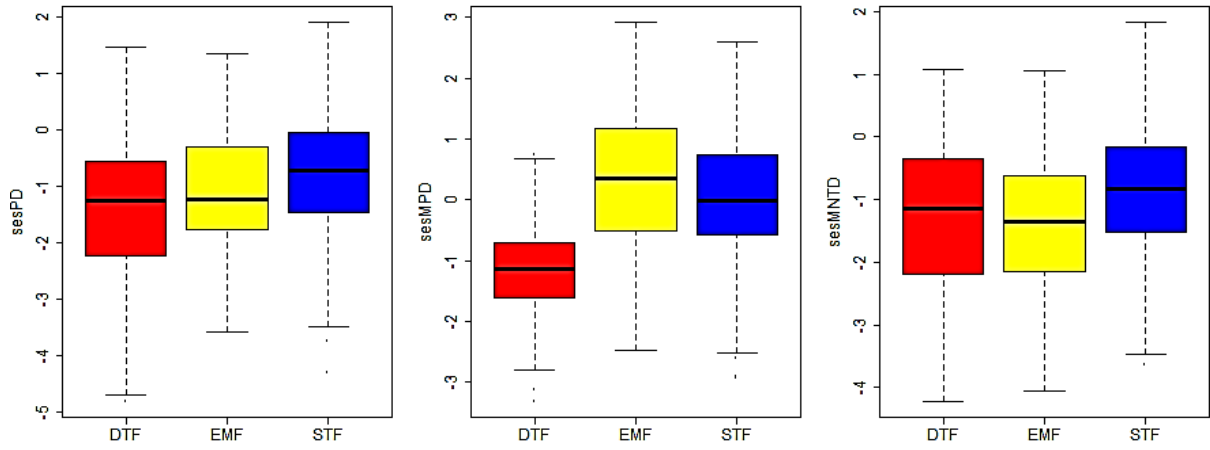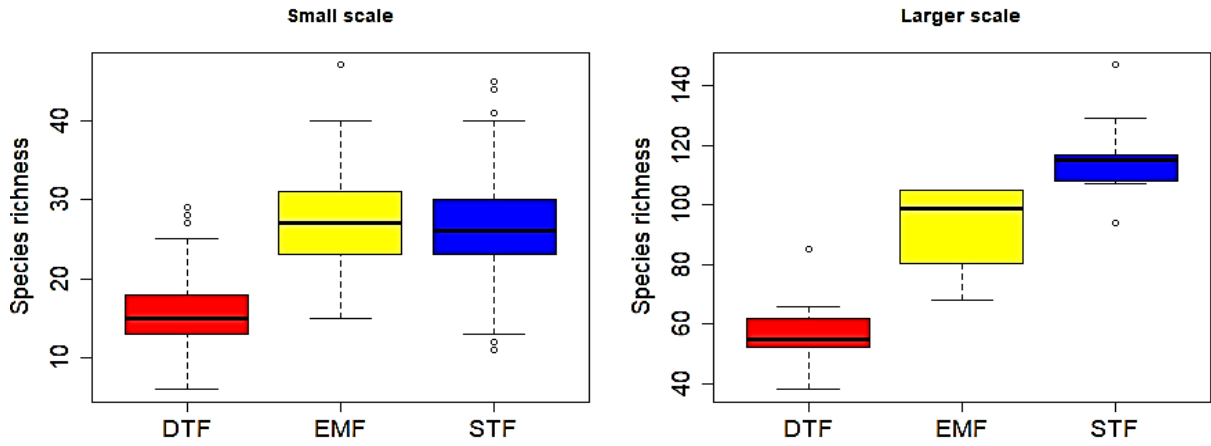

Fonte: Do autor (2019).

Figure S3 − Phylogenetic diversity calculated by site (larger scale) for three forest types: DTF (Deciduous Tropical Forest), EMF (Evergreen Moist Forest) and STF (Semideciduous Tropical Forest) located in Minas Gerais, Brazil.

Fonte: Do autor (2019).

Figure S4 − Species richness calculated by plot (small scale) and by site (larger scale) for three forest types: DTF (Deciduous Tropical Forest), EMF (Evergreen Moist Forest) and STF (Semideciduous Tropical Forest) located in Minas Gerais, Brazil.

Fonte: Do autor (2019).