

NEIL DAMAS DE OLIVEIRA JUNIOR

**EVOLUTIONARY HISTORY AND CONNECTIVITY OF THE MAIN
RIVER BASIN OF THE ATLANTIC FOREST DOMAIN**

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Magister Scientiae*.

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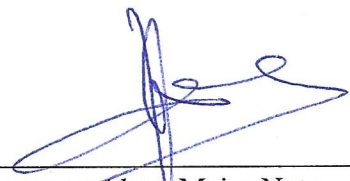
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Vanessa Pontara


Marcelo Leandro Bueno
João Augusto Alves Meira Neto
(Orientador)

Dedicado à minha família e a todos aqueles
que contribuíram pra que eu me tornasse o
ser humano que sou.

“Nada na Biologia faz sentido exceto à luz da evolução.”

Theodosius Dobzhansky

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RESUMO

OLIVEIRA-JUNIOR, Neil Damas de, M.Sc., Universidade federal de Viçosa, fevereiro de 2019. **Evolutionary history and connectivity of the main river basin of the atlantic forest domain.** Orientador: João Augusto Alves Meira Neto.

A Floresta atlântica é um dos hotspots de biodiversidade do mundo e nela se inclui a Bacia do Rio Doce, uma das maiores bacias no domínio atlântico. Importantes atividades econômicas são desenvolvidas na bacia do Rio Doce como a agricultura, produção de carne bovina e mineração, contribuindo assim para a fragmentação da paisagem e ameaçando a diversidade local. Em novembro de 2015, o rompimento da barragem de Fundão no distrito de Bento Rodrigues em Mariana causou o maior desastre com barragem de mineração da história do Brasil, liberando mais de 40 milhões de metros cúbicos de rejeitos de beneficiamento de ferro. Os ecossistemas terrestres sofreram fortes perdas de biomassa, principalmente nos fundos de vale entre a barragem de Fundão e a usina hidrelétrica de Candonga. Todavia, mensurações de riqueza ou de diversidade biológica são pouco precisas a respeito da quantidade de serviços ecossistêmicos existentes em uma comunidade. Amplas abordagens como a diversidade filogenética, a diversidade funcional e a ecologia de paisagens são importantes ferramentas para mensuração de funções ecossistêmicas, especialmente produtividade. O objetivo principal dessa dissertação foi conhecer a história evolutiva das espécies vegetais arbóreas na Bacia do Rio Doce e compreender a estrutura e a montagem de comunidades em florestas tropicais através de uma abordagem evolutiva envolvendo as métricas filogenéticas e variáveis ambientais e conhecer o atual panorama de conectividade de fragmentos na bacia, identificando áreas com grande resistência a conectividade que devem receber esforços para que se reestabeleça a conectividade. Para avaliar o potencial filogenético foram analisadas as diferentes métricas filogenéticas (Faith Index (FI) ou PD, Mean Pairwise Distance (MPD) e Mean Nearest Taxon Index (MNT)), bem como suas medidas padronizadas para o efeito da riqueza (sesPD, sesMPD e sesMNTD). Além disso foi calculado o índice de evolutionary distinctiveness (ED) usado para identificar clados com características evolutivas únicas. Para avaliar a relação das métricas filogenéticas e as variáveis climáticas de solo e clima foi utilizado a análise Generalized Least Squares (GLS) Por fim, foram analisadas as medidas de turnover filogenético (e.g. filobeta-diversidade) para medir o grau de relação entre as espécies ao longo da bacia. O atual panorama de conectividade da bacia foi avaliado através de softwares GIS e do plug in

Linkage Mapper para teste de modelos de resistência da paisagem a conectividade, gerando mapas que ilustrem a atual conectividade funcional da Bacia do Rio Doce e fundamentem planos de conservação. Nossos resultados do primeiro capítulo sugerem que variáveis ambientais e geográficas afetam a estrutura filogenética das comunidades de plantas na Bacia do Rio doce, que foram explicadas principalmente por variáveis de solo e climáticas relacionadas a relações hídricas do solo e precipitação, sugerindo uma evolução em condições de sazonalidade demarcada. As análises de filobetadiversidade mostraram que existe significativa relação entre as linhagens e variáveis geográficas, topográficas e ambientais da bacia do Rio doce, sugerindo uma tendência de agrupamento filogenético nas porções mais altas da bacia sugerindo conservantismo de nicho como resultado de grandes pressões seletivas nessas porções da bacia. Os resultados do segundo capítulo mostram que apesar de fortemente fragmentada, a bacia do Rio Doce ainda apresenta conectividade funcional principalmente na porção Oeste. O centro-norte da bacia que compreende a região de Governador Valadares é a região com maior resistência a conectividade, resultado de fortes pressões antrópicas que reduziram os remanescentes florestais, sendo necessário a intervenção através de projetos de recuperação de área degradadas para que se evite perda da biodiversidade devido a falta de conectividade. Além disso, projetos de recuperação de áreas degradadas também devem ser desenvolvidos na região de Linhares que também apresentou resistência a conectividade e está inclusa no Corredor Central da Floresta Atlântica, uma região rica em biodiversidade com alto endemismo e alto número de espécies ameaçadas, portanto, imprescindível mantê-la para manutenção da biodiversidade.

ABSTRACT

OLIVEIRA-JUNIOR, Neil Damas de, M.Sc., Universidade federal de Viçosa, February, 2019. **Evolutionary history and connectivity of the main river basin of the atlantic forest domain.** Advisor: João Augusto Alves Meira Neto.

The Atlantic Forest is one of the biodiversity hotspots in the world and includes the Doce River Basin one of the largest basins in the Atlantic domain. Important economic activities are not developed in the Rio Doce basin such as agriculture, livestock production and mining, contributing to the fragmentation of the landscape and threatening local diversity. In November 2015, the disruption of the Fundão dam in the district of Bento Rodrigues in Mariana caused the biggest disaster with the mining dam of history, releasing more than 40 million cubic meters of tailings of iron beneficiation. Terrestrial ecosystems suffered strong biomass losses, mainly in the valley funds between the Fundão Dam and the Candonga hydroelectric power plant. In 2017, 15 are mining dams were unstable in the state of Minas Gerais, threatening the local biodiversity that is the source of ecosystem functions and services, and the productivity of an ecosystem that is commonly related to the increase in Species richness. However, measurements of wealth or biological diversity are not accurate regarding the amount of ecosystem services existing in a community. Broad approaches such as phylogenetic diversity, functional diversity and landscape ecology are important tools for measuring ecosystem functions, especially productivity. The main objective of this dissertation was to know the evolutionary history of tree plant species in the Rio Doce Basin and to understand the structure and the assembly of communities in tropical forests through an evolutionary approach involving the phylogenetic metrics and environmental variables and to know the current connectivity panorama of fragments in the basin, identifying areas with great resistance to connectivity that should receive efforts to reestablish connectivity. To evaluate the phylogenetic potential, the different phylogenetic metrics (Faith index (FI) or PD, mean pairwise Distance (MPD) and mean Nearest taxon Index (MNT)) were analyzed, as well as their standardized measures for the effect of wealth (SESPD, SESMPD and SESMNTD). In addition, the evolutionary distinctiveness Index (ED) used to identify clades with unique evolutionary characteristics was calculated. To evaluate the relation of phylogenetic metrics and climatic variables of soil and climate was used the analysis Generalized Least Squares (GLS) Finally, the phylogenetic turnover measures (e.g. philobetadiversity) were analyzed to measure the degree of relationship

among species along the basin. The current panorama of basin connectivity was evaluated using GIS software and the Linkage Mapper plug in for testing models of landscape resistance to connectivity, generating maps that illustrate the current functional connectivity of the Doce River basin and support conservation plans. Our results from the first chapter suggest that environmental and geographic variables affect the phylogenetic structure of plant communities in the Doce river basin, which were explained mainly by soil and climatic variables related to relations Soil water and precipitation, suggesting an evolution in seasonally demarcated conditions. The analysis of Phylogenetic diversity showed that there is a significant relationship between the lineages and geographic, topographic and environmental variables of the Doce river basin, suggesting a tendency of phylogenetic grouping in the higher portions of the basin Suggesting niche conservatism as a result of large selective pressures in these portions of the basin. The results of the second chapter show that despite being heavily fragmented, the Doce River basin still has functional connectivity mainly in the western portion. The center-north of the basin comprising the region of Governador Valadares is the region with the highest resistance to connectivity, a result of strong anthropic pressures that reduced forest remnants, requiring intervention through projects of Degraded area recovery to avoid loss of biodiversity due to lack of connectivity. In addition, recovery projects of degraded areas should also be developed in the region of Linhares that also presented resistance to connectivity and is included in the Central corridor of the Atlantic Forest, a region rich in biodiversity with high endemism and high number of endangered species, therefore it is essential to keep it in order to maintenance of biodiversity.

Introdução Geral

A Floresta Atlântica é uma das mais diversas florestas tropicais do mundo, considerada um dos hotspots de biodiversidade do planeta (MEYERS *et al.*, 2000). Caracteriza-se por possuir uma topografia complexa, muitas vezes com gradientes ambientais abruptos, forte sazonalidade em algumas regiões e precipitação orográfica resultante da influência dos ventos oceânicos (Fundação Instituto Brasileiro de Geografia e Estatística, 1993). Devido a heterogeneidade de ambientes, a floresta atlântica abrange múltiplas fitofisionomias, sendo as principais as florestas ombrófilas densa, florestas ombrófilas mistas, florestas ombrófilas abertas, florestas estacionais semidecíduais e florestas estacionais decíduas (VELOSO, 1991) possuindo mais de 20.000 espécies de plantas, sendo 8.000 delas endêmicas (MEYERS *et al.*, 2000).

A bacia do Rio Doce (BRD), uma das mais importantes bacias hidrográficas do Brasil, encontra-se inserida com cerca de 98% de sua área no domínio atlântico. Sua porção leste que compreende toda a área da bacia no estado do Espírito Santo, abrange parte do corredor central da mata atlântica, uma das áreas de maior biodiversidade da Floresta atlântica (Instituto Mineiro de Gestão das Águas, 2010). Sendo portanto uma área de grande relevância para conservação. Dentre as principais causas de ameaça à biodiversidade do corredor central da Mata atlântica estão: uso intensivo da terra, caça, exploração de madeireiras, introdução de espécies exóticas e urbanização (LEAL E GUSMÃO CÂMARA, 2003). Na bacia do Rio Doce importantes atividades econômicas são desenvolvidas, das quais destacam-se a agropecuária, silvicultura e a mineração (INSTITUTO MINEIRO DE GESTÃO DAS ÁGUAS, 2010), o que somado a urbanização compõe as causas principais de degradação ambiental na bacia e ameaçam a sua diversidade. Desta forma, a sustentabilidade das atividades socioeconômicas na Bacia do Rio Doce passa pela conservação da biodiversidade em longo prazo, na qual é fundamental a criação e manutenção de reservas estratégicas de biodiversidade, a conexão de habitats naturais e a proteção preventiva de margens de rios para manterem, promoverem e aumentarem a estabilidade ecossistêmica (MEIRA-NETO *et al.*, 2016).

A estabilidade ecossistêmica pode ser entendida por meio de duas características dos ecossistemas: a resistência, que é a capacidade de resistir a distúrbios, e a resiliência, que é a capacidade de recuperação após os distúrbios. Os distúrbios são caracterizados principalmente pela perda de biomassa (TILMAN, 1988). Em novembro de 2015, o rompimento da barragem de fundão no distrito de Bento Rodrigues em Mariana causou o maior desastre com barragem

de mineração da história, liberando mais de 40 milhões de metros cúbicos de rejeitos de beneficiamento de ferro (FERNANDES et al., 2016; MEIRA et al., 2016). Esse incidente ficou conhecido como o “desastre de Mariana” e os impactos foram catastróficos para ecossistemas aquáticos e terrestres ao longo de grande parte da bacia do Rio Doce (MEIRA et al., 2016). Os ecossistemas terrestres, embora tenham apresentado alguma resistência aos impactos da onda de rejeitos, sofreram fortes perdas de biomassa, principalmente nos fundos de vale entre a barragem de Fundão e a usina hidrelétrica de Candonga. Não foi documentado ainda a distribuição espacial da resiliência potencial em comunidades vegetais aos distúrbios na bacia, mas há uma vasta literatura que associa o potencial de resiliência à biodiversidade (e.g., OLIVER et al. 2015; GRANADOS et al. 2016; MORI 2016, PETERSON et al. 1998). Todavia, mensurações de riqueza ou de diversidade biológica são pouco precisas a respeito da quantidade de serviços ecossistêmicos existentes em uma comunidade. Portanto, amplas abordagens como a diversidade filogenética e a ecologia de paisagens são importantes ferramentas para mensuração de funções ecossistêmicas, (GASTAUER and MEIRA-NETO, 2015; MAGNAGO et al., 2015).

As medidas de diversidade biológica baseadas em riqueza de espécies, embora úteis, não são suficientes para garantir que todos os traços funcionais e presentes na comunidade sejam expressos na amostragem (Faith, 1992). Assim, estudos que incluem medidas filogenéticas são informações fundamentais para o delineamento de áreas de conservação, pois embasam-se na singularidade de características das espécies da comunidade, selecionando assim áreas que contenham espécies com alta contribuição para a medida de diversidade, considerando cada espécie fundamental para o funcionamento das comunidades por conta da sua unicidade (FAITH, 1992, ISAAC, 2007). Espécies taxonomicamente distintas tendem a contribuir mais com a diversidade de espécies total uma vez que maiores valores de diversidade filogenética significam maior número de traços na comunidade (FAITH, 1992), que por sua vez sugerem maior número de serviços ecossistêmicos. Sendo assim, essas regiões com grandes diversidades filogenéticas são de estratégica importância para a conservação e para a manutenção dos serviços ecossistêmicos. Por fim, fatores ambientais e ecológicos combinados ajudam a explicar a diversidade de espécies e a diversidade beta das comunidades (WHITTAKER, 1972) nos gradientes ambientais (KORNER, 2007), uma vez que filtros ambientais podem ser fortes o suficiente pra selecionar apenas clados específicos para ocupar uma região, de uma maneira que os nichos estão correlacionados com o gradiente ambiental da área (JIN et al, 2015)

Não obstante, as medidas de análise da paisagem trazidos pela ecologia de paisagem são fundamentos adicionais para planejamento de ações de conservação da biodiversidade frente à perda de conectividade pela fragmentação da paisagem e às mudanças climáticas, que ameaçam a biodiversidade, colocando muitas espécies em risco de extinção (CROOK and Sanjayan, 2006). Assim, a conectividade da paisagem é fundamental para que as espécies possam de adaptar a mudanças em sua área natural de ocorrência (OPDAM E WASCHER, 2004), garantindo assim a manutenção da biodiversidade em áreas fragmentadas. Além disso a conectividade permite o movimento de espécies na paisagem em busca de recursos, colonização de novas áreas (TAYLOR, 2006) e ajuda a manter a diversidade genética através do sucesso reprodutivo de animais e plantas (CROOKS AND SANAYAN, 2006) principalmente pela transferência do pollen e dispersão de sementes (SMORK E SMOUSE, 2006) processos fundamentais para manutenção da vegetação, justificando portanto a avaliação da conectividade da paisagem como peça fundamental para conservação (SAURA & TORNÉ, 2008) uma vez que deve-se levar em conta os processos vitais que ocorrem na escala da paisagem.

Esta dissertação foi desenvolvida em dois capítulos com o objetivo de conhecer a história evolutiva das espécies vegetais arbóreas na Bacia do Rio Doce e compreender a estrutura e a montagem de comunidades em florestas tropicais através de uma abordagem evolutiva envolvendo as métricas filogenéticas e variáveis ambientais. Além disso, pretendeu-se conhecer o atual panorama de conectividade de fragmentos na bacia, identificando áreas com grande resistência a conectividade que devem receber esforços para que se reestabeleça a conectividade. Ao examinar a diversidade filogenética das comunidades arbóreas da BRD, objetivamos fornecer informações obre sua história biogeográfica e priorizar ações de conservação. Em relação a conectividade, nosso objetivo foi gerar mapas que demonstrem a conectividade dos atuais fragmentos existentes na bacia em uma abordagem abrangente para embasar estratégias de conservação (e.g. Criação de parques de conservação de diversidade biológica) dos remanescentes de floresta atlântica presentes na BRD, propondo a criação de corredores ecológicos, a fim de conservar e manter distribuído por toda a bacia o potencial de resiliência da BRD.

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Capítulo 1: Evolutionary history of tree species of the major river basin in the Atlantic Forest

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1. Abstract

The distribution pattern of species diversity is a main question to be answered in biogeography. Incorporating phylogeny in community ecology allows us to infer the patterns of distribution of species based on history of habitat preferences over time, and species function. Phylogenetic analysis can be informative about biogeographic processes that shaped community species diversity (i.e. alpha diversity). Combining environmental and ecological factors is important for the understanding of species diversity and turnover (i.e. beta diversity) among environmental gradients. since environmental filtering can be strong enough to select only specific clades to occupy a region, in a way that their niche is correlated with environmental gradients. In the present study, our goal was to reveal the biogeographic story of tree species of the Rio Doce Basin, a major river basin in the central Atlantic Forest region, and improve the understanding of community assembly and structure in tropical forests within an evolutionary approach. We expected to find a relation between the phylogenetic metrics used in our study and geoclimatic variables and a high turnover in the river basin due to environmental heterogeneity of the river basin. Using a matrix of trees occurrence for 78 sites in the DRB was extracted from NeotropTree, We generated a phylogenetic tree using all woody angiosperms found in the river basin using Phylomatic function in Phylocom 4.2 We used six different metrics to describe the evolutionary history of Rio Doce Basin: (i) Faith's phylogenetic Index (PD), (ii) Mean Nearest Taxon Distance (MNTD), (iii) Mean Pairwise Distance (MPD), as well as their standardized forms for richness standardization of the metrics to remove the effect of richness (ses): (iv) sesPD, (v) ses MPD and (vi) sesMNTD. We also calculated the evolutionary distinctiveness scores (ED) in order to describe species uniqueness. To test the relationship between phylogenetic metrics and climatic and soil variables we performed a Generalized Least squares (GLS). Finally, we performed Phylobetadiversity analysis to measure phylogenetic relationships of the species among areas using comdistnt (MNTD), comdist (MPD) functions. All analyses were performed in R software. Our results show significant relation between environmental variables and phylogenetic diversity being climatic and soil variables the main explanatory variables for the phylogenetic indexes. Phylobetadiversity analysis indicated that there is a trend of clustering patterns with increasing altitude in the DRB. Soil variables explained the most the indexes and it is mostly related to water supply for plants, suggesting that deeper evolutionary events result from a pattern of community structure that is related to the evolutionary conditions of DRB, where the communities evolved in an environment with a prominent seasonality.

Keywords: phylogenetic diversity, phylobetadiversity, community ecology, community assembly, conservation.

2. Introduction

The distribution pattern of species diversity is a main question to be answered in biogeography. The biogeographic origin of species, in combination with dispersal limitation and environmental filtering, are the principal determinants of spatial variation in the species composition of tropical forests (Cavender-Bares et al, 2016; Donoghue et al, 2008). The geographic patterns of distribution of plants is a result of a set of biotic (i.e. competition, facilitation) and abiotic variables (i.e. temperature, soil, moisture) (Jin et. al, 2015; Bueno et al. 2018; Pontara et al. 2018; Rezende et al.; 2017, 2018). However, tropical forests diversity patterns are complex and to measure diversity can be quite difficult.

Thus, incorporating phylogeny in community ecology allows us to infer the patterns of distribution of species based on history of habitat preferences over time, and species function (Swenson, 2011). In case that functional traits are conserved within phylogenetic lineages, clustered patterns of phylogenetic distribution, suggest conserved habitat use due to environmental filtering, whereas overdispersed patterns suggest evolutive convergence or competitive exclusion (Webb et al., 2002). When applied to larger areas, phylogenetic analysis can be informative about biogeographic processes that shaped community species diversity (i.e. alpha diversity) (Webb et al., 2002; Culmsee & Leuschner, 2013). Also, analysis of phylogenetic diversity can indicate important areas of conservation (Mishler et al., 2014) considering species that contributes to phylogenetic diversity because of their uniqueness (Faith 1992). That unique species distribution of the tree can be revealed by Evolutionary Distinctiveness (ED) scores (Isaac, 2007) which may indicate which species are more isolated phylogenetically and therefore, presenting peculiar genetic information has more potential to bear unique traits (Redding et al., 2010), being therefore priority to conservation.

Furthermore, adding phylogenetic information to beta diversity (Whittaker, 1972) improves the knowledge about the importance of evolutionary events driving the pattern of species distribution. (Bin et al., 2010). Phylobetadiversity incorporates evolutionary history to

beta-diversity, measuring phylogenetic relatedness among species across a geographic space, often influenced by environmental filtering and barriers (Graham and Fine, 2008). Greater values of turnover deep in the phylogeny suggests niche conservatism. In contrast, higher values of turnover in more recent clades suggest divergence in habitats (Jin et al., 2015). Combining environmental and ecological factors is important for the understanding of species diversity and turnover (i.e. beta diversity, Whittaker 1972) among environmental gradients (Korner, 2007), since environmental filtering can be strong enough to select only specific clades to occupy a region, in a way that their niche is correlated with environmental gradients (Jin et al., 2015).

Atlantic forest is known by its considerable biodiversity being one of the leading hotspots of biodiversity in the world with about 20.000 plant species of which 7000 are endemic and are regarded as a conservation priority (Meyers et al., 2000, Rezende et al. 2018). Atlantic domain harbours about 1-8 percent of the world's total biodiversity (Silva e Castelleti, 2003) being the second largest tropical forest in South America after Amazon Forest (Oliveira-Filho & Fontes, 2000). The Doce River Basin is a major river basin in the central area of Atlantic Forest with high biodiversity and with a wide range of data available for studies of biogeographic pattern of species diversity. Nonetheless, there are few studies addressing the influence of geoclimatic data on phylogenetic diversity on Doce River Basin. (Oliveira-filho 2000; Saiter et. al, 2015)

In the present study, our goal was to reveal the biogeographic story of tree species of the Rio Doce Basin and improve the understanding of community assembly and structure in tropical forests within an evolutionary approach. The knowledge of the biodiversity of Doce River Basin and the distribution range of species will improve our comprehension of the risks of phylogenetic diversity loss and adding information about local threats would enable us to refine the definition of Doce River Basin hotspots. Specifically, we ask (i) which processes and/or environmental variables, drive the community assembly across our woody plant

communities in the Doce River Basin and where within phylogenetic clades do we observe their influence; (ii) if geoclimatic variables are influencing phylobetadiversity along the basin. We expected to find a relation between the phylogenetic metrics used in our study and geoclimatic variables. Moreover, we also expect to find a high phylogenetic turnover in the river basin due to environmental heterogeneity of the river basin.

3. Materials and Methods

3.1 Study Area

This study was performed on Doce River Basin (DRB), located between latitudes 17°45' and 21°15' S e longitudes 39°30' and 43°45'W, with an area of 86.715 km² occupying parts of Minas Gerais and Espírito Santo states in Brazil (Instituto Mineiro de Gestão das Águas, 2010) (Fig 1). The DRB area is influenced by Cerrado vegetation (Instituto Mineiro de Gestão das Águas, 2010), but mostly within DRB occurs Atlantic Forest and this influence defines the basin in the Atlantic Forest domain. We analysed woody species from different physiognomies of Atlantic Forests: tropical rainforest and tropical semi deciduous forest. The semi deciduous forest is defined by the vegetation that occurs in areas of strong seasonality, characterized by a wet season with intense rainfall typical of tropical regions followed by a strong dry season (Oliveira-Filho & Fontes, 2000). As a response to that seasonality, around 20-50% of the trees lose their leaves during the dry period (deciduous) (Veloso et al., 1991). On the other hand, tropical rain forests are those areas under tropical climate conditions with average temperature of 25°C, a very well distributed precipitation along the year, therefore, the vegetation is characterized by tall evergreen trees (Veloso et al., 1991).

The DRB limits are the Negra and the Aimorés Mountains in the North, the Espinhaço Range on west side, the Caparaó Range on southeast, and the Atlantic Ocean in the east. The Rainfall regime in the DRB is divided into rainy season and dry season. The Mean Annual

Precipitation varies from 800 to 1300 mm in the rainy season and from 150-250 mm in the dry season (Instituto Mineiro de Gestão das Águas, 2010). The soil in the DRB are predominantly yellow-red latosols characterized by deep soils dystrophic with high saturation of aluminium and red ultisols characterized by variable depth and with mineral material in its constitution. Those two types of soil envelop 77,2% of the basin (Instituto Mineiro de Gestão das Águas, 2010).

3.2 Floristic data set

The matrix of trees occurrence for 78 sites in the DRB (Fig 1.) was extracted from NeotropTree, a database containing a checklist of tree species in the Neotropics (OLIVEIRA-FILHO, 2017). The checklists were obtained from occurrence records from tree different sources [a] Published floristic and quantitative surveys. [b] taxonomic monographs and [c] herbarium records available in the herbarium virtual da Flora e dos Fungos (INCT; <http://inct.splink.org.br/>). The reliability of information, expert opinion and taxonomic literature were used to verify the data. Due to high density of floristic and quantitative surveys for certain localities, data were compiled and merged into a single checklist, being kept in separate checklists in places where vegetation does not remain constant across a 5km radius. As a result, an amount of 1944 species distributed in 100 families in a total of 22007 individuals were recorded for the entire DRB.

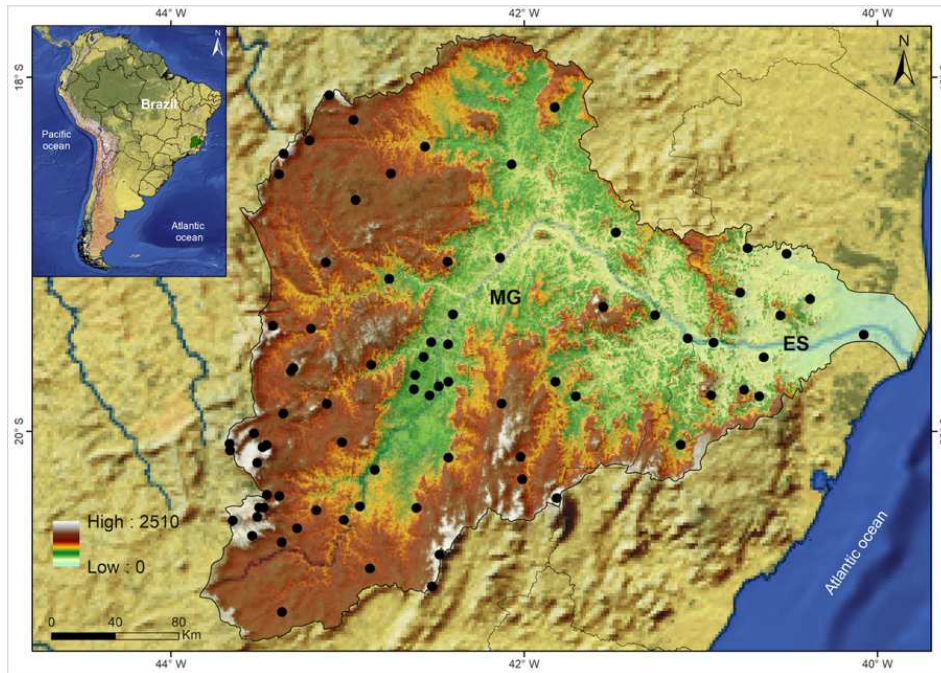


Figure 1: The Doce River Basin. The black circles represent the analysed sites. The colours represent the elevation the highest represented by white and the lowest by light green. States: MG – Minas Gerais and ES – Espírito Santo. Datum: WGS 84.

3.3 Phylogenetic Analysis

We generated a phylogenetic tree using all woody angiosperms found in the basin using Phylomatic function in Phylocom 4.2 (Webb & Donoghue, 2005) and megatree R20160415.new (Gastauer e Meira-Neto, 2017) based on APG IV (Angiosperm Phylogeny Group 2016). We excluded Ferns and Gymnosperms from Phylogenetic analysis due to their effect on the diversity metrics since they represent very long branches on the phylogeny.

We used six different metrics to describe the evolutionary history of Rio Doce Basin: (i) Faith's phylogenetic Index (PD, Faith, 1992) obtained by the sum of branches of a phylogenetic tree for all species found in a community; (ii) Mean Pairwise Distance (MPD), defined by the average phylogenetic distance among taxa in the community; (iii) Mean Nearest Taxon Distance (MNTD; Webb, 2000; Webb et al., 2002), defined by the mean phylogenetic distance from the closest relative taxon in the community. Also, we calculated the standardization of the metrics to remove the effect of richness, based on a null model (Swenson,

2014) known as standardized effect size (ses): (iv) sesPD, (v) sesMPD and (vi) sesMNTD. The negative forms or sesMPD and sesMNTD are also known as NTI (Nearest Taxon Index) and NRI (Net Relatedness Index) respectively (Webb et al., 2002; Cavender-Bares et al. 2009). Negative values of ses indicate clustering and positive values indicate overdispersion.

In order to describe species uniqueness, we calculated the evolutionary distinctiveness scores (ED) (Isaac et al., 2007). High ED scores mean that the species does not have many close relatives in the phylogenetic tree, thus being considered isolated phylogenetically. Therefore, the higher ED scores for a given community, the higher the number of evolutionary unique species (Edwards et al., 2017).

3.4 Generalized Least Squares

In order to test the relationship between phylogenetic metrics and climatic and soil variables we built linear models through generalized least squares (GLS). We included uncorrelated variables with strong explanatory power and excluded variables that has weak or none explanatory power assessing correlations. Latitude and longitude variables were used as proxies for climatic variation uncaptured by measured variables of climate and soil, therefore accounting for spatial autocorrelation. Variance inflation factors (VIF) less than five for each explanatory variable (Quinn and Keough, 2002) and we used Akaike Information Criterion (AIC) to compare the models.

3.5 Phylobetadiversity Analysis

Phylobetadiversity among areas was measured using `comdistnt` (MNTD), `comdist` (MPD), and `Unifrac` functions in the ‘picante’ package in R (Kembel et al., 2010; R Development Core Team, 2013). `Comdist` is a phylobetadiversity measure that computes the mean phylogenetic distance among species occurring in two different sites (Webb et al., 2008).

Comdistnt measures the mean phylogenetic distance between every species in a plot and the nearest phylogenetic neighbor in another site (Duarte et al., 2014). It is, therefore, a “terminal node” metric (Swenson, 2011). COMDIST and COMDISTNT were computed in the R environment, using the package picante 1.6–2 (Kembel et al., 2010). As some methods are more sensitive to variation in deeper phylogenetic nodes (COMDIST) while others capture variation mostly associated with shallower nodes (COMDIST, UniFrac), using several indices to analyze phylobetadiversity patterns might help us to understand to what extent phylobetadiversity levels are explained by more basal or recent nodes (Swenson, 2011). The correlation between these beta diversity indices and geographic distance was first assessed with a Mantel test based on Pearson’s product-moment correlation with 9999 permutations.

4. Results

4.1 Phylogenetic diversity and environmental variables

There is a strong correlation between phylogenetic diversity and species richness (Fig. 2). The MNTD showed an opposite result to that found for PD and SR, as expected when there are more species of the same clades. The best model for ses.MPD and ED was the full model, including soil and climatic variables (Table 1). We found that climate is the best explanatory model to explain sesPD and sesMNTD distribution in the DRB. For species richness (SR), the pure soil model explained the data better than a model with just climatic model. The best climatic model for SR included the same climatic variables as the model for PD (SR value was strongly positively correlated with PD) (Fig. 2; Table 1).

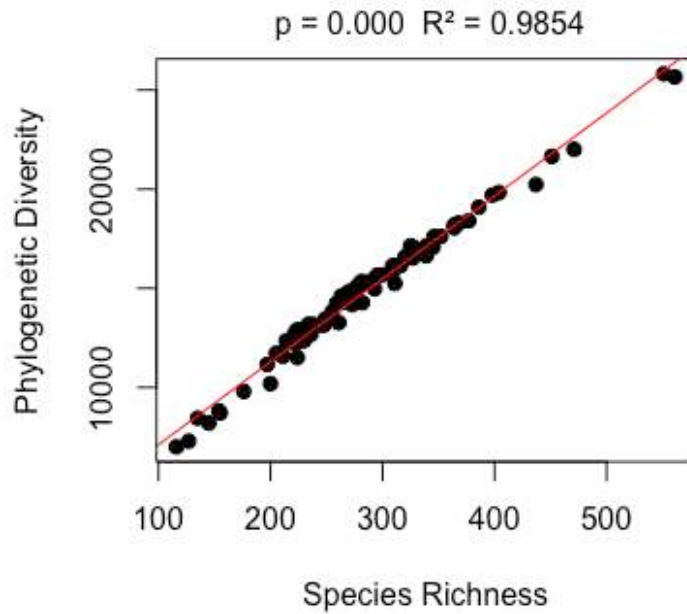


Figure 2: Correlation between Phylogenetic Diversity (PD) and Species Richness (SR) of Atlantic Forest species in the Doce River Basin.

Table 1: Delta akaike Information Criterion (AIC) values for distinct models tested to explain species richness (SR) and standardized indexes of Phylogenetic Diversity (PD), Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD): sesPD, sesMPD, sesMNTD and for Evolutionary distinctiveness (ED). Variables included are TempMax: Max temperature of warmest month; TempSeas: Temperature seasonality; TempMin: Minimum Temperature of coldest month; PrecAnn: Annual precipitation; CloudItcp: Cloud interception; Grassy cover; SoilWaterStorage, WaterExcDur; Alt/Altitude: Elevation; Ranked Rockiness; RankedTBS: measure of soil fertility; Ranked Sand: ; Ranked Drainage.

Models	SR	sesPD	sesMPD	sesMNTD	ED
Climate	1.23	0	7.27	0	29.22
Soil	0	30	0.37	22.35	15.09
Climate + Soil	9.43	1.81	0	4.35	0
Variables included	SoilWaterStorage/GrassyCover/WaterExcDur	TempMax/CloudItcp/Alt/PrecAnn/RankedRockiness	CloudItcp/Altitude/RankedTBS/SoilWaterStorage/	RankedSand/RankedRockiness/TempSeas/TempMax/Alt	RankedDrainage/GrassyCover/SoilWaterStorage/TempMin/TempSeas

4.2 Phylobetadiversity

We found significant relations between the metrics of Phylobetadiversity (BetaMPD and betaMNTD) and the variables of environment, geographic distance and elevation (Table 1.) Both metrics presented the same value when compared to elevation, but BetaMNTD is slightly greater than BetaMPD regarding the relationship with environment and distance.

Table 1. Mantel test for the phylobetadiversity metrics. P values are in parenthesis.

	BetaMPD	BetaMNTD
Elevation	0.5839***	0.5839***
Environment	0.4567***	0.7114***
Distance	0.5839***	0.6901***

*** significance of the Mantel test ($p < 0.001$)

5. Discussion

As we expected, geoclimatic variables are influencing tree species richness and community structure in the DRB. Soil and climatic conditions have a strong effect on the distribution of plant species richness and phylogenetic diversity of woody species richness and phylogenetic diversity of woody plant communities in DRB. Our results suggest soil (e.g. soil water storage and water deficit duration) as an important environmental filter since it is the best explanatory variable for variation in SR and PD. Species richness is highly correlated with phylogenetic diversity (Fig. 2), suggesting that phylogenetic diversity in the DRB is highly explained by soil variables. Species richness is explained better by soil variables (Slik et al,

2009) and soil characteristics influences the capacity to store water and make nutrients (minerals) available for plants; therefore, they explain strong patterns of the distribution of plant species (Ricklefs, 2013). Consequently, plants distributions are segregated by geomorphic patterns (Phillips et al., 2003), and many different soil habitats emerge from the topography of the DRB. Both sesMPD and ED (metrics related to deeper branches in the phylogenetic tree) are influenced by soil variables related to water availability (i.e. ranked drainage for ED and soil water storage affecting both, ED and sesMPD), suggesting that deeper evolutionary events result from soil and topographic evolutionary conditions within DRB. Also, soil fertility is included in the model as one predictive variable of sesMPD, therefore affecting the phylogenetic distribution deeper in the phylogeny (Sanders, 2011).

Climate is influencing the number of lineages (sesPD) and the recent diversification of taxa (sesMNTD) in the DRB. Precipitation seasonality might be involved since precipitation is known to affect trees phylogenetic diversity (Slik, 2009) and there is evidence for its influence in the eastern portion of Atlantic forest (Rezende et al., 2018). The seasonality gradient from east to west in the Atlantic Forest, a very well understood pattern in Atlantic forest (Oliveira-filho & Fontes, 2000), which also shapes directly the plant physiognomy of the DRB. Furthermore, elevation and associated temperatures are known to be important factors that shapes Atlantic forest communities (Oliveira-Filho & Fontes, 2000). Increasing altitude, evident in the gradient from east to west within RDB, leads to changes in climate trends such as decreasing atmospheric pressure, decreased temperature which implies in altered humidity as well, and increased radiation (Korner, 2007). Thus, due of gradient topography, there are environments with different microclimate and edaphic characteristics that affects the number of lineages able to establish and persist (Sander, 2011).

The temperature variables driving the species diversity in either latitudinal and altitudinal gradients, also was highlighted by Qian & Ricklefs (2016). The correlation between

elevation and phylogenetic relatedness in elevational gradients in the tropics has been often observed (Culmsee and Leuschner, 2013; Qian, 2016; Zhang et al, 2016). Our findings of decreasing sesPD, sesMNTD and sesMPD with elevation, results in a clustered pattern in high altitudes for deep and tip branches of the phylogenetic tree. This suggests a strong environmental filtering acting at higher altitudes promoting clustering trends of the phylogenetic structure. Therefore, niche conservatism explains communities' assembly in higher altitudes, differently from other studies correlating elevation and phylogenetic overdispersion of communities (Qian & Ricklefs 2016; Zhang et al 2017; Qian, 2018; Pontara et al., 2018). Consequently, abiotic factors related to elevation that affects directly the establishment of species such as lower temperatures, reduced soil depth and water storage capacity (Zhang et al., 2016), also are shaping the communities in the DRB.

In larger areas such as the one we are focusing in this study, phylogenetic clustering would reflect biogeographical processes instead of ecological ones because clades diversify at a regional scale (Webb, 2002). Qian & Ricklefs (2016) propose that in evolutionary history, angiosperm species distributed in low and high elevations belonged to old families. As the geographic distance were reduced between low and high elevations and because high altitude harbors smaller habitat areas, new families and other higher altitude taxa were less likely to originate in these regions. Due to majority area in the lowlands, the probability of new young family-level clades arise is greater in these areas (Qian & Ricklefs, 2016). But, our data suggests that recent evolutionary events have been less frequent on lowlands since sesMNTD is greater in these areas (Fig 2, Appendice).

Phylogenetic turnover was significant for both the tips and the deep branches of the phylogenetic tree, with high turnover among clades (Swenson 2011) and among species. Our analysis showed that phylobetadiversity (betaMPD and betaMNTD) is correlated with environmental variables (Baldeck et al., 2016; Jin et al., 2015; Hardy et al., 2012), which likely

reflects strong environmental filtering that prevents some species to establish in certain areas such as high altitude sites. This is related due to strong rockiness presence, temperature variables or even precipitation gradient present in the DRB (Pontara et al., 2018). In tropical trees communities, environmental variables related to rainfall and dry season are among the main drivers of phylogenetic turnover (Hardy et al., 2012; Swenson, 2011; Pontara et al., 2018). We did not specifically address our analysis to those variables since we tested phylogenetic turnover correlation to environment including other variables related with the ones described above. However, since water deficit duration and soil water storage were explanatory variables for species richness and the latter explaining sesMPD and ED, it is an evidence that water-related variables and temperature are shaping the communities in the DRB delimiting species distribution. Moreover, our results related to significant relation between phylogenetic turnover and elevation, corroborating our results of phylogenetic structure and reinforcing the evidence for phylogenetic niche conservatism. In fact, evolutionary lineages might conserve their climatic niche (Gastauer et al., 2015), because there is a strong correlation between the phylogenetic turnover (betaMPD and betaMNTD) and spatial distance (Gastauer et al., 2015) since broader scales encompasses high heterogeneity of habitats (Cavender-Bares, 2009).

Therefore, we conclude that niche conservatism of species is influencing the species diversity distribution in the DRB because our results suggests that environmental variables are related to phylogenetic diversity along the river basin, providing evidence of strong environmental filtering shaping the communities, as we expected. Climate and soil variables are the most explanatory variables in this study. Although we have evidence for the decrease in the number of lineages with precipitation we must take into account orographic precipitation that happens in the west portion of the basin which encompasses Espinhaço Range, which probably is filtering species because of temperature and soil more than precipitation, something to be elucidated in further studies.

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7. Appendix

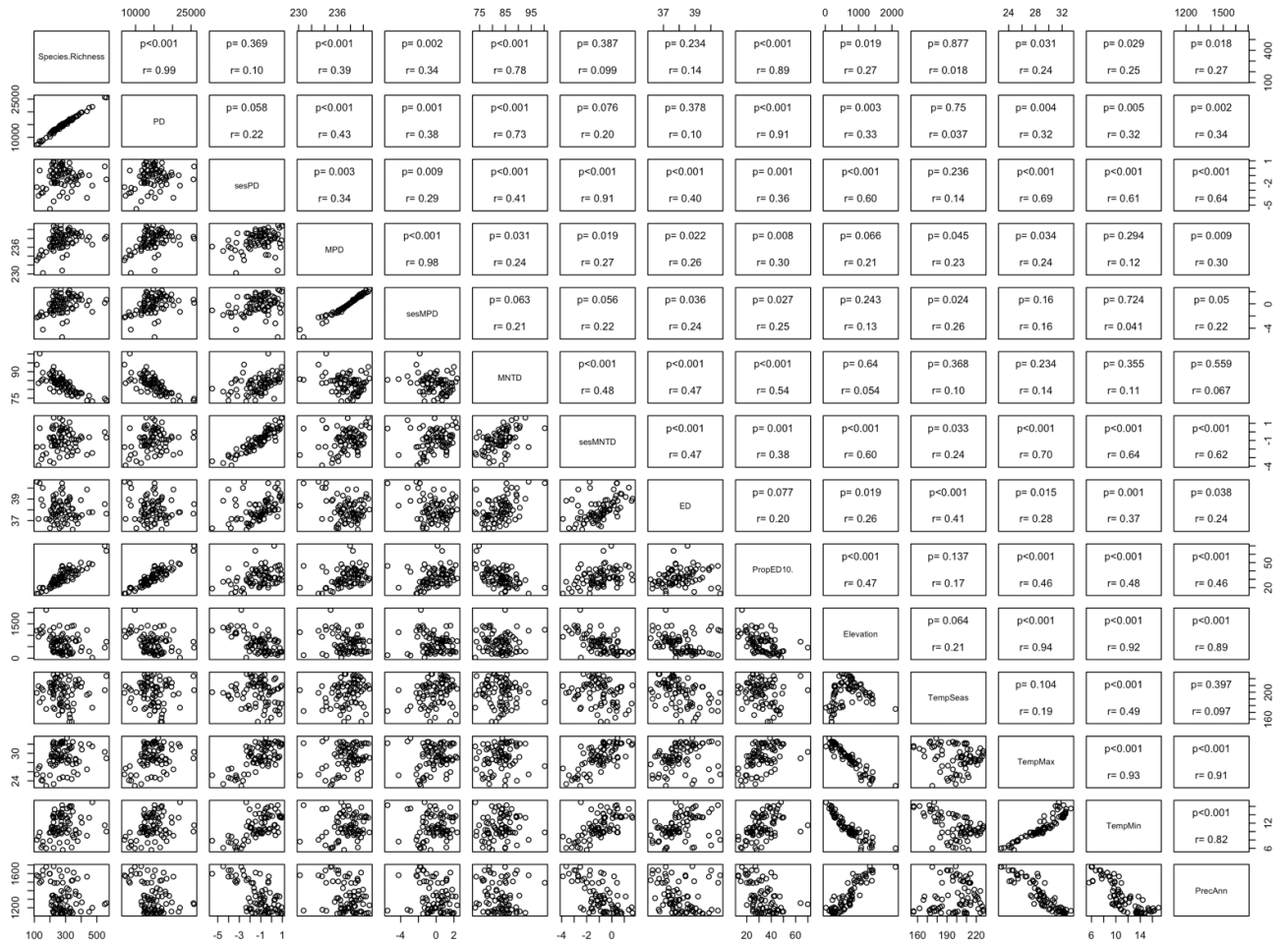


Figure 1. Correlations between, Species Richness, phylogenetic metrics (sesPD, sesMPD and sesMNTD) and environmental variables.

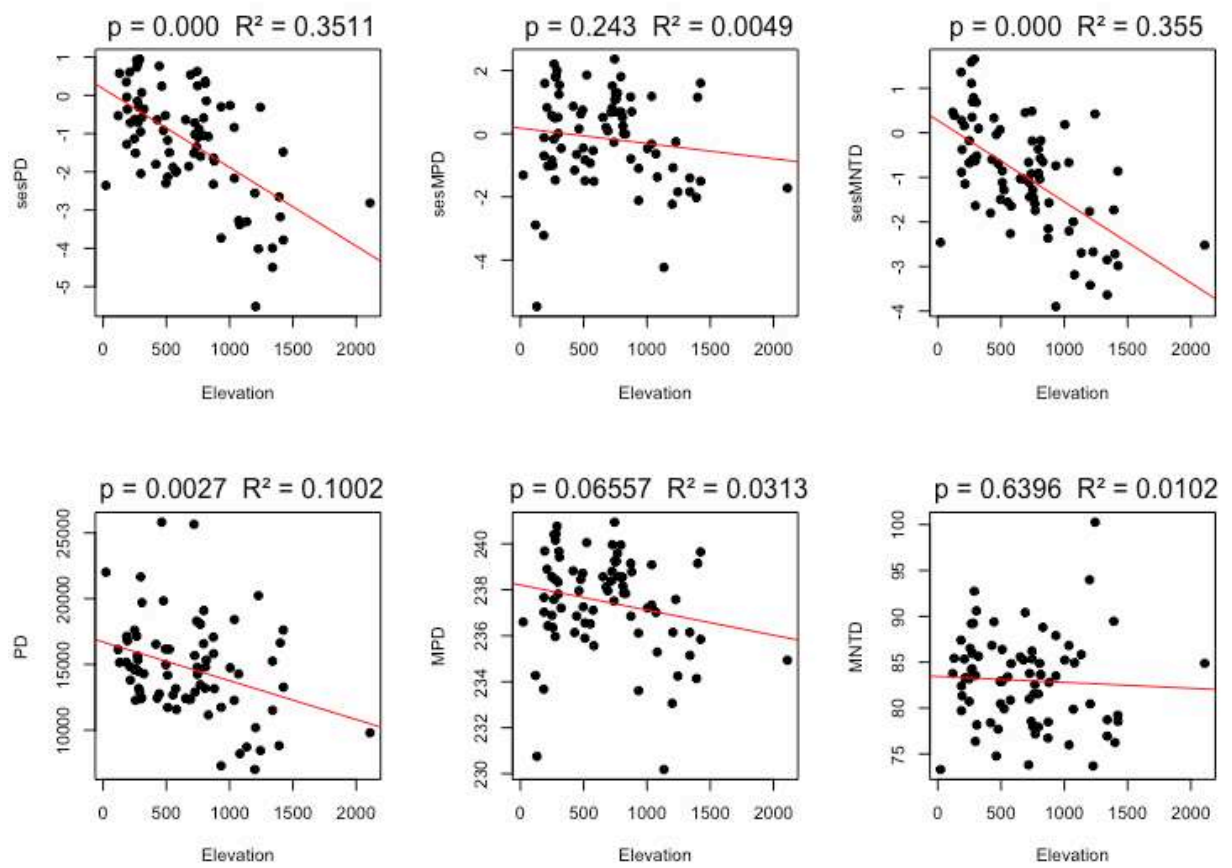


Figure 2. Correlations between all phylogenetic metrics and elevation in the Doce River Basin. Only sesPD and sesMNTD presented significant correlation with elevation.

Capítulo 2: Tropical Forest Connectivity at basin level: a study case from Atlantic Forest

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1. Abstract

The probability of a propagule to reach a given site where it can establish and persist is affected by distance from the source. Fragmented landscapes often promote habitat isolation can difficult or impede the movement of species affecting its range distribution if they are unsuitable for species existence. Studies evaluating landscape connectivity are fundamental to ensure that ecological conservation planning will cover all vital processes occurring at a landscape scale. Based on the land-cover classification of Doce River Basin, we used a habitat /non-habitat approach to evaluate the connectivity of the DRB for tree species. based on circuit theory we built 6 models of resistance surface based on habitat and non-habitat areas. We ran analysis using GIS and Linkage Mapper plug-in to generate least cost paths maps. Our results showed that the DRB is quite fragmented but still remains functionally connected. The center-north of the basin that comprises a region of Governador Valadares is a region with greater resistance to the connectivity, as a result of strong anthropic pressures that reduce the forests, being necessary an intervention through projects of recovery of degraded areas so that the loss is avoided due to a lack of connectivity. In addition, land reclamation projects in degraded areas should also be organized in the region of Linhares because it is inserted on the central corridor of Atlantic Forest, a region with high biodiversity with a high level of endemism and a high number of endangered species, and it is therefore it is important to the maintenance of biodiversity.

Keywords: fragmentation, landscape ecology, conservation, corridors

2. Introduction

The probability of a propagule to reach a given site where it can establish and persist is affected by distance from the source, in other words, the larger the distance, the smaller is the probability of a species to reach suitable habitat and establish (Hanski and Gilpin, 1997). Fragmented landscapes often promote habitat isolation can difficult or impede the movement of species affecting its range distribution if they are unsuitable for species existence (Crooks and Sanjayan, 2006; Matos et al., 2017). In contrast, areas with suitable habitat act as corridors for the dispersal of species and ensure their movement in the landscape (e.g. landscape connectivity). Therefore, landscape connectivity is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993 see also With et al, 1997; Saura et al., 2011).

Landscape connectivity is a major concern in ecology and land conservation planning (Saura et al., 2011). In a climate change scenario, connectivity is very important to alleviate the consequences of the changes in the environmental conditions allowing species to accommodate to the changes in their natural range (Opdam and Wascher, 2004) and guarantee the maintenance of biodiversity in fragmented areas. A path that is well connected, will receive more dispersers and will provide also more propagules (Taylor et al., 1993). In addition, landscape connectivity allows species movement in the landscape to collect resources, to colonize new habitats (Taylor, 2006), and helps to maintain genetic diversity through pollen and seed dispersal (Smork and Smouse, 2006). These vital processes may be affected by deficiency on landscape connectivity, risking the permanency of plant populations in a landscape (Crooks and Sanjayan, 2006). Therefore, studies evaluating landscape connectivity are fundamental to ensure that ecological conservation planning will cover all vital processes occurring at a landscape scale.

Modelling connectivity for plant species is challenging, because there are considerable number of factors that affects functional connectivity in plants. Pollen and seed dispersal are both dependent on biotic and abiotic factors, which in turn is affected by landscape (Auffret et al., 2017). Using resistance distance to model connectivity is more advantageous than simply use Least Cost Distance, taking into account different levels of suitability for dispersal of plants and animals (McRae, 2006), from hostile environments to patch mosaics (Thiele et al., 2017). This approach is advantageous because it accounts for the random movements in the landscape, considering more than one possible path (Mc Rae 2006; Thiele et al., 2017), therefore, providing solid data for conservation planning and decision making (Fuller et al., 2006; Correa Ayram et al., 2014).

Here, we use landscape connectivity tool to analyze the Doce River Basin evaluating connectivity of tree species at the landscape scale. The DRB is a major river basing inserted in the Atlantic Forest domain, where many important economic activities are developed such as agriculture, livestock production and mining, (Instituto Mineiro de Gestão das Águas, 2010). Those activities are the main cause of fragmentation in this high diverse region (Saiter et al. 2015, Capítulo 1). This way, we used a comprehensive dataset on the composition of tree communities across the bacia do Rio Doce (BRD), and based on the land-cover classification of Doce River Basin provided by Agência Nacional de Aguas (ANA) through geonetwork opensource project, we used a habitat /non-habitat approach to evaluate the connectivity of the DRB for tree species, where habitat was defined as all native forest remnants and all other types of land cover was considered non-habitat. Therefore, as non-habitat areas present high resistance to connectivity, we aim to identify areas which lack of connectivity in the DRB that needs attention for conservation planning. Based on the satellite images we aim to create maps of the current fragments of native forest in the DRB. Finally, we will use land cover to generate

maps showing areas with high resistance and show the best fit for least cost corridors based on effective resistance using Jaccard index as a proxy for connectivity.

3. Materials and Methods

3.1 Study area

The area of this study is the Doce River Basin (hereafter referred as DRB), which occupies parts of Minas Gerais and Espírito Santo, with a total area of 86 715 km², between latitudes 17°45' and 21°15' S e longitudes 39°30' and 43°45'W. (Instituto Mineiro de Gestão das Águas, 2010). Most part of the river basin is enveloped in Atlantic Forest Domain and we used tree species from two different physiognomies: Tropical rainforest with well distributed rainfall along the year and with an average temperature of 25°C (Veloso et al., 1991) and tropical semideciduous forest characterized by a strong seasonality, with a prominent dry season and a wet season with intense rainfall. During dry season the mean precipitation is from 150 to 250 mm, and in the wet season it varies between 800 to 1300mm (Instituto Mineiro de Gestão das Águas, 2010). The DRB area is comprised between Atlantic Ocean and Espinhaço Range from east to west, Negra and Aimorés Mountain in the north limits and Caparaó Range on southeast limits. In the DRB the soils are predominantly yellow-red latosols, and red ultisols being the first characterized by deep soils dystrophic with high saturation of aluminium and the latter with variable depth and with mineral material in its constitution. Those two types of soil constitute 77,2% of the river basin. (Instituto Mineiro de Gestão das Águas, 2010).

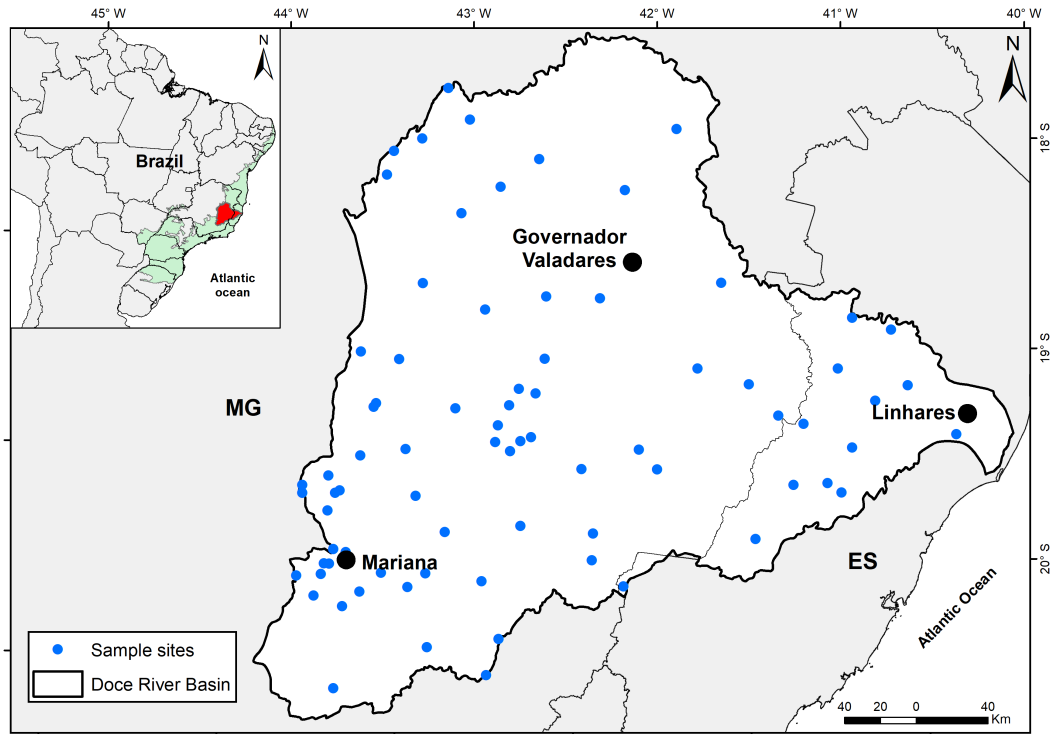


Figure 1. Doce River Basin location and the 78 sites used in our analysis (blue circles); the main cities within Doce River Basin (black circles). Green color represents the original area of Atlantic Forest.

3.2 Floristic data set

The matrix of trees occurrence for 78 sites in the DRB (Fig 1.) was extracted from NeotropTree, a database containing a checklist of tree species in the Neotropics (Oliveira-filho, 2017). The checklists were obtained from occurrence records from tree different sources [a] Published floristic and quantitative surveys. [b] taxonomic monographs and [c] herbarium records available in the herbarium virtual da Flora e dos Fungos (INCT; <http://inct.splink.org.br/>). The reliability of information, expert opinion and taxonomic literature were used to verify the data. Due to high density of floristic and quantitative surveys for certain localities, data were compiled and merged into a single checklist, being kept in separate checklists in places where vegetation does not remain constant across a 5km radius. As a result, an amount of 1944 species distributed in 100 families in a total of 22007 individuals were recorded for the entire DRB.

3.3 Data collection of soil uses and occupation

In this study we used the classification of soil uses and occupation provided by Agencia Nacional de Aguas (ANA) from 2014 (see Fig 2A). The classification includes 12 classes: Native vegetation, pastures, reforestation area, rock outcrop, open areas, agriculture areas, beaches, mining areas, urban areas, airports, roads and water. The native vegetation of the DRB was strongly suppressed by anthropogenic activity and most part of the forest Remnants are constrained to the steeper areas of the land. Moreover, the pastures are also degraded with low soil cover, compaction and intense trampling (Agência Nacional de Aguas, 2013).

Our methodology was based on circuit theory (McRae, 2006) also known as effective resistance. We built 6 models of resistance surface based on habitat and non-habitat areas (Table 1. Appendices) The resistance value added to a cell can be understood as the cost (risk of mortality or difficulty) of moving across the cells. We considered low resistance value (resistance =1) for habitat areas (Native forest remnants) and higher resistance values (resistance =100) for other land cover types, based on cell characteristics.

3.4 Data Analysis

We ran the models using Linkage Mapper Tool (McRae and Kavanagh, 2011) that model linkages between areas based on resistances and core habitat areas. Linkage mapper calculates cost-weighted distance from one core area to another and those values are used to generate least cost corridors and least cost paths (LCP). Cost-weighted distance is normalized by LCP between areas, producing a normalized least cost corridor values so the cells along the LCP will equal 1. Then Normalized least cost corridors are put together to generate the final network of corridors of cost-distance.

After running the LCP analysis on Linkage Mapper, we used the Jaccard index to model the relation among pairs of plots and Euclidean Distance and Least Cost Distances through Generalized Linear Models (GLM) (Thiele et al., 2017) using MuMIn, Car, gof, vegan and reshape2 packages in R 3.4.3 version (R core team, 2017). The aim was to use Jaccard index as a proxy for connectivity models based on floristic similarities between areas. We used Quasi-binomial distribution testing linearity with function `cumres` from package `gof`. We selected the best model using `MumIn` package, selecting the best model based on quasi AIC values, through dredge function. We limited the model selection for those with only one predictive variable and considered adequate the models that presented quasiAIC under 2.00. We also calculated chi-squares and P value using function `Anova` from `Car` package. Three models were the best fit for connectivity: (i) Euclidean distance ($P=2.418e-06$ AIC=0.00); (ii) model 3 ($p= 6.614e-07$, AIC= 1.59) and (iii) model 5 ($P = 7.221e-07$, AIC = 1.59). Because straight lines are not always possible in the landscape and because simpler models are easier to implement, our choice was to use the model 3 of connectivity.

4. Results

The map of fragments of DRB shows that the river basin is highly fragmented, especially the areas in the north, center and east (Fig 2A). Most part of the forest remnants are located in the west, south and southeast portion of the river basin, therefore, it presents high functional connectivity. Regions that presented high levels of fragmentation (or less forest remnants) presented high resistance to connectivity for tree species, encompassing the Governador Valadares Region and Linhares. An intermediate resistance in the southwest of the basin (fig 2B). Based on the map with least cost corridors there are areas in the DRB presenting

very poor functional connectivity such as the Governador Valadares and Linhares regions and areas like the southwest of the basin (Fig 2C).

The least cost path map outcome shows that areas around Governador Valadares municipality are not connected due to greater resistance of the matrix, resulted from anthropogenic activity (mainly pastures and agricultural areas) that caused reduction of forest remnants and therefore increased landscape resistance to connectivity. Areas in the north of Governador Valadares are also presenting high resistance to corridors for connectivity as well as Linhares region.

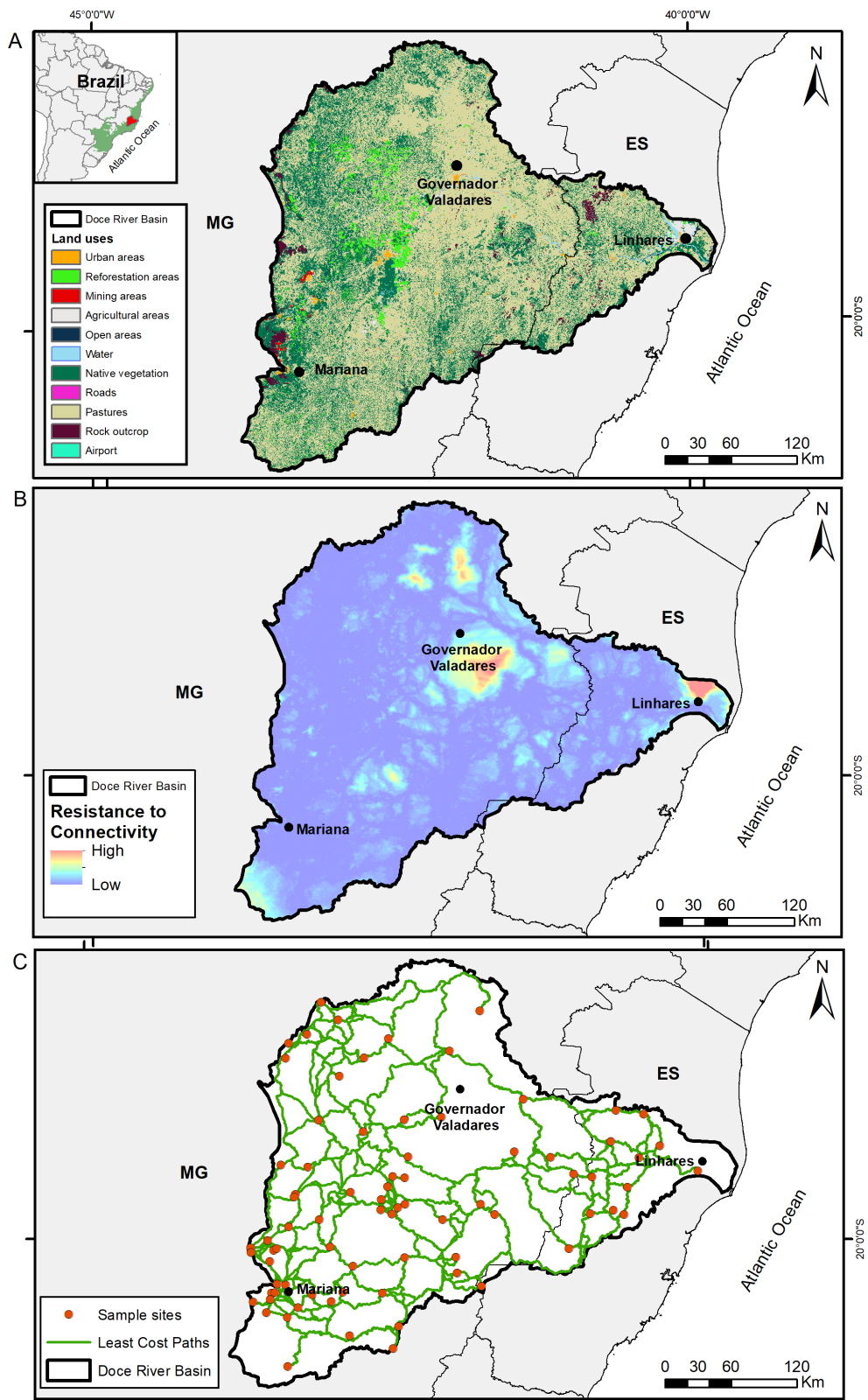


Figure 3. Maps generated based on resistance distance. (A) Land uses of the Doce river basin provided by Agência Nacional de Águas. (B) Resistance to connectivity map based on the reclassification of land uses. (C) Least-Cost paths map. Black circles are the main municipalities, and red circles are the sample sites.

5. Discussion

The weakest functional connectivity is located mainly in the central area of Rio Doce Basin in the Governador Valadares region, likely resulted of intensive use and occupation of land. Hostile environments for most species are common in agricultural landscapes worldwide such as arable fields, intensive used grasslands, whereas suitable areas for dispersal and migration are rare (Thiele & Schirmel, 2017). In the Governador Valadares region most part of the forest patches have been converted in pastures, whereas Linhares region was mostly converted into agricultural areas. Therefore, these regions have gone through habitat loss, which enhances the distance among patches and landscape resistance and difficult landscape connectivity (Hanski, 1998).

Patches of native vegetation in the DRB are abundant mainly in the west portion, although the majority of them have reduced size. Most of the forest remnants in the Doce River Basin are constrained to steeper areas (Agencia Nacional de Águas, 2013), due to mountainous topography present in this region. However, small patches can be used by dispersers as stepping stones to reach bigger patches. Nonetheless, in the west portion of the DRB there is greater probability of connectivity (or less resistance of connectivity). Previous studies have shown the importance of small fragments or free-standing trees in the matrix for the maintenance of landscape connectivity (Luck and Daily, 2003; Mueller et al, 2014). On the other hand, the susceptibility to habitat loss and fragmentation is higher for species with higher demand of interior habitat and limited movement capacity (Laurance 1990; Pfeifer et al., 2017).

Current plant distribution may not be a result of current landscape connectivity. Lindborg and Eriksson (2004) found out that the current diversity of plant species in grasslands in Sweden is not result of the current connectivity but it is related to the historical landscape connectivity. There may be a large time lag between landscape changes and populations demise

(Eriksson and Ehrlén 2001) and it reflects the capacity of persistence of plant populations in isolated or deteriorating environments (Lindborg and Eriksson, 2004). Therefore, the DRB current distribution of plant species is a result of the historical occupation of the river basin and population studies may be helpful to understand the dynamic of plant populations in response to the fragmentation over history and also help to make decisions to protect some areas.

The matrix surrounding fragments may affect the direction of dispersal. Certain land uses such as roads, waterways and agricultural areas acts as barriers to some disperser keeping them away of these regions promoting less probability of dispersion (Taylor et al., 2006). In the north of Governador Valadares region, there is an area that presents connectivity towards north direction but, there is too much resistance to be connected with any point in the south, meaning that it is somehow isolated from the areas from the south of the DRB. As a consequence, important processes such genes flow may be compromised towards the south and from the south, therefore, it is one of the priority areas to manage so it become reconnected with the southern part of the DRB.

Landscape connectivity has three main components: 1) patterns and behaviors of species movement; 2) structure of resource patches (size and arrangement) and 3) the matrix (Taylor et al., 2006). The first two components are not always possible to manage properly since species inherent behavior cannot be altered and enhance patches area or moving the patch is not feasible due to political, social and economic constraints. The matrix is commonly greater in area than remnants of native vegetations thus, managing it may be more important than managing only forest remnants in order to promote functional connectivity, even though the decisions may include high political and economic costs (Taylor et al, 2006). This may be a wise approach in the Governador Valadares and Linhares regions, to increase habitat area and promote functional connectivity. Since functional connectivity for plants involves not only

dispersal from source area but also successful establishment and development in the receptor patch (Auffrey et al., 2017), it is important to ensure that there will be paths with enough area to receive propagules and restore the functional connectivity. A path that is well connected, in turn, will receive more dispersers and will provide also more propagules (Taylor et al., 1993). The southwest of the basin is a high altitude area and very important for conservation because it is part of the areas that have higher precipitation in the basin, supplying the river with water. In addition, presented intermediate level of resistance and attention must be given to this region as well, in order to restore connectivity.

Priority Areas for Biodiversity Conservation in the DRB accounts for 2.450,00 hectares (or 28% of DRB area) of which 109,000 ha (4.46% of total Priority Area) are in Integral Protection Conservation Units (Agencia Nacional de Águas, 2013). This is a very low amount of protected areas and new conservation units should be created to ensure the protection of the biodiversity in the DRB. The portion of DRB located in the Espírito Santo State is inserted in the Central Corridor of Atlantic Forest, an area with high level of endemism and with a high amount of endangered species (Instituto Mineiro de Gestão das Águas, 2010). Nevertheless, our results shows that the region of Linhares municipality presents high resistance to connectivity, which certainly affects the connectivity of the central corridor of Atlantic Forest. Therefore, this region should be a target of restoration projects of forest remnants.

6. Conclusion

Despite the highly fragmented landscape, our study showed that the DRB is functionally connected in the west portion for tree species. The central, southwest, east and north areas of the DRB are strongly affected by habitat loss and have great resistance to corridors. Therefore, restoration and land reclamation projects in these areas are encouraged to attenuate the lack of connectivity, ensuring the persistence of plant populations and maintenance of biodiversity and

vital processes for plants permanency. However, those areas are not the only areas with high resistance to corridors for dispersion. The extreme east portion of the DRB in the municipality of Linhares also needs attention, especially because it is inserted on the Central Corridor of Atlantic Forest, a region with considerably high biodiversity, endemism and high number of endangered species.

It is important to highlight that Governador Valadares is one of the largest cities within RDB, and despite the fact that is the area with least probability of connectivity, it does not justify focusing all the investments in this region. There are other areas affected by the incorrect land management. Smaller municipalities have less resources to implement policies to guarantee the integrity of forest remnants. Therefore, public policies must include the cities with less resources and also focus on less degraded areas in order to avoid loss of fragments and therefore reducing connectivity in the DRB, affecting biodiversity and ecological processes.

7. Appendix

Table 1: Models of Resistance created to model connectivity

Resistance Value	Euclidean Distance	Model 1	Model 2	Model 3	Model 4	Model 5
1	-	Native Vegetation	Native Vegetation	Native Vegetation	Native Vegetation	Native Vegetation
60	-	Open Areas, Reforestation, Pastures	Reforestation, Rock Outcrops, Pastures		Open Areas, Reforestation, Rock Outcrops, Pastures	Open Areas, Rock Outcrops, Pastures
70	-	Rock Outcrop	Open Areas	-	-	Reforestation
90	-	Agriculture areas, beaches, mining areas, urban areas, airports, roads,	Agriculture areas, beaches, mining areas, urban areas, airports, roads,	-	Agriculture areas, beaches, mining areas, urban areas, airports, roads,	Agriculture areas, beaches, mining areas, urban areas, airports, roads,
100	-	Ocean, Water	Ocean, Water	All other classifications	Ocean, Water	Ocean, Water

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Conclusões Gerais

Nosso estudo mostra que variáveis ambientais e geográficas modelam a distribuição de espécies na Bacia do Rio Doce bem como influenciam a estrutura das comunidades. Clima e solo influenciam a diversidade filogenética, o primeiro influenciando o número de linhagens presentes e o segundo quando em conjunto com o clima afetando os ramos mais profundos e de topo da árvore filogenética. A análise de filobeta-diversidade demonstrou uma tendência ao agrupamento filogenético em regiões mais altas da bacia, evidenciando fortes filtros ambientais

associados a história evolutiva da vegetação da Bacia do Rio Doce. Existe uma relação significativa das linhagens presentes na bacia com altitude, distância geográfica e variáveis ambientais, reforçando ainda mais a força dos filtros ambientais que influenciaram na estruturação da vegetação da bacia ao longo de sua história evolutiva.

As análises de conectividade funcional mostraram que a porção oeste da bacia possui maior conectividade e, portanto, maior capacidade de movimento entre os dispersores e polinizadores, responsáveis pelo sucesso reprodutivo das plantas. No entanto, as porções centro-norte que inclui o município de Governador Valadares e leste que inclui o município de Linhares e a porção do extremo sudoeste da bacia possuem áreas com forte nível de degradação e portanto a conectividade funcional está comprometida, principalmente devido ao reduzido número de remanescentes florestais, se fazendo necessário a intervenção imediata através de projetos de recuperação de área degradadas e manejo da matriz da paisagem para que se evite perda da biodiversidade devido a falta de conectividade. Também, é necessário que se desenvolva projetos de recuperação de áreas degradadas na região de Linhares que também apresentou resistência a conectividade e está inclusa no Corredor Central da Floresta Atlântica, uma região rica em biodiversidade com alto endemismo e alto número de espécies ameaçada.