

Community Assembly as the Basis for Species Selection for Tropical Forest Restoration in Global Change Scenario

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Abstract

Background Tropical forests hold high biodiversity, which challenges the selection of species for forest restoration. For a site-specific restoration is required the understanding of the main influences ruling the assemblages. We aimed to answer three questions. 1) how do environmental variables influence taxonomic, phylogenetic diversities, and the phylogenetic structure in the of Rio Doce Basin (TFRD)? 2) How do environmental variables, phylogenetic structure and the main types of seed dispersal relate to each other? 3) Which information of the TFRD assemblages can be used for ecological restoration and conservation in global change scenario? We used 78 sites with their checklists to calculate taxonomic, and phylogenetic diversities, phylogenetic structures, and dispersal proportions. Then, we related the diversities of the sites to their bioclimatic variables and built GLM models.

Results Species richness was influenced negatively by water excess duration, by water deficit duration, and positively by maximum temperature, and temperature seasonality. Water regime drives diversity and phylogenetic community structure in the TFRD more than other variables. Annual precipitation and maximum temperature presented the clearer influences on diversity and phylogenetic structure. Zoochory was positively, and anemochory, autochory were negatively related to sesMPD.

Conclusions By choosing the lineages with high fitness for each site, the functioning and the stability of ecosystems should increase. The addition of species with anemochory and autochory increases functional and phylogenetic diversity in areas with extreme water excess or water deficit, important in a global change scenario. A high proportion of zoochory allows the communities to function conserving dispersers, biodiversity, and services.

1. Background

Environmental degradation is one of the largest threats that are being looked at in the current global change scenario. Large-scale land degradation by agriculture, urbanization and mining are increasing in the tropics (Nazareno and Vitule 2016; Nunes et al. 2019) and require forest restoration activities to reduce the loss of biodiversity and the loss of ecosystem services (Poorter et al. 2016; Ellison et al. 2017; Filoso et al. 2017; Bustamante et al. 2019; Matos et al. 2020). In the Brazilian Rio Doce Basin, the largest river basin (86,715 km²) fully inside the Atlantic Tropical Forest Domain, Brazil, a history of land degradation including a recent tailing dam collapse in 2015 (Edwards and Laurance 2015; Meira et al. 2016; Meira-Neto and Neri 2017), accumulated a vegetation deficit of 7,160 km² to achieve compliance with actual environmental legislation (Pires et al. 2017). Native vegetation of the basin, mainly seasonal tropical forest, holds high levels of diversity (Neves et al. 2020), challenging the restoration of such large areas. Besides choosing the adequate site-specific restoration strategy (Holl and Aide 2011; Brancalion et al. 2017), the selection of locally adapted species is necessary to reconstitute taxonomic, functional and phylogenetic diversities (Temperton et al. 2005; Li et al. 2018), safeguarding community stability and the performance of ecosystem services (Pillar et al. 2013; Kang et al. 2018), especially in global changing scenarios (Bakker and Wilson 2004; Harris et al. 2006; Wolff et al. 2018). Thus, the understanding of the environmental influences ruling the vegetation assemblages is required to select locally adapted species for planting or seeding in restoration projects in current and in future assembly rules scenarios (Gastauer et al. 2018).

For deeper understanding of which factors play in the assemblage of those Tropical Forests of the Rio Doce Basin (TFRD), rules of community assembly can be assessed by means of tree species composition of forest remnants responding to environmental variables, influencing the taxonomic diversity as well as phylogenetic diversity and structure. This is because (Niño et al. 2014) ecological niches are major drivers of tropical communities largely determined by environmental variables that limit in different ways the species distributions (Weiher and Keddy 1995; Weiher et al. 2011; Götzenberger et al. 2012).

Among the most usable niche determinants in vegetation are the bioclimatic variables (Hijmans et al. 2005; Fick and Hijmans 2017) which are capable of model spatial distributions of plant species for many different purposes (Phillips et al. 2006; Austin 2007; Wüest et al. 2015; Heringer et al. 2019) allowing predictions in plant communities based on niches (Keddy 1992; Carnaval and Moritz 2008). Niche conservatism and niche convergence, as well as their effects on phylogenetic structures, are useful tools for empirical studies that evaluate environmental filtering and competition as causes of phylogenetic clustering and phylogenetic overdispersion, respectively (Losos 2008; Swenson 2009; Wiens et al. 2010; Boukili and Chazdon 2017). As bioclimatic variables can filter in, and out lineages that have niches conserved or convergent, the phylogenetic structure may vary depending on the phylogenetic signal of selected traits (Blomberg et al. 2003; Lebrija-Trejos et al. 2010). In addition, the bioclimatic determination of niches can help to predict future trends in the assembly rules, since climate change models (IPCC 2013) indicate some future bioclimatic scenarios.

Besides ecological niches, the main dispersal types are also central in the community assembly since dispersal limitations can play an important role for forests (Hubbell 2001; Gilbert and Lechowicz 2004; Hardy 2008; Weber et al. 2014). Dispersal types are not only important as drivers of community assembly, but also can inform how these types are aligned with phylogenetic lineages and how these types are conserved or not in the phylogenetic lineages (i.e., phylogenetic signal) (Carrión et al. 2017; Chen et al. 2018).

Therefore, the knowledge about the community assembly of tropical forest communities with high biodiversity is essential for planning of restoration actions, increasing the stability and functioning of the restored and conserved ecosystems (Reich et al. 2012; Oliver et al. 2015; Mori 2016). Since phylogenetic ecology can shed light on the understanding of rules of community assembly and ecological functioning of tropical forests (Paine et al. 2012; Oliveira et al. 2014; González-Caro et al. 2014), we aimed to answer the following questions. 1) How do bioclimatic variables influence taxonomic, and phylogenetic diversities, and the phylogenetic structure in the tropical forests of a river basin (TFRD)? 2) How do environmental variables, phylogenetic structure and the main types of seed dispersal relate to each other in the TFRD assemblages? 3) What of the answers to the previous questions can be used in the ecological restoration of TFRD in a global change scenario, as well as in the conservation of biodiversity and ecosystem services?

2. Materials And Methods

2.1 Study sites/surveys

This study was performed on Tropical Forests of the Rio Doce Basin (TFRD), located between latitudes 17°45' and 21°15' S and longitudes 39°30' and 43°45'W, with more than 86.000 km² occupying parts of Minas Gerais and Espírito Santo states in Brazil (Fig 1). The TFRD are essentially secondary forests with only few of them classified as old growth forests. The TFRD area may be influenced by different floras (i.e., Cerrado and Campos Rupestres) on western watersheds, and mountain tops, but Atlantic Tropical Forest flora defines the basin within

the domain of Atlantic Forest. We analyzed woody species from subtypes of Atlantic Tropical Forests: seasonal tropical forest and tropical rainforest.

The seasonal tropical forest is defined by a seasonality characterized by a rainy season characteristic of tropical forests followed by a dry season during the winter. As a response to that seasonality, around 20-50% of the trees lose their leaves during the dry period (deciduous). The tropical rain forests are under tropical climate conditions with average temperature of 25°C, and with a very well distributed precipitation along the year, characterized by tall evergreen trees (Oliveira-Filho and Fontes 2000).

The TFRD limits are watersheds of Serra Negra, and Aimorés mountains northwards, the Espinhaço Range on west, the Brigadeiro, and the Caparaó Ranges on southeast, and the ocean in the east. The rainfall regime in the basin is generally divided into rainy season during the summer, and dry season during the winter. The Mean Annual Precipitation varies from 1200 to 1900 mm. The soil of the TFRD are predominantly dystrophic Red-Yellow latosols, deep soils characterized by high aluminium contents, and dystrophic Red Cambisols, a type of shallower soils (Nunes et al. 2000; Marangon et al. 2013; Soil Department of Universidade Federal de Vicosa 2020).

The database has 78 locations of TFRD extracted from NeotropTree, with checklists of tree species (Oliveira-Filho 2014). The checklists are records of papers, monographs, dissertations and thesis as well herbaria records available in the Flora and Fungi Virtual Herbarium (2020). Because the high number of checklists for some sites, the data was compound into one checklist list. A total of 22007 trees of 1944 species within 100 families were analyzed for TFRD (Oliveira-Junior et al. 2020).

2.2 Phylogenetic community structure

We produced a phylogenetic tree with all woody angiosperms recorded in the basin using Phylomatic function in Phylocom 4.2 (Webb and Donoghue 2005) and megatree R20160415.new (Gastauer and Meira-Neto 2017) based on APG IV (The Angiosperm Phylogeny Group 2016). Ferns and gymnosperms were omitted because of their outcome on the phylogenetic metrics they are very distinct and old phylogenetic lineages.

We used the following metrics to explain phylogeny of TFRD in each community: (i) Faith's phylogenetic Index (PD) (Faith 1992) found by the sum of phylogenetic branches for all species ; (ii) Mean Pairwise Distance (MPD), the mean phylogenetic distance among species; (iii) Mean Nearest Taxon Distance (MNTD) (Webb 2000; Webb et al. 2002), the mean phylogenetic distance between the closest related species. Also, we calculated the standardized effect size (ses) of PD, MPD and MNTD to eliminate the richness effect based on a null model (Swenson 2014). Negative ses show phylogenetic clustering and positive ses show phylogenetic overdispersion.

We used evolutionary distinctiveness scores (ED) as species exclusivity (Isaac et al. 2007). If a species does not have close relatives in a community phylogeny, that species is considered unique and ED scores high (Edwards et al. 2017).

2.3 Environmental variables

For each localization of the surveys, we gathered elevation (United States Geological Survey 2019) and extracted the 14 bioclimatic variables from WorldClim: Annual Mean Temperature, Isothermality, Temperature Seasonality, Maximum Temperature of the Warmest Month, Minimum Temperature of Coldest Month, Mean Temperature of Wettest Quarter, Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month and

Precipitation Seasonality (Fick and Hijmans 2017). Additionally, we used WaterExcDur, WaterExcSev, WaterDefDur and WaterDefSev from diagrams of Walter (Walter and Lieth 1967; Walter 1986; Oliveira-Filho 2014) for modelling. All bioclimatic variables are derived from the monthly or daily temperature and rainfall values in order to produce ecologically important variables used for niche modelling with high consistency (García-Callejas and Araújo 2016; Morales-Barbero and Vega-Álvarez 2019). The applied bioclimatic variables signify annual means (Booth 2016; Kendal et al. 2018), seasonality (Hereford et al. 2017; Tonkin et al. 2017) and severe environmental factors (e.g., duration and severity of water excess and deficits) that influence species distribution and performance (e.g., Amissah et al., 2018).

2.4 Phylogenetic signal of dispersal types

Phylogenetic signal of dispersal types means the trend of species with zoochory, anemochory, and autochory to be more related than by chance or to be less related than by chance. If the signal shows the pool of species with a dispersal type more related between each other than null models, the phylogenetic signal is clustered and means that the dispersal type has been predominantly conserved within the phylogenetic lineages under niche conservatism. The opposite, when a signal shows the species less related than calculated by null models, the phylogenetic signal is overdispersed and means that the dispersal type is predominantly convergent (homoplasy). In order to test if dispersal types presented phylogenetic signal, the net relatedness index - NRI among all species of the same dispersal type (DispersalNRI) was calculated. The same was calculated for nearest taxon distance - NTI (DispersalNTI). This calculation was done reordering species labels 999 times through phylogeny. DispersalNRI values significantly greater than zero (more than 1.96 sd, and more than -1.96 sd) indicate phylogenetic signal. Phylogenetic signal of dispersal type was considered significant when the observed MPD or MNTD occurred in the lowest 2.5% of the null models (significance of 0.05) (Gastauer et al. 2017).

2.5 Modelling

To outline the environmental predictor variables that best describe species richness and phylogenetic structure of sampled tree communities, we build for each response variable a global general linearized model containing all 15 predictor variables.

We scaled the explaining variables. Then, we used the dredge function of the MuMIn package (Bartón 2018) to model-select all possible combinations of five or less uncorrelated predictive variables ($r < 0.6$, https://github.com/rojaff/dredge_mc) that most parsimoniously explained our data. We considered models with five or less predictive variables to avoid overfitting. We used the Akaike Information Criterion (AIC) for selection of the best models (Symonds and Moussalli 2011). All models with ΔAIC less than 2 were considered equally parsimonious. When more than one model was selected, we calculated model-averaged parameters and unconditioned standard errors weighted by the likelihood ratio using the 'model.avg' function of the MuMIn package. The function performs significance tests for each predictor estimated in this average model. The resulting global models were confirmed by plotting residuals versus adjusted values as well as residuals versus predicts.

For modelling percentages of zoochorous, anemochorous and autochorous species within surveys, we build global models containing the same 15 environmental predictor variables plus species richness, sesMPD, sesMNTD and sesPD. For model selection, we proceed as described above.

3. Results

Modelling species richness, only one global model containing five environmental variables was selected, with four significant trends (Table S1), indicating that richness is influenced negatively by water excess duration and by water deficit duration meanwhile is positively influenced by the Maximum temperature of the warmest month as well as is positively influenced by seasonal temperature (Figure 1).

For further response variables, more than one model was selected (Table S1). 14 models containing the all variables except Precipitation during Wet Period, and Minimum Temperature explain sesPD. However, only two trends were significant: annual precipitation reduces sesPD, and water excess duration increases sesPD (Table S2, Figure 2).

For sesMPD, six models were selected containing 10 out of the 15 predictor variables (Tables S1, S2). In the averaged model, only two trends were significant: annual precipitation reduces and water excess duration increases sesMPD (Figure 2).

For sesMNTD, the two significant trends were: increasing maximum temperature of the warmest month, and increasing isothermality increase sesMNTD (Table S2, Figure 2).

The percentage of zoochory species increases with increasing sesMPD, with water excess duration, with water deficit severity, and decreases with water excess severity (Figure 3).

The percentage of species with anemochory decreases with increasing sesMPD and increases with increasing water excess severity (Table S3, Figure 4).

The percentage of autochory increases as sesMPD decreases, as water deficit severity decreases, and is positively related to the water excess severity (Table S3, Figure 4).

Anemochory, and autochory presented DispersalNRI clustered phylogenetically showing that these dispersal types are conserved within phylogenetic lineages throughout the phylogenetic tree (Table 1). Zoochory, and anemochory presented clustered DispersalNTI, showing that these dispersal types are conserved within phylogenetic lineages towards the tips of the phylogenetic branches (Table 1).

4. Discussion

4.1 How do bioclimatic variables influence taxonomic, and phylogenetic diversities, and the phylogenetic structure in the tropical forests of a river basin (TFRD)?

Water regime drives species richness and phylogenetic community structure in the TFRD more than other types of environmental variables. At least one among annual precipitation, water excess duration, water excess severity, and water deficit severity were significant in all averaged models, except for the model for sesMNTD. Species richness, sesPD, sesMPD and percentage of zoochory were affected by water excess duration. All dispersal types were explained partially by water excess severity. Temperature regime was the second most important important regime. Maximum temperature of the warmest month and isothermality explained sesMNTD. Maximum temperature of the warmest month, and temperature seasonality explained partially species richness. Among the variables, water excess duration, annual precipitation, maximum temperature and isothermality influenced the

phylogenetic diversity and phylogenetic structure. The effects of temperature on richness, and on sesMNTD suggest environmental filtering effects causing phylogenetic clustering driven by decreasing maximum temperature of the warmest month and decreasing isothermality (i.e., increasing temperature variation). Therefore, the lower temperature and the less temperature variation in different seasons, the more environmental filtering.

The percentage of species with zoochory, anemochory or autochory were related to phylogenetic structures (i.e., sesMPD) in different ways. Increasing zoochory increases phylogenetic distances between species (i.e., increasing sesMPD) meanwhile increasing anemochory, and autochory decrease phylogenetic distances between species (i.e., decreasing sesMPD). The opposite relation of zoochory with sesMPD was not because zoochory is convergent, but because the less zoochory, the more abiotic dispersion (i.e., anemochory + autochory) that is clustered for MPD (i.e., DispersalNRI more related than by chance), suggesting anemochory, and autochory as homologies in the TFRD metacommunity. Only zoochory decreased with increasing water excess severity, and appears to be the only dispersal type benefited with increasing water surplus. Water excess severity was positively related to anemochory, and autochory, and might be interpreted as stresses influencing positively these dispersal types. Water deficit severity influenced negatively autochory.

The answer of the first question shows how environmental variables influence taxonomic, and phylogenetic diversities as well as phylogenetic structure in the tropical forests of that large river basin (TFRD). Seven environmental variables were found to influence the taxonomic diversity, phylogenetic diversity and phylogenetic structure in averaged models: water excess duration, water excess severity, water deficit duration, water excess severity, maximum temperature, temperature seasonality, and isothermality. As water excesses and water deficits increase in number of days, the species richness decreases. As the maximum temperature and the temperature seasonality decrease, the species richness decrease. Thus, more days of water excesses or more days of water deficits in TFRD are associated with loss of species richness as well as lower maximum temperatures and lower temperature variation between seasons. Therefore, the found global model shows that increasing the number of days with excess or deficit of water, decreasing temperatures, and decreasing temperature variation, decrease species richness.

Still answering the first question, as annual precipitation decreases and there are more days of water excess, sesPD and sesMPD increase; as maximum temperature and isothermality increase, sesMNTD increases. Thus, the lower annual precipitation, the more water excess days, the higher temperature variation, and the higher maximum temperatures in TFRD, the greater the phylogenetic diversity and phylogenetic distances between species. However, as the more days with water excess (i.e., days with higher precipitation than evapotranspiration) cause higher sesPD and sesMPD, it is possibly because benefits the zoochory that is positively-related to mean phylogenetic distances (see zoochory discussion below). Therefore, higher precipitation promotes decreasing sesPDs and sesMPDs (i.e., phylogenetic clustering) in the TFRD similarly to effects of environmental filters found in tropical vegetation (Gastauer and Meira-Neto 2013; Miazaki et al. 2015), but does not cause species richness loss. Phylogenetic effects in tropical vegetation that can be explained by plant-plant interactions, density-dependence effects (Paine et al. 2012; Kraft et al. 2015; Carrión et al. 2017; Cadotte and Tucker 2017; Meira-Neto et al. 2018), and environmental filtering that has been reported as cause of phylogenetic effects in many different groups of species, especially plants. For instance, environmental filtering promotes phylogenetic effects in protists, in diatoms (Leibold et al. 2010; Singer et al. 2018; Keck and Kahlert 2019), and likely causes phylogenetic clustering in plant communities of tropical forests when associated with species richness decreasing (Gastauer

and Meira-Neto 2013; Parmentier et al. 2014). Therefore, the increasing annual precipitation in the TFRD that shortens phylogenetic distances might be an environmental filter effect because of excessive water. High precipitation may cause temporarily flooding stresses (Bueno et al., 2014; Pontara et al., 2016), and, consequently, may filter out lineages without conserved traits of flooding tolerance, but species richness does not decrease with the increasing annual precipitation. Alternatively, increasing annual precipitation would promote competition, and/or density dependent effects. For instance, high precipitation might cause competition increasing, and higher density-dependent effects by increased water resources and increased plant growing (see Tilman 1988). However, the forests with largest trees in TFRD, which would indicate stronger competition, are in low altitude sites with lower precipitation (Lopes et al. 2002; Camargos et al. 2008; Souza et al. 2012, 2013). The only clear result is that as precipitation increases, PD, and MPD decrease as an effect of increasing percentages of species with abiotic dispersal (see dispersal discussion below). Therefore, environmental filtering, competition and density dependent effects do not explain the PD and the MPD variation in TFRD. On the other hand, temperature regime can explain environmental filtering because species richness and sesMNTD decrease as maximum temperature decreases, indicating that the lower the maximum temperature, the closer the relatives in the TFRD communities and the lower the species density. High and low temperatures have been reported as environmental filters in forests, but high temperatures are rather filters in tropical dry forests, and low temperatures are rather filters associated with high altitudes or latitudes in temperate forests (Qian et al. 2014; Qian 2018). Therefore, our results suggest that the seasonal TFRD are environmentally filtered by low temperatures that cause decreasing species richness, and decreasing phylogenetic distance between species of their communities by filtering in species with conserved traits within phylogenetic lineages.

4.2 How do environmental variables, phylogenetic structure and the main types of seed dispersal relate to each other in the TFRD assemblages?

The percentage of species with zoochory, anemochory and autochory was significantly related to sesMPD and not to sesMNTD or sesPD, which means that the main association of dispersal types with the communities' phylogenies is throughout the entire phylogenetic tree (i.e., sesMPD). As the DispersalNRI is clustered for abiotic dispersal types, the clustered sesMPD reinforce that anemochory and autochory are conserved in phylogenetic branches originated in old nodes congruently with the decreasing sesMPD as anemochory and autochory. As a consequence, the increasing proportion of zoochory is not caused by its preeminence as homoplasy in the TFRD metacommunity, but because abiotic dispersal decreases. Thus, increasing anemochory and autochory reduce the sesMPD distances between species congruently with their clustered DispersalNRI in the TFRD metacommunity.

Zoochory is phylogenetic clustered towards the tip of phylogenetic tree according to its DispersalMNTD. That means the species with zoochory are predominantly clustered in lineages with conserved zoochory diversified from recent nodes. Despite zoochory is clustered towards the tip of phylogenetic tree, zoochory is not clustered throughout the entire phylogenetic tree. Anemochory is also clustered according to its DispersalMNTD. Autochory is not clustered towards the tip of phylogenetic tree in TFRD, suggesting lack of recent diversification of lineages with conserved autochory.

The dispersal types responded to water regime. The dominant dispersal type in TFRD is zoochory that varies from 50% up to more than 95% of the tree species in evergreen and seasonal Atlantic Tropical Forests (Tabarelli and Peres 2002). In the TFRD, the minimum zoochory percentage found in a forest was 53% and the maximum was

81% (data not shown). As dominant dispersal type, zoochory responded positively to water excess duration, and water deficit severity meanwhile anemochory and autochory were not influenced by those explaining variables. However, zoochory responded in an opposite way from the two abiotic dispersal types to water excess severity. Zoochory also responded in an opposite way from autochory to water deficit severity. Thus, zoochory seems to be impaired meanwhile anemochory and autochory seem to be benefitted in sites with extreme severity of water excess or water deficit.

As anemochory and autochory are clustered in some phylogenetic branches in the TFRD metacommunity, the presence of these dispersal types in restored TFRD will allow those species to improve the functional and phylogenetic diversity of restored forests by representing entire phylogenetic branches, especially in those TFRD with extreme water regimes (i.e., high severity of water excess, and high severity of water deficit). Therefore, the relation between severity of water excess, and severity of water deficit with the two abiotic dispersal types deserves attention since extreme water regimes are increasing according to forecasted climate scenarios in the most of the Atlantic Forest distribution (IPCC 2013). As a consequence, the proportion of anemochory and autochory may increase in the TFRD during the next decades in a global change scenario.

4.3 What of the answers to the previous questions can be used in the ecological restoration of TFRD in a global change scenario, as well as in the conservation of biodiversity and ecosystem services?

Species selection is not the restoration project itself. Most selected species may not be able to thrive under the harsh initial conditions of the restoration sites. This means that the selected species must be used in TFRD restorations to add taxonomic and phylogenetic diversity in order to improve the suitability and long-term stability of the restored ecosystems. For that, our databank delivered as supplementary material will offer the basis for the species selection. The results sequence shows how the TFRD community assembly rules are central to the species selection for the planned large-scale restoration in the basin, which includes mitigating the Mariana disaster that compromised the service of water purification in the basin. 1) The environmental filtering promoted by low temperatures (i.e., low maximum temperatures) drops the taxonomic diversity shortening the phylogenetic distance between species, predominantly filtering in species of some recently diversified lineages. Temperatures in TFRD are also related with altitude (data not shown). Thus, the use of some lineages better fitted for TFRD restoration in sites with low maximum temperatures (i.e., high altitudes inside the basin) should enhance the performance of restored forests. 2) Possibly the water purification is the most affected ecosystem service by the main players of global change, such as forests degradation, agriculture (Cabel et al. 1982), urbanization (Zhao et al. 2013), and environmental disasters (Lambertz and Dergam 2015; Meira et al. 2016; Meira-Neto and Neri 2017). Water purification should be restored in all regions of the basin through forest restoration. We understand that tree species with good fitness to the bioclimatic profiles of restored sites will enhance the ecosystem service of water purification, especially in areas with low maximum temperature, and high annual precipitation, improving the functioning and the stability of restored forests (Cadotte et al. 2009, 2012; Isbell et al. 2015; Brancalion et al. 2017). 3) In a global change scenario that predicts increasing climate variance for TFRD (IPCC 2013), the inclusion of species with anemochory and autochory in restoration practices increases functional and phylogenetic diversity when associated with a large proportion of species with zoochory, especially in areas with current or predicted extreme water excess or extreme water deficit. 4) A large proportion of species with zoochory in restored forests is mandatory because it assembles communities with high taxonomic, and phylogenetic diversity with the cobenefit of carbon stock (Matos et al. 2020), conserving dispersal services (Tabarelli and Peres

2002; Jansen et al. 2014), conserving dispersers, and conserving the threatened ecological interactions of tropical forests (Janzen 1986).

List Of Abbreviations

Tropical Forests of the Rio Doce Basin - TFRD

Faith's phylogenetic Index (PD)

Mean Pairwise Distance (MPD),

Evolutionary distinctiveness (ED)

Mean Nearest Taxon Distance (MNTD)

Standardized effect size (ses) of PD - sesPD

Standardized effect size (ses) of MPD - sesMPD

Standardized effect size (ses) of MNTD - sesMNTD

Net relatedness index - NRI

Nearest taxon distance - NTI

Net relatedness index of the same dispersal type - DispersalNRI

Nearest taxon distance of the same dispersal type - DispersalNTI

Declarations

Ethics approval and consent to participate

All sampling and analysis were carried out in accordance with Brazilian law. The data were shared between the authors.

Consent for publication

All authors agree with the publication of this manuscript.

Availability of data and material

Data will be shared as demanded.

Competing interest

None.

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Authors contributions

JAAMN conceived and designed the analyses, wrote and edited the paper, performed the analyses; NDOJ collected data and performed analyses, wrote the paper; NS collected data and performed analyses; ATOF collected the data and developed part of the analyses tools; MLB performed the analyses, wrote the paper; VP performed the analyses and wrote the paper; MG performed the analyses, wrote the paper, developed part of the analyses tools.

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Tables

Table 1 - Phylogenetic signal of dispersal types as DispersalNRI (MPD), and DispersalNTI (MNTD) for anemochory, autochory, and zoochory. Dispersal types: AN - anemochory, AU - autochory, and ZO - zoochory. Calculated by Phylocom with randomization method 2, by mean of 999 runs. Ntaxa, number of species; MPD, mean phylogenetic distance calculated for species by actual data; MPD.rnd, mean phylogenetic distance calculated by randomization; NRI, Net Relatedness Index; MPD.rank.Low, how many times the MPD was lower than MPD.rnd; MPD.rank.Hi, how many times the MPD was higher than MPD.rnd; MNTD, mean nearest taxon distance calculated for species by actual data; MNTD.rnd, mean nearest taxon distance calculated by randomization; NTI, Nearest Taxon Index; MNTD.rank.Low, how many times the MNTD was lower than MNTD.rnd; MNTD.rank.Hi, how many times the MNTD was higher than MNTD.rnd; runs, number of randomizations. *p<0.05, **p<0.01, ***p<0.001.

Type	ntaxa	MPD	MPD.rnd	MPD.sd	NRI	MPD.rankLow	MPD.rankHi	runs
AN	330	209.0239	220.9857	1.4227	8.4076***	999	0	999
AU	161	191.2269	221.1116	2.0766	14.3909***	999	0	999
ZO	1432	221.3495	221.1048	0.3678	-0.6653	247	752	999
Type	ntaxa	MNTD	MNTD.rnd	MNTD.sd	NTI	MNTD.rankLo	MNTD.rankHi	runs
AN	330	56.0852	61.3007	1.8922	2.7563**	996	3	999
AU	161	67.5397	71.9932	3.4141	1.3044	899	100	999
ZO	1432	44.6573	48.8249	0.3891	10.71***	999	0	999

Figures

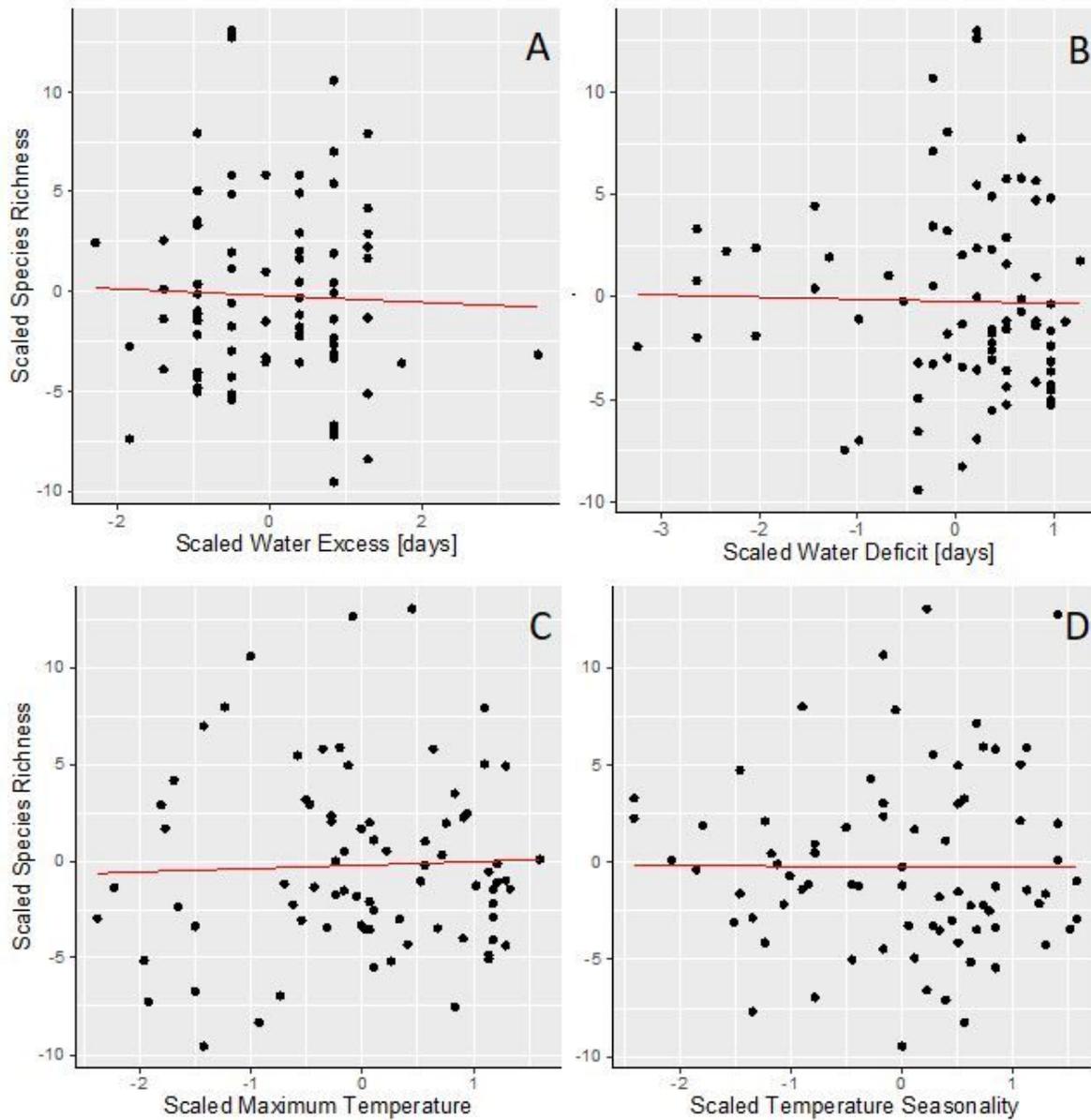


Figure 1

The explanatory A- water excess duration (Water excess [days]), B- water deficit duration (Water deficit [days]), C- maximum temperature of the warmest month (Maximum temperature) and D- temperature seasonality and the response variable species richness of the global GLM model for fragments of the Rio Doce Basin, Brazil. Water excess duration (estimate = -0.108760, $P= 4.82e-15$), water deficit duration (estimate = -0.108465, $P< 2e-16$), maximum temperature of the warmest month (estimate = 0.073362, $P= 4.47e-06$), temperature seasonality (estimate = 0.065411, $P=1.45e-13$).

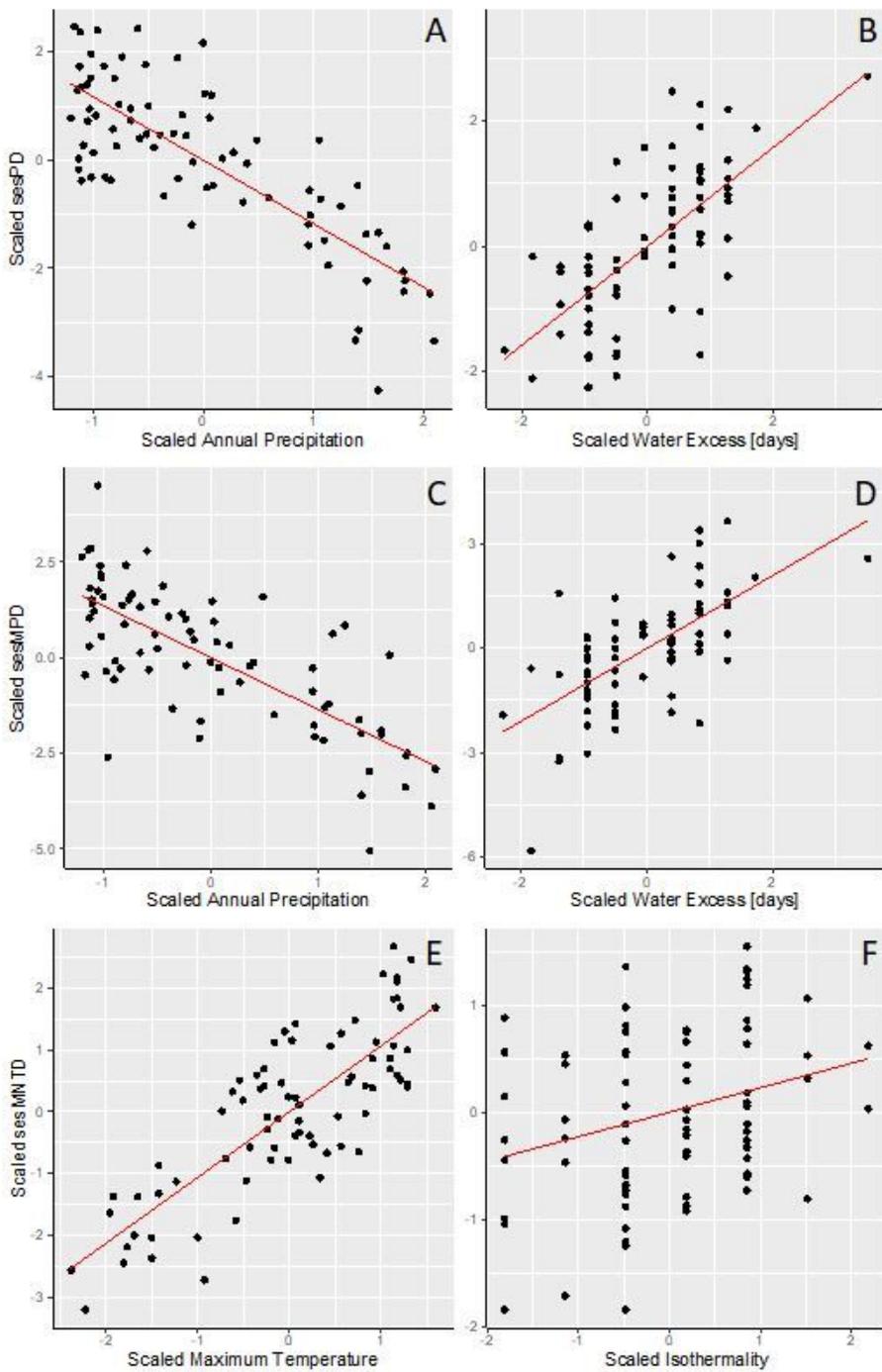


Figure 2

A, and B - The explanatory variables mean annual precipitation (Annual precipitation) and water excess duration (Water excess [days]), and the response variable standard size effect of phylogenetic diversity (sesPD) of the global GLM model for fragments of the Rio Doce Basin, Brazil. Annual precipitation (estimate = -1.173858, $P=0.003$); Water excess (estimate = 0.786778, $P=0.00332$). C, and D- The explanatory variables mean annual precipitation (Annual precipitation) and minimum temperature of the coldest month (Minimum Temperature) and the response variable standard size effect of mean phylogenetic distance (sesMPD) of the global GLM model for fragments of the Rio Doce Basin, Brazil. Annual precipitation (estimate = -1.353912, $P=0.00357$); Water excess (estimate = 1.052365, $P=0.00368$). E, and F- The explanatory variables maximum temperature of the warmth

month, and the isothermality, the response variable of sesMNTD of the global GLM model for fragments of the Rio Doce Basin, Brazil. Maximum temperature (estimate = 1.06510, $P=0.00389$), isothermality (estimate = 0.22868, $P=0.04736$).

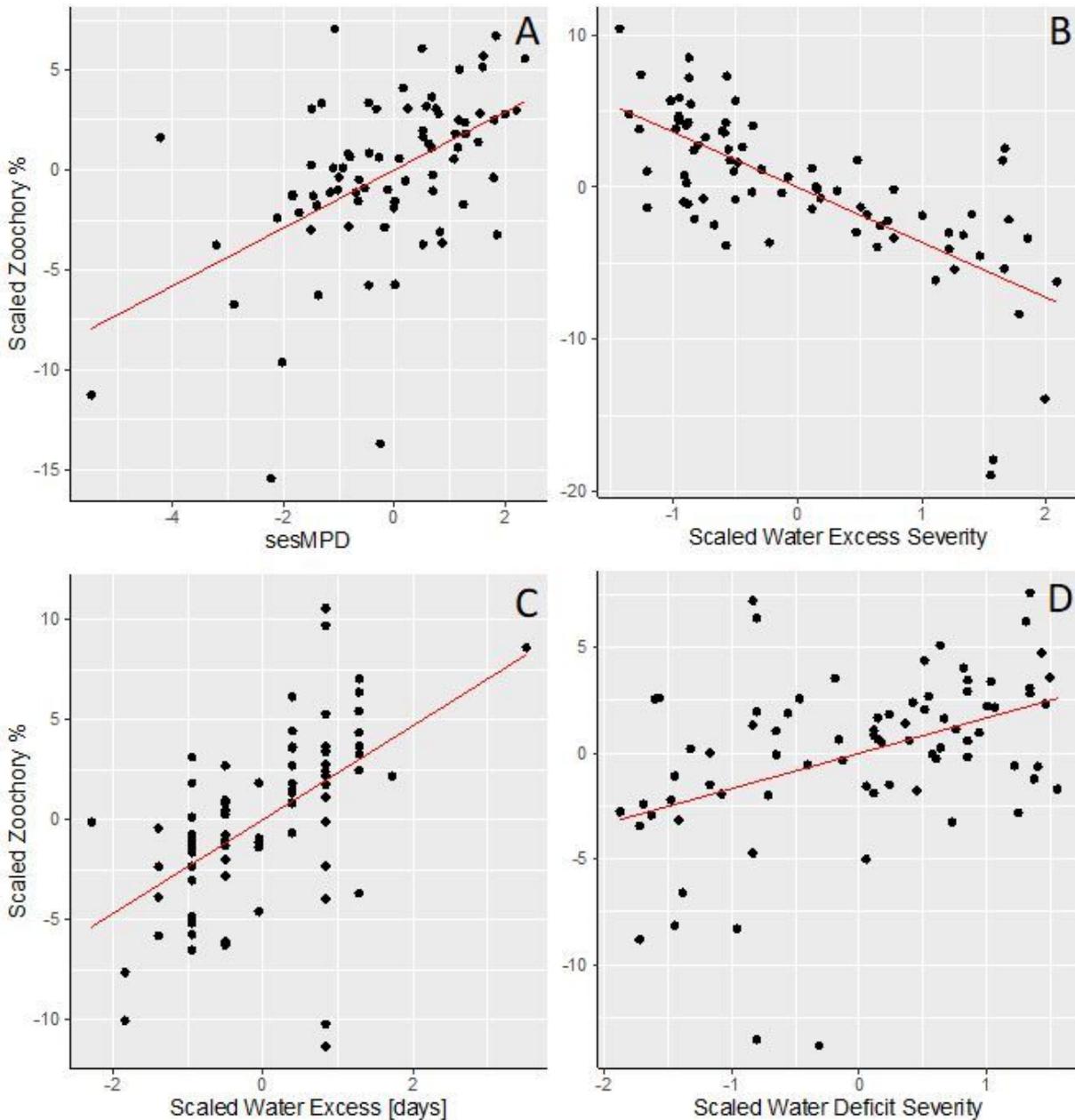


Figure 3

The explanatory variables standard size effect of A- mean phylogenetic distance (sesMPD), B- water excess severity, C- water excess duration (Water excess [days]), D- water deficit severity, and the response variable percentage of species with zoochory (Zoochory %) of the global GLM model for fragments of the Rio Doce Basin, Brazil. SesMPD (estimate = 1.4483, $P= 1.56e-05$), water excess severity (estimate = -3.6250, $P= 1.84e-05$), water excess duration (estimate = 2.3493, $P= 0.0144$), water deficit severity (estimate = 1.6785, $P=0.01964$).

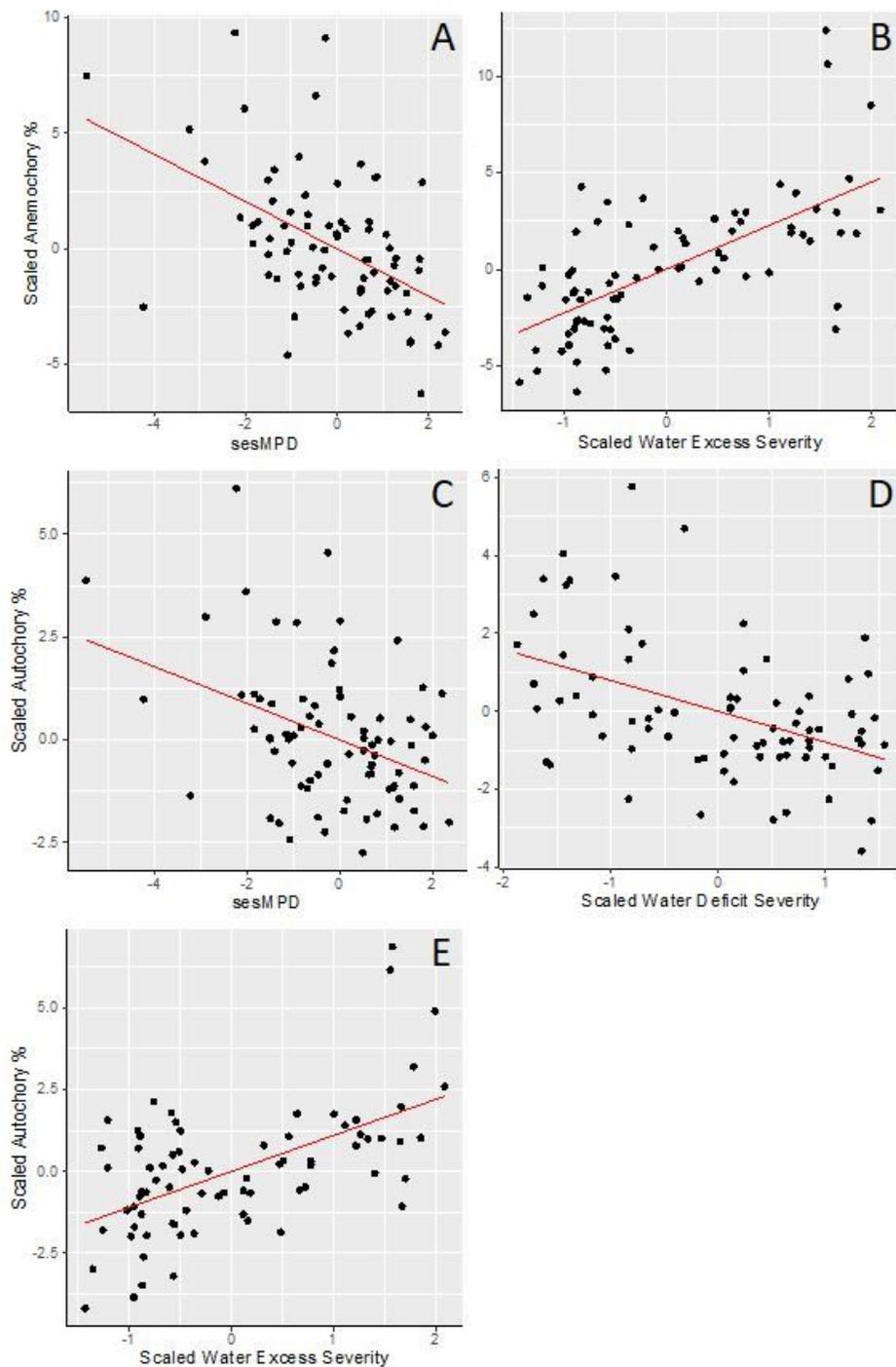


Figure 4

A, and B- The explanatory variables standard size effect of mean phylogenetic distance (sesMPD), water excess severity and the response variable percentage of species with anemochory (Anemochory %) of the global GLM model for fragments of the Rio Doce Basin, Brazil. SesMPD (estimate = -1.02441, $P= 4.82e-05$), water excess severity (estimate = 2.26164, $P= 0.00181$). C, D, and E- The explanatory variables standard size effect of mean phylogenetic distance (sesMPD), water deficit severity, and water excess severity, and the response variable percentage of species with autochory (Autochory %) of the global GLM model for fragments of the Rio Doce Basin, Brazil. SesMPD (estimate = -0.4452, $P=0.00186$), water deficit severity (estimate = -0.7936, $P=0.00935$), water excess severity (estimates = 1.1008, $P=0.00188$).

Supplementary Files

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- [Supplementarymaterial3.0.docx](#)