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Ecological indicators as tools to monitor the effects of climate change on Tropical dry forest

"Documento Definitivo"

Doutoramento em Biologia e Ecologia das Alterações Globais
Especialidade de Ecologia e Biodiversidade Funcional

Ana Cláudia Pereira de Oliveira

Tese orientada por:
Professora Doutora Cristina Branquinho
Professor Doutor Renato Garcia Rodrigues

Documento especialmente elaborado para a obtenção do grau de doutor

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2020

NOTA PRÉVIA

A presente tese apresenta resultados de trabalhos já publicados (capítulos 2 e 3) ou em preparação para publicação (capítulos 4 e 5), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos Pós-Graduados da Universidade de Lisboa, publicado no Diário da República II série nº 57 de 23 de março de 2015. Tendo os trabalhos sido realizados em colaboração, o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, 5 de Outubro de 2020.

Ana Cláudia Pereira de Oliveira

Aos meus pais, Ruth e Israel,

e ao Infali Turé

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"Tudo o que pode fazer ou sonha que pode, comece.
A audácia contém gênio, poder e magia”
W.H.Murray, The Scottish Himalayan Expedition, 1951

“Pedras no caminho?
Guardo todas, um dia vou construir um castelo…”
(Fernando Pessoa)

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Abstract

Drylands (hyper-arid, arid, semi-arid and dry sub-humid areas) cover about 47% of global land surface and harbour about 39% of the world´s population, encompassing the least developed countries, poorest and highly dependent on natural resources. The need to anticipate the impacts of climate change on drylands is indisputable due to their high vulnerability to climate and environmental changes (leading to desertification), as both disturbances are key threats to biodiversity and to ecolosystem services delivery, essential to human well-being. Diversity metrics (taxonomic and functional) are complementarily used to monitoring ecosystems' response to climate. With this in mind **the main aim of this thesis was to identify potential ecological indicators based on both taxonomic and functional plant diversity metrics, to be used as tools to monitor the effects of climate change on Tropical dry forest.** Caatinga, one of the most diverse ecosystems in Neotropical seasonally dry forests, and more vulnerable to climate change in Brazil, was used as a case study. The aridity index was considered as an adequate variable to assess the effects of climate change on vegetation. In this study, a very rich database with information on the occurrence of around 1 000 plant species in this ecosystem was used. It contained data derived from different sources, collected with different sampling methodologies and sampling efforts in space and over time. By applying a re-sampling methodology, plant species abundance was estimated along a spatial climate gradient. This information is essential to assess the response of diversity metrics, especially those that require abundance data, such as functional metrics. Thirteen plant functional traits (PFT) were studied, which determine species' responses to the environment, and allow to assess the response of functional metrics to climate. Of the 13 PFT studied, eight responded to aridity, which affected the functional structure of Caatinga vegetation. Clustering analysis based on the 13 PFT was used to group species into seven main functional groups responding to aridity. Functional groups with the presence of chemical defense and CAM (crassulacean acid metabolism) photosynthetic pathway were those whose relative abundance increased most with increasing aridity. Thus, they were proposed as ecological indicators to track aridity effects on the plant community functional structure. Based on the previously described results, a global analysis of complementary diversity metrics was made to assess the susceptibility of the plant community, from a taxonomic and functional point of view, along the aridity gradient. In more arid sites, there was a higher functional diversity supported by a few plant species (low species richness) with unique functions, suggesting low resilience to environmental change. Contrastingly, less arid sites showed lower functional diversity but higher functional redundancy among species. Overall, this work's findings support the use of complementary plant diversity metrics as warning ecological indicators of climate change impacts on the Caatinga ecosystem. In adition, the response of the plant community along the spatial climate gradient provides indications on how it might change over time under a global aridity increase, contributing to improve predictions on the effects of climate change. As projections are not very encouraging, it is crucial that we taxonomically and functionally conserve and restore these dry forests in order to mitigate the predicted negative impacts of climate change in the Caatinga ecosystem.

Key-words: Brazilian Caatinga, climate change, diversity metrics, dryland ecology, plant functional traits

Resumo

As terras secas (hiper-áridas, áridas, semi-áridas e sub-húmidas secas) cobrem cerca de 47% do globo terrestre e abrigam cerca de 39% da população mundial. Ocorrem maioritariamente em países menos desenvolvidos, mais pobres e altamente dependentes dos recursos naturais. A necessidade de antecipar os impactos das alterações climáticas nas terras secas é indiscutível devido à sua alta vulnerabilidade a alterações climáticas e ambientais (tendo como consequência a desertificação), já que ambas constituem importantes ameaças para a biodiversidade e para a prestação de serviços de ecossistema essenciais para o bem-estar humano. Métricas de diversidade (taxonómicas e funcionais) são usadas de forma complementar para monitorizar a resposta dos ecossistemas ao clima. Assim, **o principal objetivo desta tese é identificar potenciais indicadores ecológicos, baseados métricas taxonómicas e funcionais, que possam ser usados como ferramentas para monitorizar os efeitos das alterações climáticas na Floresta tropical seca**. A Caatinga, um dos ecossistemas mais diversos das Florestas Neotropicais sazonalmente secas, mas também dos mais vulneráveis às alterações climáticas no Brasil foi a área estudada. O índice de aridez foi considerado uma variável adequada para avaliar os efeitos das alterações climáticas na vegetação. Para este estudo, utilizamos um banco de dados muito rico com informações sobre a ocorrência de cerca de 1 000 espécies de plantas neste ecossistema, obtida a partir de dados provenientes de diferentes fontes, recolhidos com diferentes metodologias e esforços de amostragem no espaço e ao longo do tempo. Aplicando uma metodologia de reamostragem, a abundância de espécies de plantas foi estimada ao longo de um gradiente espacial de clima. Tais informações são essenciais para avaliar a resposta das métricas de diversidade, especialmente aquelas que requerem dados de abundância, como métricas funcionais. Foram estudadas 13 características funcionais da planta (CFP), que determinam as respostas das espécies ao meio ambiente e permitem avaliar a resposta das métricas ao clima. Das 13 CFP estudadas, oito responderam à aridez, que por sua vez afetou a estrutura funcional da vegetação da Caatinga. A análise de agrupamento com base nos 13 CFP foi usada para agrupar espécies em sete grupos funcionais principais que respondem à aridez. Os grupos caracterizados pela presença de defesas químicas e via fotossintética CAM (metabolismo ácido das crassuláceas) foram aqueles cuja abundância relativa aumentou mais com o aumento da aridez. Assim, estes foram propostos como indicadores ecológicos para rastrear os efeitos a aridez na estrutura funcional da comunidade vegetal. Com base nos resultados descritos anteriormente, foi feita uma análise global de métricas complementares de diversidade para avaliar a suscetibilidade da comunidade de plantas, do ponto de vista taxonómico e funcional, ao longo do gradiente de aridez. Em locais mais áridos, verificou-se uma maior diversidade funcional suportada por algumas espécies de plantas (baixa riqueza de espécies) com funções únicas, sugerindo baixa resiliência. Em contraste, locais menos áridos mostraram menor diversidade funcional, mas maior redundância funcional entre as espécies. No geral, as conclusões deste trabalho apoiam o uso de métricas complementares de diversidade vegetal como indicadores ecológicos de alerta dos impactos das mudanças climáticas no ecossistema da Caatinga. Além disso, a resposta da comunidade vegetal ao longo do gradiente espacial do clima fornece indicações sobre possíveis alterações ao longo do tempo sob um aumento da aridez global, contribuindo para melhorar as previsões sobre os efeitos das alterações climáticas. Como as projeções não são muito animadoras, é fundamental que conservemos e restauremos taxonómica e funcionalmente estas florestas secas, a fim de mitigar os impactos negativos previstos das alterações climáticas no ecossistema da Caatinga.

Palavras chave: Caatinga brasileira, alterações climáticas, métricas de diversidade, ecologia de terras secas, características funcionais de plantas

Chapter 1

General Background

1 General Background

1.1 Climate change and dryland systems

Climate change is the variability of climate-defining variables that persist over a long period (minimum 30 years) and may have natural, anthropogenic causes or both (IPCC 2019). However, general circulation models simulating the behavior of the climate system indicate that part of the global climate change observed, especially in the last four decades, is caused by anthropogenic greenhouse gas (GHG) emissions (IPCC 2019). These gases change the atmosphere as well as its composition and hence the regulation of heat energy (Karl and Trenberth 2003; Fleming 2020).

Future climate scenarios indicate changes in temperature regimes and rainfall patterns, but also a higher frequency of extreme weather phenomena such as more frequent and severe droughts (IPCC 2014). Thus, climate change will have mostly negative impacts on various natural and social systems, and can alarmingly impact global biodiversity (Bellard et al. 2012; Peñuelas et al. 2013).

Since biodiversity is essential for ecosystem functioning (e.g. nutrient cycling, primary productivity, decomposition) it is legitimate to assume that the more diverse the ecosystem, the greater the ecosystem ability to maintain its processes and functions in the face of climate change (Hooper et al. 2005). In addition, the impacts of climate change on biodiversity can also be reflected in human livelihood and well-being (Mooney et al. 2009; Cardinale et al. 2012), because when ecosystems change to a different state, their ability to provide ecosystem services also changes (Carpenter *et al.*, 2009). As a result, there is an urgent need to develop and implement adequate actions to reduce biodiversity vulnerability and increase resilience, especially in highly vulnerable ecosystems to climate change, such as drylands.

Dryland systems are characterized by a combination of high evaporation, low rainfall, and human activities such as livestock grazing, the collection of wood and non-wood forest products, fire use, and soil cultivation (Safriel et al. 2005; Pennington et al. 2009; FAO 2019). These systems are found in most of the world´s terrestrial biomes and ecoregions and have a large proportion of common species and distinct habitats **(Figure 1.1).**

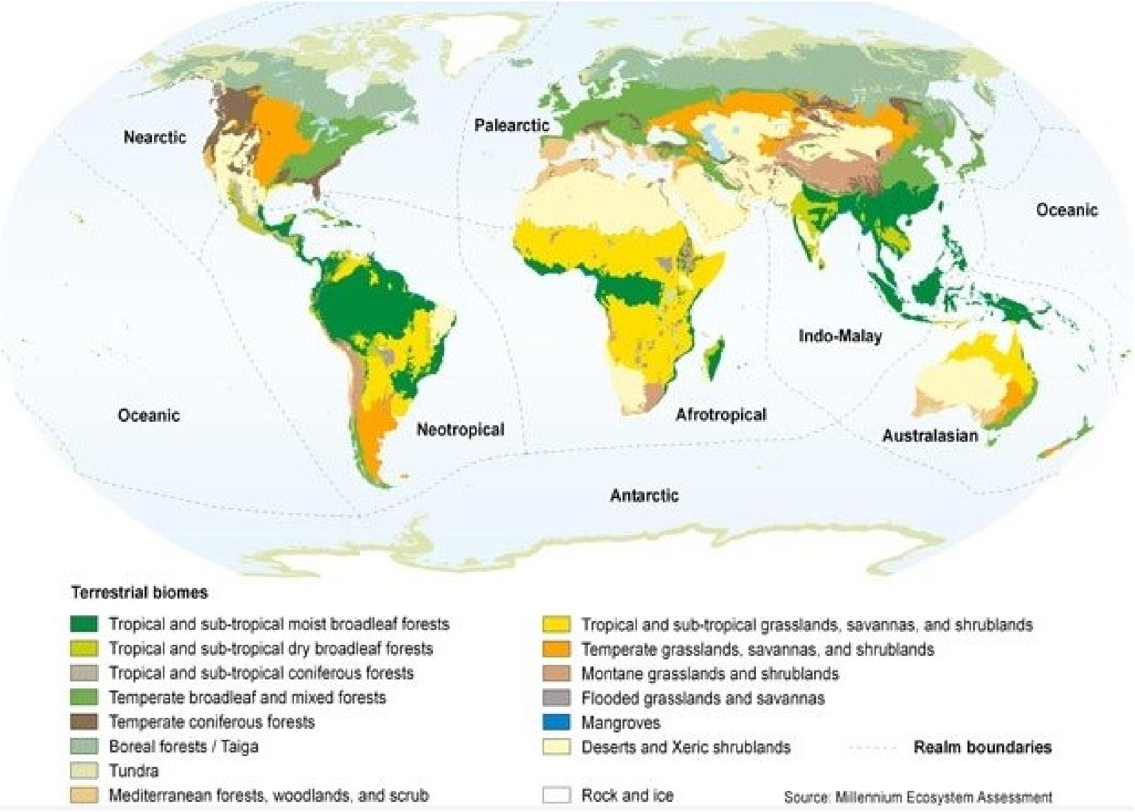


Figure 1.1. World's ecorregions categorized within eight biogeographic realms. (Source: Millenium Ecosystem Assessment)

Drylands covered about 41% of terrestrial ecosystems up to 2007 (Reynolds et al. 2007) **(Figure 1.2)**, which currently has increased to almost 47% (Koutroulis 2019) with an expected expansion up to 56% until 2100 (Huang et al. 2016). Also, this cover may expand even more due to an aridity increase associated with climate change (Dai 2011; Feng and Fu 2013; IPCC 2019). The population inhabiting drylands was 35% up to 2000 and this value increased to 39%, accompanying the terrestrial cover increase (Koutroulis 2019).

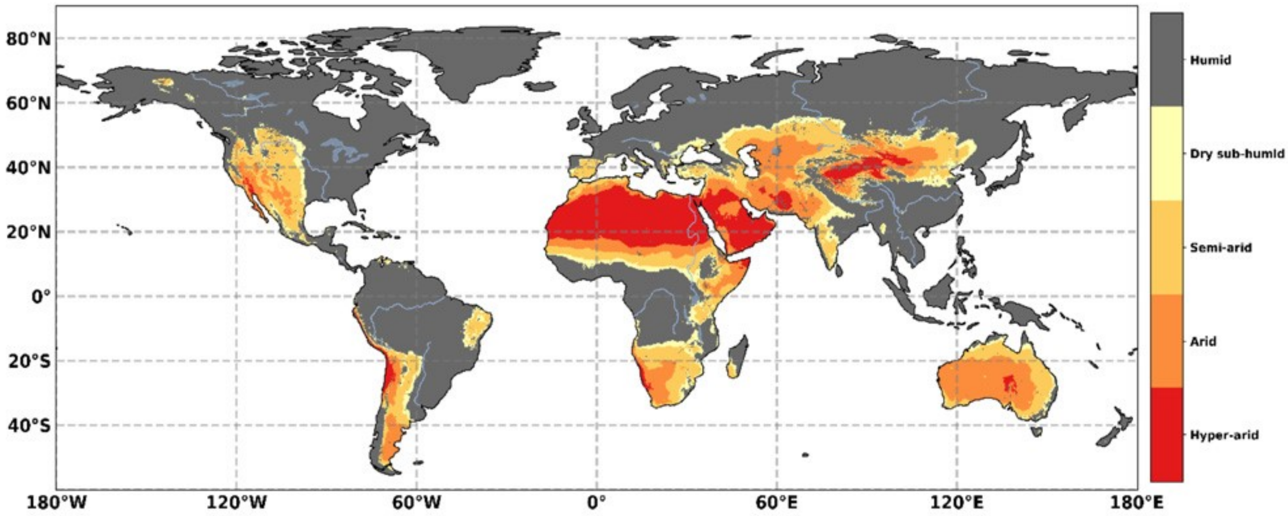


Figure 1.2. Distribution of drylands around of the world, including four dryland systems that compose the aridity gradient (hyper-arid, arid, semi-arid and dry subhumid). (Extrated from https://www.ipcc.ch/srccl/chapter/chapter-3/)

Due to the multiplicity and complexity of the processes acting in these systems, the aridity index (AI) is widely used to classify the different drylands subtypes **(Figure 1.2)**. This index is calculated as the ratio of average annual precipitation and potential evapotranspiration (Thornthwaite 1948). Thus, the dryland system can be classified into four subtypes from less arid to more arid namely: (i) dry subhumid between 0.50 and 0.65 AI; (ii) semi-arid represented by 0.20 to 0.50; (iii) arid from 0.05 to 0.20; and (iv) hyper-arid lower than 0.05 AI.

Drylands show a gradient in primary productivity decreasing from dry subhumid, semi-arid, and arid to hyper-arid areas (Safriel et al. 2005). Population density within drylands increases with decreasing aridity from 71 persons per square kilometre in the dry sub-humid drylands to 10 persons in hyper-arid drylands. In parallel, with the decrease in aridity, there is a decrease in the sensitivity of dryland ecosystems to human impacts that contribute to land degradation. Within this context, the risk of land degradation is highest in the median section of the aridity gradient represented by semi-arid, where both population pressure (population density) and sensitivity to degradation are of intermediate values (Safriel et al. 2005). Consequently, all dryland subtypes, in particular the median section (semi-arid), are strongly vulnerable to climate and environmental changes, including desertification process **(Figure 1.3)**.

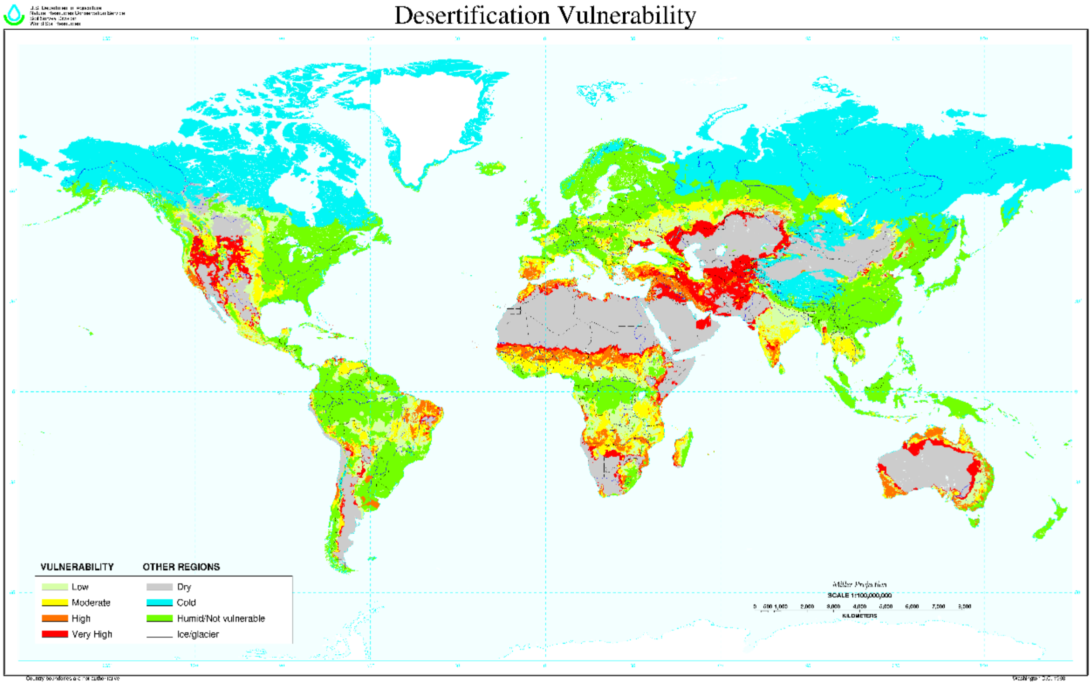


Figure 1.3. Different scales of desertification vulnerability within dryland systems and other regions (Extracted from USDA-NRCS website)

1.2 Detecting climate change effects on diversity

1.2.1 Diversity metrics

There is a consensus that climate change will impact ecosystem structure and functioning (Maestre et al. 2012; Nunes et al. 2017; Berdugo et al. 2020). To develop actions for biodiversity conservation at a global, regional and local scales, as well as to analyse many questions in ecology, it is essential to know the biological diversity of ecosystems and, consequently, its functioning (Begon et al. 2007).

Taxonomic and functional metrics, as biodiversity surrogates, have been suggested to be used to assess the impact of environmental drivers with different intensities, on biodiversity (Branquinho et al. 2019). Species richness is a classic example of traditional metrics (Cadotte et al. 2011). Normally, species richness, defined as the number of species in a certain area, is related to the distribution of the number of individuals among species that have been established in alpha (α), gamma (γ), and beta (β) diversity (Whittaker 1960; Magurran 2004). Alpha diversity is based on the total number of species at a local scale; while gamma diversity is based on the sum of species´ number recorded at a regional scale; beta diversity works at a global and/or regional scale and is the change of species among these communities/localities (Whittaker 1960; Magurran 2004).

The abundance and equitability of each species are also included in taxonomic metrics as well as the Simpson index, which measures the probability that two random individuals in a community belong to the same species (Brower & Zarr 1984; Ricotta 2005). However, these measures do not consider the functions of species within the ecosystem (Cianciaruso et al. 2009). For these reasons, the use of taxonomic metrics alone, may not capture key changes in plant communities, and their functional consequences, due to environmental changes (Ricotta, 2005).

Due to the potential link to ecosystem functioning and maintenance, the inclusion of functional metrics has been complementary to traditional metrics in assessing the response of plant communities to environmental changes (Petchey and Gaston 2006; De Bello et al. 2007; Laliberte and Legendre 2010; Swenson and Weiser 2010; Pillar et al. 2013; Matos et al. 2017; Nunes et al. 2017; Sfair et al. 2018). Functional metrics have received increasing attention by encompassing morphological, behavioral, and ecological differences among individuals and species that can interfere with species growth, reproduction and survival (Violle et al. 2007; Swenson and Weiser 2010). Several functional metrics have been proposed over time from Rao´s quadratic entropy (Botta‐Dukát 2005) to indexes for different diversity components such as functional richness, evenness and divergence (Mouchet et al. 2010). Recently, an index called functional dispersion was proposed as a multivariate measure of species dispersion within the trait space, consisting of the mean distance of species to the community centroid, weighted by their abundances (Laliberté & Legendre, 2010).

Another interesting metric is the weighting of the trait´s values of each species by their abundance in the community (community weighted mean – CWM). This allows us to identify the contribution of each trait within the community (Lavorel et al. 2008; Dias et al. 2013). This approach considers the biomass contribution of a given species within a community, assuming that the effects will be greater the greater their contribution (*mass ratio hypothesis* - Grime 1998). Conversely, when trait data include continuous values, the CWM corresponds to the trait value weighted by its relative abundance (Lavorel et al. 2008). To calculate these functional metrics, it is necessary to collect information about one or a set of functional traits, which are morphological, physiological and/or phenological features measured in each species or individuals (Canadell et al., 2007; Violle et al., 2007).

Plant functional traits have greatly improved the understanding of the effects of environmental changes on biodiversity and ecosystem functioning (Petchey and Gaston, 2006; Nunes *et al.*, 2017). They are associated with plants´ adaptive strategies to climate, soil resources, disturbance (e.g. competition and land-use changes) and defense/protection needs (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). Hence, certain traits may be used to predict changes in environmental factors (Lavorel and Garnier 2002; Suding et al. 2008). For instance, plant traits such as *growth form* and *leaf traits* are associated with photosynthetic production and ecophysiological adaptation, e.g. to drought stress. *Spinescence* provides defense against herbivory while reducing heat or drought stress. The *photosynthetic pathway* (C3, C4 and CAM – Crassulacean acid metabolism) describes nutrient and water use efficiency. As well, the s*eed dispersal mode* determines the distance species can cover (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013, 2016).

Despite the success of functional diversity *per se* or together with traditional taxonomic metrics, these do not reflect the species´ abilities to ensure the maintenance of ecosystem processes e.g. if disturbances lead to species loss.

Thus, functional redundancy has been proposed (Walker 1992; de Bello et al. 2007). This metric has a relationship with species and functional diversity. That is, some species perform similar roles in communities and ecosystems, and redundant species can, therefore, be lost with minimal impact on ecosystem processes (Lawton and Brown 1994). Low redundancy occurs when there is a positive linear relationship between species and functional diversity because each species has a relatively unique trait (Petchey and Gaston 2006; Sasaki et al. 2009). This positive linear relationship indicates functional traits are lost or trait space dimensionality decreases from a system as species diversity declines (Petchey and Gaston 2006; Sasaki et al. 2009). This low redundancy indicates that ecosystem functioning is not robust concerning changes in diversity caused by environmental drivers (Petchey and Gaston 2006; Sasaki et al. 2009). In contrast, high redundancy occurs when one new species with new and still unrepresented functional traits is added in the community. Thus, functional diversity may quickly increase at lower diversity levels and subsequently increase at declining rates as functional redundancy increases. High redundancy indicates high robustness in the ecosystem relative to environmental drivers (Petchey and Gaston 2006; Sasaki et al. 2009).

1.2.2 Abundance data to measure diversity metrics

Most of the applications of biodiversity-based information require the use of abundance data (Mouillot et al. 2011; Maestre et al. 2012). It has been suggested that dominant species composing 80% of the relative abundance of a community (sometimes corresponding to a low number of species), can capture the main effects of environmental drivers on key ecosystem processes (Grime 1998; Lavorel and Garnier 2002; Hooper et al. 2005). Yet, for large datasets, species abundance data is often not available. For instance, in biological research, the Global Biodiversity Information Facility (GBIF) is becoming a reference database for researchers, with records containing occurrences of hundreds of millions of species worldwide. Another example, specific for dryland ecosystems, is the Dryflor database, which has so far recorded the occurrence of 4 660 woody plants species, based on 835 inventories (Banda et al. 2016). However, defining methodologies to transform basic-biodiversity occurrence data (e.g. species presence/absence) into abundance data to be used in many applied ecological studies, remains highly challenging regardless of has been a goal for a long-time (Gleason, 1920; Conlisk et al. 2009).

Several methods towards this end have been developed, including (i) regression approaches, using a truncated Poisson or negative binominal distribution methods (Augustin et al. 1998; He & Gaston 2000; Pearce & Boyce 2006; Conlisk et al. 2009; Hwang & He 2011), (ii) methods based on the number of cells occupied in a rectangular grid (Gerrard & Chaing 1970; Kunin 1998; Joseph et al. 2006), (iii) the zero-inflated count model (Barry & Welsh 2002), and (iv) model count data, where a first model is fitted to account for occurrence, and then a second model follows to show abundance once presence is predicted (Welsh et al. 1996; Guisan & Kienast 1998). Nevertheless, these studies have not always been successful. They require knowledge on the average area occupied by an individual of a given pecies, but this information is rarely available. There is also a lack of knowledge about abundance levels associated with a given occurrence map. Since different species exhibit different distribution patterns - two species with the same total occupancy area can have different abundances for the number of occupied cells (Gaston 1996; Gaston et al. 1998; Kunin 1998). Count data are difficult and expensive to collect for techniques that deal with overdispersion as a zero-inflated count model and count data model (Nielsen et al. 2005).

As more biodiversity-databases are available, the more we need to have tools to make the most of them, in terms of conservation and ecosystem functioning. These datasets hold a lot of precious knowledge (Soranno et al. 2015) that needs to be worked out for different specific aims, and to address several societal challenges, from species conservation to ecosystem services provisioning. Added, the database should be considered as a shared knowledge about biodiversity that is necessarily collective (Canhos et al., 2006). Despite a large number of observations recorded and publication of results in the past centuries, in many cases primary observation and data collected are not disseminated among researchers in several fields of knowledge, which would also ensure their preservation for future generations (Canhos et al., 2006). Advancing information technology, data integration, and scientific communication have consolidated how biodiversity-change monitoring is performed (Pereira et al. 2013; Matos et al. 2017).

1.2.3 Ecological indicators

The term indicator is derived from the Latin word *indicare* that means to point or proclaim. An indicator is a cost-effective and valuable tool that allows summarizing a complex set of information retaining only the essential significance of the aspects being analyzed (Walz 2000; EPA-SAB 2002; Heink and Kowarik 2010). Good indicators should be distinguishable variables, easy to measure and to interpret, and representative of what will be evaluated (Rodrigues & Gandolfi, 2001). Additionally, ecological indicators should be effectively used to characterize, monitor and assess the impacts on biodiversity of several drivers as well as consider the re-establishment of ecosystems structure and functions (Block et al. 2001).

This tool is widely used for the assessment of environmental conditions (Branquinho et al. 2015; Koch et al. 2016; Varela et al. 2018). The use of ecological indicators represents a scientific analysis with a numerical or descriptive categorization of environmental data and is often based on partial information that reflects the status of extensive ecosystems (Van Straalen 1998; Manoliadis 2002). The repeated use of ecological indicators in monitoring programs can assist, for example, in detecting environmental changes in early stages or assessing the efficiency of measures taken to improve environmental quality (Van Straalen 1998; Branquinho et al., 2015). In tropical forests, ecological indicators have been used to monitor ecologically restored areas and the estimators normally used are the diversity (e.g., richness and abundance of organisms and diversity of species within functional groups), vegetation structure (e.g., soil cover by vegetation and biomass) and ecological processes (e.g., nutrient cycling, biological interactions and seed dispersal) (Belloto et al., 2009; Rodrigues et al. 2011).

1.2.4 Space-for-time approach

The substitution of space-for-time is an alternative widely used in biodiversity modeling to infer past or future trajectories of ecological systems from spatial gradients (Gosz 1992; Blois et al. 2013; Matos et al. 2017; Nunes et al. 2017). In contrast, climatic projections based on time series data normally focus on structural and compositional features of systems neglecting spatial heterogeneity within sites as well as functional dynamics (Pickett 1989; Blois et al. 2013; Damgaard et al. 2019). The substitution of space-for-time assumes that time is a surrogate for an operational environment, and the past is a series of such environments (Pickett 1989).

Even using both time series data and spatial gradient strategies, it is a huge challenge for the scientific community to detect the impacts of environmental and climate change on ecosystems at an early stage (Scheffer et al. 2009). This is particularly important when considering that recent studies have shown a short resilient period, the ghost period, before ecosystems transition from a favorable to an undesirable state (Vidiella et al. 2018). Moreover, ecosystems transition can be rapid or abrupt (Scheffer et al. 2001; Dakos et al. 2019). However, during a drought period, an area can be continuously disturbed and show little vegetation but still be able to recover after a rainy season. On the other hand, once it turns to desert, for example, it is nearly impossible to return to the previous state. In this situation, the new equilibrium state is adverse and improper for most species adapted to the previous state (Scheffer et al. 2009).

A model by Vidiella et al. (2018) identified the short resilient period through soil degradation levels in a semi-arid ecosystem. During these periods, interventions aimed at the ecological restoration of these areas may be a successful strategy protecting drylands facing tipping points (Vidiella et al., 2018). To anticipate and identify these impacts, action can be taken to delay or stop the ecosystem change from a favorable to an undesirable state as well as increase the ecosystem resilience to climate change (Sousa-Silva et al. 2018). Therefore, it is urgent to overcome these challenges and to detect the impacts of environmental and climate change on ecosystems at an early stage to avoid irreversible damages.

1.3 Case study

1.3.1 Caatinga – Seasonally dry tropical forest (SDTF)

Caatinga is a Brazilian ecosystem that covers 912 529 km^2, corresponding to 11% of Brazil (da Silva et al. 2018). The name “Caatinga” originated from the indigenous word Caá-Tinga (white woods) to distinguish this vegetation - without leaves in the dry season - from other types of vegetation (Prado 2003). Despite the name Caatinga having persisted to this day, during the 19th century Carl Friedrich von Martius recognized this ecosystem as a phytogeographical unit and called it the “Kingdom of Hamadryades”. This name symbolizes the nymphs that emerged from a period of depression, after rains, giving rise to festive moments and temporary pleasure (Ab´Saber, 2003).

This Brazilian ecosystem shows high spatial heterogeneity due to habitat and temporal heterogeneity associated with climate, which results in higher floristic diversity, physiognomies and community structure (Andrade-Lima 1981; Araújo et al. 2005; Rodal et al. 2008). Its floristic composition changes from open vegetation dominated by herbaceous and shrubs species in rocky outcrops of the driest areas to semi-deciduous forests dominated by woody species in richer and wetter soils (Fernandes and Queiroz 2018). This heterogeneous environment results in an ecosystem with high species turnover forming an ecological pattern of community structure organization (Banda et al. 2016). Indeed, species turnover in the environment can occur because of historical and spatial restrictions, interspecific interactions, or due to the wide variety of randomly occurring species (Baselga 2010).

These characteristics make Caatinga the most diverse seasonally dry tropical forest ecosystem, housing 1 112 plant species (Banda et al., 2016). Fabaceae is the richest family followed by Euphorbiaceae, Malvaceae, and Asteraceae (Moro et al. 2014). Of the 1 112 plant species, around 30% are endemic (Giulietti et al., 2002). Cactaceae is the most notable example of high endemism in Caatinga, with 50% of its species being unique to this ecosystem (Fernandes and Queiroz 2018). Moreover, 350 of the species present are considered endangered and a conservation priority by the Brazilian Ministry of Environment, Cactaceae being the most threatened (Giulietti et al. 2002; MMA 2016).

Caatinga aggregates a wide structural variety and complex floristic composition, adapted to the existing climate and geoenvironment (Queiroz 2006). In general, plants in this ecosystem have adaptive strategies to survive in the semi-arid environment, such as: i) small plants due to water deficit along the year, resulting in discontinuous plant´s growth; ii) shrub and trees with spinescence against pathogens and herbivorous as well as reduced water loss; iii) succulent plants that retain water, ensuring their survival during dry seasons; v) plants with short reproductive cycles (annual); vi) foliage with strong deciduous character in response to a long period of water deficit; and; vii) pinnate or twice pinnate leaves, corresponding to small photosynthetic units (Rizzini 1997; Prado 2003; Paganucci de Queiroz 2006) **(Figure 1.4).**

1 Caatinga landscape before a period of drought.
Photo: SMorais, SOS Caatinga

2 Caatinga landscape 20 days after rain.
Photo: SMorais, SOS Caatinga

3 Open vegetation in Caatinga
Photo: ACPOliveira

4 *Cereu jamacaru*
Cactaceae
Photo: ACPOliveira

5 Annual plants
Habranthus sylvaticus
Amaryllidaceae
Photo: DFernandes

6 Spinescences (thorns)
Photo: RQueiroz

7 Twice pinnate leaves
Anadenanthera colubrina
Fabaceae
Photo: RQueiroz

8 *Encholirium spectabile*
Bromeliaceae
Photo: ACPOliveira

Figure 1.4. A brief illustration of structural variety from Caatinga, which has: (i) irregular seasonal vegetation influenced by climatic variability (1 and 2); (ii) many vegetation types such as open vegetation (3 and 4); (iii) a majority low vertical structure (3); (iv) adaptive strategies to survive in the semi-arid environment (e.g.; Crassulacean acid metabolism (CAM – 4), annual plants (5), spinescence (6), twice pinnate leaves (7), plants with leaves arranged in a rosette (8).

Despite its singular representativeness and great importance, Caatinga is the least known, studied and protected among Brazilian ecosystems, and has been scientifically neglected for many years (Santos et al. 2011; Moro et al. 2016). Although there is a considerable number of very recent works (e.g., Sfair et al. 2018; Silva and Souza 2018; Pinho et al. 2019; Ribeiro et al. 2019). The lack of knowledge about this ecosystem could be associated with its high irregular seasonal vegetation implying continuous sampling efforts and/or a low number of research teams or senior researchers in the region (Santos et al. 2011; Da Costa et al. 2015). The lack of protected status for Caatinga is associated with an unknown and strong dependence on its natural resources by populations living in this ecosystem (Banda et al. 2016; Sfair et al. 2018). In addition, the region suffers from a lack of public policies that would ensure sustainable development and, consequently, increases the threat to Caatinga conservation (Santos et al. 2011; Melo 2018).

Caatinga's main threats with potentially irreversible impacts, are human activities and climate change (Ribeiro-Neto et al. 2016; da Silva and Barbosa 2018). In Caatinga, human activities increased significantly with the colonization of this ecosystem by the first Europeans who landed in Brazil. These activities included the killing of indigenous people to conquer space for large settlements dedicated to subsistence agriculture, and livestock farming along large rivers (Hemming, 1978; Puntoni, 2002). Since then, agricultural activities forward-looking family production have often been associated with low technological methods showing an absence of conservationist soil management practices (Sfair et al. 2018). Grazing has been highlighted as the main livestock farming since colonization. In 2017, nine million goats, able to eat all plant parts (i.e., from flower to litter) were estimated to live in Caatinga, endangering the composition, dynamics, and functioning of this ecosystem (Guimarães Filho and Goes, 1998).

In addition, native vegetation extraction is another human activity that threatens Caatinga, with millions of cubic meters of native vegetation being consumed all year in the region. This consumption is mainly associated with firewood and coal production that support steel production and plaster factories (Ramos et al., 2014; Albuquerque et al. 2018). At the same time, Caatinga is one of the ecosystems that show higher vulnerability to the negative impacts of any climatic variability (i.e. reduction or long periods without rainfall) (da Silva et al. 2018). Caatinga threats and vulnerabilities to climate change have already been identified and are further described below. Extremely long drought periods such as the one that occurred between 2010 and 2016, clearly demonstrated the vulnerability of this ecosystem and its population to climate change, with serious socio-economic and environmental consequences (Alvalá et al. 2017; Buriti and Barbosa 2018; Marengo Orsini et al. 2018). Drought conditions occur typically in Caatinga, but they have recently become more frequent and prolonged (Buriti and Barbosa 2018). According to climate projections, the future of this ecosystem is threatened as a temperature increase in Caatinga is expected by 2100 (IPCC 2011). Climatic projections also indicate a reduction in rainfall (Magrin et al. 2014; Buriti and Barbosa 2018).

Anthropogenic actions and climate change together may facilitate the process of erosion, productivity decrease, aggravating the soils' environmental degradation.

Reducting leaf deposition on the soil surface can unprotect it from direct solar radiation and increase the direct impact of rainwater on exposed soil, thus favouring erosion processes, and decreasing nutrients deposition (i.e. carbon and nitrogen) (Bochet et al. 2006; Zuazo and Pleguezuelo 2009). Furthermore, these factors can accelerate the desertification process in this ecosystem which already includes more than 60% of the areas susceptible to desertification in Brazil (Hauff 2010) **(Figure 1.5)**.

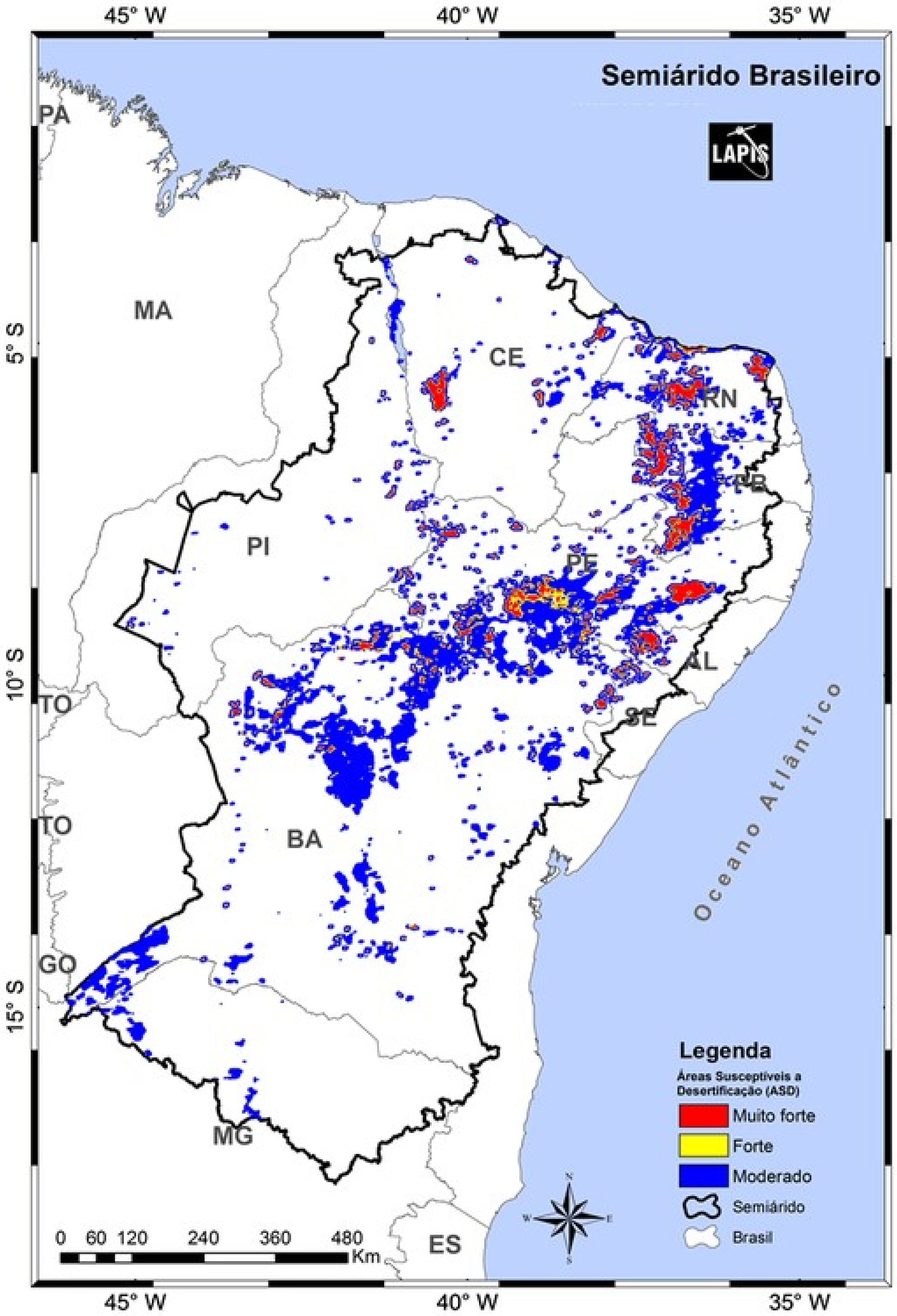


Figure 1.5. Desertification map in the semi-arid from Brazil. (Source: Lapis – Laboratório de Análise e Processamento de Imagens de Satélites). Legend: Areas susceptible to desertification (ASD) – blue areas are moderately susceptible; yellow areas are strongly susceptible; red areas are extremely susceptible. Black outline limits the semi-arid region under analysis; with area represents Brazil country limits.

1.4 Objectives and structure of the thesis

It is a consensus that the increase in aridity associated with climate change can lead to biodiversity change and loss. Having this in mind, we proposed a general question, ***can we develop ecological indicators of the impacts of climate change on the structure and functioning of Tropical dry forest based on both taxonomic and functional plant biodiversity metrics****?* Given this narrative, the **main objective** of this study ***was to identify potential ecological indicators based on both taxonomic and functional plant diversity metrics which can be used as tools to monitor the effects of climate change on Tropical dry forest***.

The thesis is structured in six chapters (**Figure 1.6**). The **General Background (Chapter 1)** frames the problematic of the effects of climate change on the diversity of dryland systems, while addressing the need to assess the response of plant diversity metrics to track and anticipate these effects on this ecosystem. A brief description of the tropical dry forest (Brazilian Caatinga) is given in the introduction.

As more biodiversity-databases are available, the more we need to have tools to make most of them, in terms of conservation and ecosystem functioning. To evaluate trends in biodiversity change, species abundance is required. Yet, for large datasets, species abundance data is often not available. Thus, estimating abundance from presence-absence data is a crucial step to track biodiversity changes. However, estimating it from presence data, particularly at wider scales, remains a challenge. This challenge gains even greater importance for areas that have remarkably high biodiversity, as is the case of Caatinga, a Neotropical seasonally dry forests. We had available a database with information of more than 1 000 plant species of Caatinga collected since 2008 by University of Vale do São Francisco (UNIVASF). Yet, this database lacked information on species abundances. In **Chapter 2** we aimed at developing tools to transform species presence/absence data into estimations of species abundance. Specifically we followed the following steps: 1) develop and apply a re-sampling methodology to estimate species abundance from species presence/ absence data; 2) improve and evaluate abundance data reliability for further ecological interpretation, by focusing on sites with a minimum sampling effort and on plant species with a minimum number of occurrences along the study area; 3) compare the taxonomic diversity and composition of the databases obtained from the previous steps, including the proportion of endemism and exotic species, to evaluate their potential to support Caatinga's plant conservation strategies and studies on ecosystem structure and functioning.

Drylands are experiencing an overall increase in aridity that is predicted to intensify in the future due to climate change. This may cause changes in the structure and functioning of dryland ecosystems, affecting ecosystem services and human well-being. Therefore, detecting early signs of ecosystem change before irreversible damage takes place is important. In **Chapter 3** we used a space-for-time substitution approach to study the response of the plant community to aridity in a Tropical dry forest (Caatinga, Brazil), and infer potential consequences of climate. We addressed thirteen functional traits related to plant strategies to deal with water limitations. We hypothesized that aridity is a strong environmental filter acting on the functional structure of plant communities in this tropical dry forest. We expect to find i) an increase in the relative abundance of drought-adapted traits towards stress-avoidant strategies (e.g., summer deciduousness) and ii) a reduction in functional diversity for most traits as a result of climatic filtering.

To find tools to early detect the effects of increasing aridity on ecosystems is extremely urgent to avoid irreversible damage. In this context the use of plant functional groups (groups of species sharing the same traits) might have some interest. **In chapter 4**, we aim at identifying the Caatinga's main plant functional groups based on multiple traits and assess changes in functional groups abundance along a spatial gradient of aridity (aridity index between 0.27 and 0.69) in a tropical dry forest (Caatinga). Our objective was to assess changes in plant community functional structure along a spatial aridity gradient in tropical dry forest, by grouping plant species into functional groups base on multiple traits. The interpretation of the functional group's patterns along the aridity gradients could be used to track climate change impacts over time.

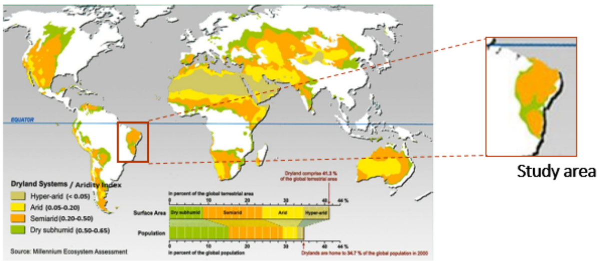
There are several biodiversity-based metrics to describe the ecosystem structure and functioning. Taxonomic diversity metrics provide strong evidence that diversity promotes ecosystem stability and functioning, contributing significantly to many ecosystem services. Even so, taxonomic metrics consider all species and individuals as equivalents disregarding e.g. their functional role and how they affect ecosystem functioning. The study of species functional traits allows to overcome this limitation, providing a more mechanistic link between species and multiple ecosystem functions. Additionally, functional redundancy can be used as a measure of detecting potential loss of species that carry out unique roles in important ecosystem processes as well as reorganization and renovation of the ecosystem after the disturbance, which can significantly affect and change ecosystem functioning. Due to the complementary character of these metrics, it is important to evaluate how they change along environmental gradients, and how can we interpret the observed patterns to better anticipate changes in the structure and functioning of the ecosystems to be studied over time. Thus, in **Chapter 5** we aim at assessing changes in plant taxonomic and functional diversity metrics along a spatial aridity gradient in the Caatinga ecosystem, assuming that these can give indications about climate change impacts over time. We hypothesized that complementary diversity metrics will respond differently to aridity in this tropical dry forest, namely that with increasing aridity we will find: (i) a decrease in species richness to only those highly adapted to drought; (ii) a decrease in functional diversity due to environmental filtering; (iii) an increase in functional redundancy between species sharing the same drought-adapted traits.

The thesis ends with a **General Discussion (Chapter 6)** considering the implications and opportunities these results have anticipating future impacts of climate change on drylands. In this chapter new perspectives on the potential of diversity metrics as universal indicators to monitor and track the responses of drylands to climate change are also pointed out and future challenges and research lines that can be drawn from this work are identified.

Chapter 1 – General Background

Why in drylands? → Drylands are experiencing climatic events of novel magnitudes that can cause a shif between alternative ecological regimes

Map of the World's drylands



Aridity can impact

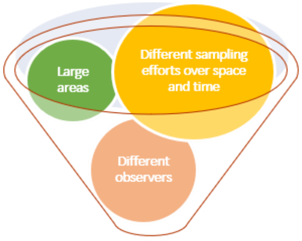
Processes

How identify potential ecological indicators as tools to monitor the effects of climate change in drylands?

Chapter 2 – Database and re-sampling methodology

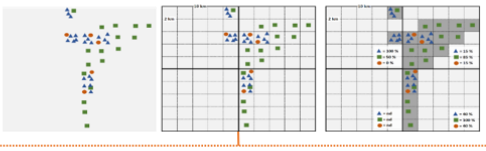
Why resample the data? → To estimate plant species abundances from species presence data.

Database collected over/by:



Raw database – 24.317 individuals
937 species
(with aquatic communities and undetermined species)

Re-sampling methodology



DB1 Database - 5.235 individuals
Without aquatic communities and undetermined species
(323 Sampling Units; 791 Species)

DB2 Database - 2.111 individuals
Without under sampled units
(38 Sampling Units; 532 Species)

DB 3 Database - 1.867 individuals
Without rare species
(113 Sampling Units; 48 Species)

Can support...

Conservation purposes

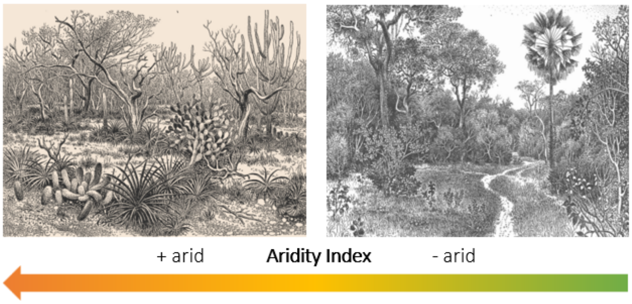
Understanding ecosystems structure and functioning

Re-sampling proved to be an importante tool for obtaining abundance data essential for the development of plant-based indicators of ecosystem structure and functioning.

Chapter 3 - Aridity as main environmental filter of the plant community functional structure

What is the impact of aridity on plants functional structure? → Changes in the structure and functioning of ecosystems, affecting ecosystem services and human well-being.

Increasing Aridity			
Functional Dispersion		**Community weighted mean**	
Vegetative Strategies			
Growth Form	ns	Shrub	🟠
Leaf phenology type	🟠	Evergreen	🟠
		Deciduous	🟢
Leaf thickness	🟠	Leaf thickness	🟠
Photosynthetic pathways	🟢	Crassulacean Acid Metabolism (CAM)	🟢
Reproductive Strategies			
Dispersal strategy	ns	Autochory	🟠
		Zoochory	🟢
Fruit type	🟢	Fleshy fruit	🟢
Defense Strategies			
Spinescence presence	🟢	Thorn/Acule	🟢
Chemical defense exudation	🟢	Latex/Resin	🟢
Positive (green circles), negative (orange circles) and no significance Spearman´s correlation. P-value: small circle (< 0.05); médium circle (< 0.01); large circle (0.001).			



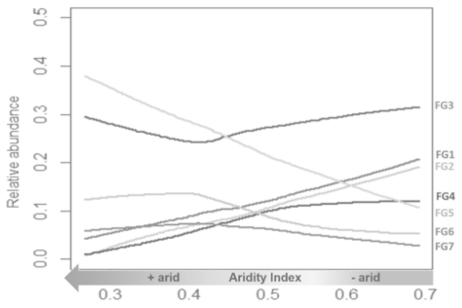
A future increase in aridity may affect the functional structure of tropical dry forests.

continue…

Chapter 4 - Functional groups as ecological indicators

Can functional groups be used as ecological indicators to track the effect aridity on the plant community?

Crucial to track the effect o aridity over time on ecosystems and to early warn us about ecological regime shifts.



FG3 - Deciduous trees with pivoting root but without chemical defense

FG1 - Shrub/Herb without leaves arrangende in a rosette and without CAM

FG5 - Trees with chemical defense

FG4 - Evergreen trees with pivoting root but without chemical defense

FG6 - CAM plants

FG2 -Trees with tuberous root without chemical defense

FG7 - Plants with leaves arranged in a rosette

● Increase arid

● Decrease arid

Functional Groups FG5 and FG6 were the best ones to be used over time to track the effect of aridity on the tropical dry forest.

Chapter 5 – Response of the taxonomic and functional metrics to aridity

How do diversity metrics change along an aridity gradient?

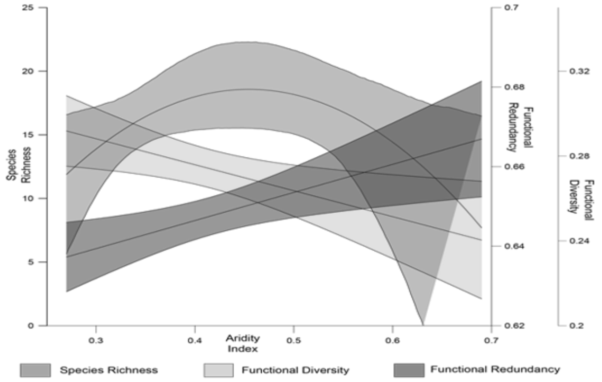
To assess the susceptibility of the plant community to climate, from a taxonomic and functional point of view.

More arid sites

- Higher functional diversity supported by a few plant species with unique functions
- Low resilience (lower functional redundancy among species

Less arid sites

- Lower functional diversity
- More resilicence (higher functional redundancy among species)



The complementary plant diversity metrics can be used as warning ecological indicators of climate change on the ecosystem.

Chapter 6 - General Discussion

Did diversity metrics prove effective for tracking of the effects of climate change?

Diversity metrics have proven to be essential tools to monitor the effects of climate change on Tropical dry forest.

Figure 1.6. Framework of the thesis.

References

Ab' Saber. NA (2003) Os domínios de natureza no Brasil: potencialidades paisagísticas. Ateliê Editorial, São Paulo,160p

Albuquerque UP, Araújo E de L, de Castro CC, Alves RRN (2018) People and natural resources in the Caatinga. In: Caatinga: The Largest Tropical Dry Forest Region in South America

Alvalá RCS, Cunha APMA, Brito SSB, et al (2017) Drought monitoring in the Brazilian Semiarid region. An Acad Bras Cienc 1–15. https://doi.org/http://dx.doi.org/10.1590/0001-3765201720170209

Andrade-Lima D (1981) The caatinga dominium. Rev Bras Botânica 149–153

Araújo EL, Silva KA, Ferraz EMN, et al (2005) Diversidade de herbáceas em microhabitats rochoso, plano e ciliar em uma área de caatinga, Caruaru, PE, Brasil. Acta Bot Brasilica. https://doi.org/10.1590/S0102-33062005000200011

Augustin NH, Mugglestone MA, Buckland ST (1998) The role of simulation in modelling spatially correlated data. Environmetrics. https://doi.org/10.1002/(SICI)1099-095X(199803/04)9:2<175::AID-ENV294>3.0.CO;2-2

Banda KR, Delgado-Salinas A, Dexter KG, et al (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. Science (80-). https://doi.org/10.1126/science.aaf5080

Barry SC, Welsh AH (2002) Generalized additive modelling and zero inflated count data. Ecol Modell. https://doi.org/10.1016/S0304-3800(02)00194-1

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Begon M, Townsend C, Harper JL (2007) Ecologia: de Indivíduos a Ecossistemas

Bellard C, Bertelsmeier C, Leadley P, et al (2012) Impacts of climate change on the future of biodiversity. Ecol. Lett.

Bellotto, A., Viani, R.A.G., Nave, A.G., Gandolfi, S. e Rodrigues, R.R. (2009) - Monitoramento das áreas restauradas como ferramenta para avaliação da efetividade das ações de restauração e para redefinição metodológica. In: Rodrigues, R.R.; Brancalion, P.H.S. e Isernhagen. (Orgs.) - Pacto pela restauração da mata atlântica: Referencial dos conceitos e ações de restauração florestal. LERF/ESALQ, Instituto BioAtlântica, São Paulo, p.132-150.

Berdugo M, Delgado-Baquerizo M, Soliveres S, et al (2020) Global ecosystem thresholds driven by aridity. Science (80-). https://doi.org/10.1126/science.aay5958

Block WM, Franklin AB, Ward JP, et al (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. Restor Ecol. https://doi.org/10.1046/j.1526-100X.2001.009003293.x

Blois JL, Williams JW, Fitzpatrick MC, et al (2013) Space can substitute for time in predicting climate-change effects on biodiversity. Proc Natl Acad Sci U S A 110:9374–9. https://doi.org/10.1073/pnas.1220228110

Bochet E, Poesen J, Rubio JL (2006) Runoff and soil loss under individual plants of a semi-arid Mediterranean shrubland: Influence of plant morphology and rainfall intensity. Earth Surf Process Landforms. https://doi.org/10.1002/esp.1351

Botta-Dukát Z (2005) Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Branquinho C, Serrano HC, Nunes A, et al (2019) Essential biodiversity change indicators for evaluating the effects of Anthropocene in ecosystems at a global scale. In Casetta, E., Marques da Silva, J. & Vechhi, D. (eds) From Assessing to Conservating Biodiversity. History, Philosophy and Theory of the Life Sciences, vol 24. Springer, Cham.

Branquinho, C., Matos, P., Pinho, P. Lichens as ecological indicators to track atmospheric changes: future challenges. In: Lindenmayer, D.; Barton, P.; Pierson, J. (Eds.). Indicators and surrogates of biodiversity and environmental change. Australian Copyright, 2015. p. 77-90. ISBN 978-1-4987-4870-4

Brower, J.E.; Zarr, J.H. 1984. Field and laboratory methods for general ecology. W. C. Brown Publishers, Dubuque, Iowa, USA. 226 pp

Buriti CO, Barbosa HA (2018) Um século de secas: por que as políticas hídricas não transformaram o semiárido brasileiro?

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol.

Canadell, JG, Pataki, DE, Pitelka, LF (eds) (2007) Terrestrial Ecosystems in a Changing World. Berlin Heidelberg: Springer-Verlag.

Canhos, D.A.L.; Souza, S.; Canhos, V.P. (2006). Coleções biológicas e sistemas de informação. (disponível em http://www.dpi.inpe.br/referata/arq/12_candinha/ pdf)

Cardinale BJ, Duffy JE, Gonzalez A, et al (2012) Biodiversity loss and its impact on humanity. Nature

Carpenter SR, Mooney HA, Agard J, Capistrano D, et al (2009) Science for Managing Ecosystem Services: Beyond the Millennium Ecosystem Assessment. Proc Natl Acad Sci U S A https://doi.org/10.1073/pnas.0808772106

Cianciaruso M V., Batalha MA, Gaston KJ, Petchey OL (2009) Including intraspecific variability in functional diversity. Ecology. https://doi.org/10.1890/07-1864.1

Conlisk E, Conlisk J, Enquist B, et al (2009) Improved abundance prediction from presence-absence data. Glob Ecol Biogeogr 18:1–10. https://doi.org/10.1111/j.1466-8238.2008.00427.x

Cornelissen JHC, Lavorel S, Garnier E, et al (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot.

Da Costa GM, Cardoso D, De Queiroz LP, Conceição AA (2015) Variações locais na riqueza florística em duas ecorregiões de caatinga. Rodriguesia. https://doi.org/10.1590/2175-7860201566303

da Silva JMC, Barbosa LCF (2018) Impact of human activities on the Caatinga. In: Caatinga: The Largest Tropical Dry Forest Region in South America

da Silva JMC, Leal IR, Tabarelli M (2018) Caatinga: The largest tropical dry forest region in South America

Dai A (2011) Drought under global warming: A review. Wiley Interdiscip. Rev. Clim. Chang.

Dakos V, Matthews B, Hendry AP, et al (2019) Ecosystem tipping points in an evolving world. Nat Ecol Evol. https://doi.org/10.1038/s41559-019-0797-2

Damgaard C, Strandberg M, Kjær C, Sørensen PB (2019) Use “risk of system failure” rather than additive aggregation methods of indicators when assessing habitat quality. Ecol Indic. https://doi.org/10.1016/j.ecolind.2019.105564

De Bello F, Lepš J, Lavorel S, Moretti M (2007) Importance of species abundance for assessment of trait composition: An example based on pollinator communities. Community Ecol. https://doi.org/10.1556/ComEc.8.2007.2.3

Dias ATC, Berg MP, de Bello F, et al (2013) An experimental framework to identify community functional components driving ecosystem processes and services delivery. J Ecol. https://doi.org/10.1111/1365-2745.12024

EPA-SAB, 2002 Environmental Protection Agency–Science Advisory Board, 2002. A Framework for Assessing and Reporting on Ecological Condition: An SAB Report. EPA-SAB-EPEC-02-009, EPA Science Advisory Board, Washington, D.C.

FAO (2019) The State of Food and Agriculture 2019. Moving forward on food loss and waste reduction. Rome. Licence: CC BY-NC-SA 3.0 IGO

Feng S, Fu Q (2013) Expansion of global drylands under a warming climate. Atmos Chem Phys. https://doi.org/10.5194/acp-13-10081-2013

Fernandes MF, Cardoso D, de Queiroz LP (2020) An updated plant checklist of the Brazilian Caatinga seasonally dry forests and woodlands reveals high species richness and endemism. J Arid Environ. https://doi.org/10.1016/j.jaridenv.2019.104079

Fernandes MF, Queiroz LP de (2018) Vegetação e flora da Caatinga. Cienc Cult 70:51–56

Fleming RJ (2020) The Rise and Fall of the Carbon Dioxide Theory of Climate Change

Gaston KJ (1996) Biodiversity. A Biology of Numbers and Difference. In: Blackwell Science

Gaston KJ, Blackburn TM, Lawton JH (1998) Aggregation and interspecific abundance-occupancy relationships. J Anim Ecol. https://doi.org/10.1046/j.1365-2656.1998.6760995.x

Gerrard DJ, Chaing HC (1970) Density Estimation of Corn Rootworm Egg Populations Based upon Frequency of Occurrence. Ecology 51:237–245. https://doi.org/10.2307/1933659

Giulietti AM, Harley RM, Queiroz LP de, et al (2002) Plantas endêmicas da Caatinga. In: Sampaio EVSB, Giulietti AM, Virgõnio J, Gamarra-Rojas CFL (eds) Vegetação e flora das caatingas. APNE / CNIP, Recife, PE., pp 103–115

Gleason HA (1920) Some Applications of the Quadrat Method. Bull Torrey Bot Club 47:21–33. https://doi.org/10.2307/2480223

Gosz JR (1992) Gradient Analysis of Ecological Change in Time and Space: Implications for Forest Management. Ecol Appl 2:248–261. https://doi.org/10.2307/1941859

Grime JP (1998) Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. J. Ecol.

Gross N, Börger L, Soriano-Morales SI, et al (2013) Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. J Ecol 101:637–649. https://doi.org/10.1111/1365-2745.12063

Guimarães Filho, C.; Góes, J. G. "Desempenho reprodutivo de caprinos na Caatinga sob diferentes taxas de lotação". *Pesquisa Agropecuária Brasileira* 1998, 23:309-314.

Guisan A, Kienast F (1998) Predicting the potential distribution of plant species in an Alpine environment. J Veg Sci

Hauff SN (2010) Representatividade do Sistema Nacional de Unidades de Conservação na Caatinga. Programa Das Nações Unidas Para O Desenvolv

He, Gaston (2000) Estimating Species Abundance from Occurrence. Am Nat 156:553–559. https://doi.org/10.2307/3079057

Heink U, Kowarik I (2010) What are indicators? On the definition of indicators in ecology and environmental planning. Ecol Indic. https://doi.org/10.1016/j.ecolind.2009.09.009

Hemming, J. (1978). Red gold. The conquest oj the Brazilian Indians. Cambridge, Harvard University Press.

Hooper DU, Chapin FS, Ewel JJ, et al (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr. https://doi.org/10.1890/04-0922

Huang J, Yu H, Guan X, et al (2016) Accelerated dryland expansion under climate change. Nat Clim Chang. https://doi.org/10.1038/nclimate2837

Hwang WH, He F (2011) Estimating abundance from presence/absence maps. Methods Ecol Evol. https://doi.org/10.1111/j.2041-210X.2011.00105.x

IPCC (2019) IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse gas fluxes in Terrestrial Ecosystems

IPCC (2014) Climate Change 2014

IPCC (2011) Summary for Policymakers. In: IPCC Special Report on Renewable Energy Sources and Climate Change Mitigation. In: Cambridge University Press

Joseph LN, Field SA, Wilcox C, Possingham HP (2006) Presence-absence versus abundance data for monitoring threatened species. Conserv Biol 20:1679–1687. https://doi.org/10.1111/j.1523-1739.2006.00529.x

Karl TR, Trenberth KE (2003) Modern Global C(1) Karl, T. R.; Trenberth, K. E. Modern Global Climate Change; 2003; Vol. 302.limate Change

Koch NM, Branquinho C, Matos P, et al (2016) The application of lichens as ecological surrogates of air pollution in the subtropics: a case study in South Brazil. Environ Sci Pollut Res. https://doi.org/10.1007/s11356-016-7256-2

Koutroulis AG (2019) Dryland changes under different levels of global warming. Sci Total Environ 655:482–511. https://doi.org/10.1016/J.SCITOTENV.2018.11.215

Kunin WE (1998) Extrapolating species abundance across spatial scales. Science (80-). https://doi.org/10.1126/science.281.5382.1513

Laliberte E, Legendre P (2010) ALaliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91(1), 299–305. http://doi.org/10.1890/08-2244.1 distance-based framework for measuring functional diversity from multiple . Ecology. https://doi.org/10.1890/08-2244.1

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct. Ecol.

Lavorel S, Grigulis K, McIntyre S, et al (2008) Assessing functional diversity in the field - Methodology matters! Funct. Ecol.

Lawton JH, Brown VK (1994) Redundancy in Ecosystems. In: Biodiversity and Ecosystem Function

Rodrigues, R.R.; Gandolfi, S. Conceitos, tendências e ações para recuperação de florestas ciliares. In: Rodrigues, R.R.; Leitão Filho, H.F. (Eds.). Matas ciliares: conservação e recuperação. 2 ed. São Paulo: EDUSP/FAPESP, 2001. p. 235-248.

Maestre FT, Quero JL, Gotelli NJ, et al (2012) Plant species richness and ecosystem multifunctionality in global drylands. Science (80-). https://doi.org/10.1126/science.1215442

Magrin GO, Marengo JA, Boulanger J-P, et al (2014) Central and South America. In: Barros VR, Field CB, Dokken DJ, et al. (eds) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovenmetal Panel on Climate

Change. Cambridge University Press, Cambridge, United Kingdon and New York, NY, USA, pp 1499–1566

Magurran AE (2004) Measuring of Biological Diversity

Manoliadis OG (2002) Development of ecological indicators - A methodological framework using compromise programming. In: Ecological Indicators

Marengo Orsini JA, Alves LM, Alvala RCS, et al (2018) Climatic characteristics of the 2010-2016 drought in the semiarid northeast Brazil region. An Acad Bras Cienc. https://doi.org/10.1590/0001-3765201720170206

Matos P, Geiser L, Hardman A, et al (2017) Tracking global change using lichen diversity: towards a global-scale ecological indicator. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.12712

Melo FPL (2018) The socio-ecology of the Caatinga: Understanding how natural resource use shapes an ecosystem. In: Caatinga: The Largest Tropical Dry Forest Region in South America

MMA M do MA (2016) Unidades de Conservação por Bioma (CNUC/MMA, Brasília-DF, Brasil). www.mma.gov.br/images/arquivo/80112/CNUC PorBiomaFev16.pdf.

Mooney H, Larigauderie A, Cesario M, et al (2009) Biodiversity, climate change, and ecosystem services. Curr. Opin. Environ. Sustain.

Moro MF, Lughadha EN, Filer DL, et al (2014) A catalogue of the vascular plants of the Caatinga Phytogeographical Domain: A synthesis of floristic and phytosociological surveys. Phytotaxa. https://doi.org/10.11646/phytotaxa.160.1.1

Moro MF, Nic Lughadha E, de Araújo FS, Martins FR (2016) A Phytogeographical Metaanalysis of the Semiarid Caatinga Domain in Brazil. Bot Rev. https://doi.org/10.1007/s12229-016-9164-z

Mouchet, M.A., Villéger, S, Mason, N.W.H., et al (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24:867-876. doi: 10.1111/j.1365-2435.2010.01695.x

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. PLoS One. https://doi.org/10.1371/journal.pone.0017476

Nielsen SE, Johnson CJ, Heard DC, Boyce MS (2005) Can models of presence-absence be used to scale abundance? Two case studies considering extremes in life history. Ecography (Cop) 28:197–208. https://doi.org/10.1111/j.0906-7590.2005.04002.x

Nunes A, Köbel M, Pinho P, et al (2017) Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. Agric For Meteorol. https://doi.org/10.1016/j.agrformet.2017.03.007

Paganucci de Queiroz L (2006) The Brazilian Caatinga: Phytogeographica patterns inferred from distribution data of the Leguminosae

Pearce JL, Boyce MS (2006) Modelling distribution and abundance with presence-only data. J Appl Ecol 43:405–412. https://doi.org/10.1111/j.1365-2664.2005.01112.x

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. Annu Rev Ecol Evol Syst. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Peñuelas J, Sardans J, Estiarte M, et al (2013) Evidence of current impact of climate change on life: A walk from genes to the biosphere. Glob. Chang. Biol.

Pereira HM, Ferrier S, Walters M, et al (2013) Essential biodiversity variables. Science (80-.).

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2016) Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot. https://doi.org/10.1071/bt12225_co

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot. https://doi.org/10.1071/BT12225

Petchey OL, Gaston KJ (2006) Functional diversity: Back to basics and looking forward. Ecol. Lett.

Pickett STA (1989) Space-for-Time Substitution as an Alternative to Long-Term Studies. In: Long-Term Studies in Ecology. Springer New York, New York, NY, pp 110–135

Pillar VD, Blanco CC, Müller SC, et al (2013) Functional redundancy and stability in plant communities. J Veg Sci. https://doi.org/10.1111/jvs.12047

Pinho BX, Tabarelli M, Engelbrecht BMJ, et al (2019) Plant functional assembly is mediated by rainfall and soil conditions in a seasonally dry tropical forest. Basic Appl Ecol. https://doi.org/10.1016/j.baae.2019.08.002

Prado DE (2003) As caatingas da América do Sul. In: Ecologia e Conservação da

Caatinga

Puntoni, P. A Guerra dos Bárbaros. Povos e a colonização do sertão nordeste do Brasil, 1650-1720. São Paulo: Hucitec/USP/ FAPESP, 2002.

Ramos M.A., Cavalcanti M.C.B.T. & Vieira F.J. (2014) Recursos madeireiros (p. 105–113). In: Albuquerque U.P. (Org.). Introdução a Etnobiologia. Recife: NUPEEA. 189 p.

Reynolds JF, Maestre FT, Kemp PR, et al (2007) Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences. In: Terrestrial Ecosystems in a Changing World

Ribeiro-Neto JD, Arnan X, Tabarelli M, Leal IR (2016) Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. Biodivers Conserv. https://doi.org/10.1007/s10531-016-1099-5

Ribeiro EMS, Lohbeck M, Santos BA, et al (2019) Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J Ecol. https://doi.org/10.1111/1365-2745.13177

Ricotta C (2005) Through the jungle of biological diversity. Acta Biotheor.

Rizzini CM (1997) Prefácio da 2ª Edição. In: Tratade De Fitogeografia Do Brasil: Aspectos ecológicos; sociológicos e florísticos

Rizzini, C.T. 1979. Tratado de Fitogeografia do Brasil: aspectos sociológicos e florísticos. HUCITEC/ USP, São Paulo.

Rodal MJN, Martins FR, Sampaio EV de SB (2008) Levantamento quantitativo das plantas lenhosas em trechos de vegetação de caatinga em Pernambuco. Rev Caatinga 21:192–205

Rodrigues RR, Gandolfi S, Nave AG, et al (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. For Ecol Manage. https://doi.org/10.1016/j.foreco.2010.07.005

Safriel U, Adeel Z, Niemeijer D, et al (2005) Chapter 22: Dryland Systems

Santos JC, Leal IR, Almeida-Cortez JS, et al (2011) Caatinga: The scientific negligence experienced by a dry tropical forest. Trop Conserv Sci. https://doi.org/10.1177/194008291100400306

Sasaki T, Okubo S, Okayasu T, et al (2009) Two-phase functional redundancy in plant communities along a grazing gradient in Mongolian rangelands. Ecology. https://doi.org/10.1890/08-1850.1

Scheffer M, Bascompte J, Brock WA, et al (2009) Early-warning signals for critical transitions. Nature

Scheffer M, Carpenter S, Foley J, et al (2001) Catastrophic shifts in ecosystems RID F-2386-2011. Nature. https://doi.org/10.1038/35098000

Sfair JC, De Bello F, De Frana TQ, et al (2018) Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. Environ Res Lett. https://doi.org/10.1088/1748-9326/aa9f5e

Silva AC, Souza AF (2018) Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. PLoS One. https://doi.org/10.1371/journal.pone.0196130

Soranno PA, Bissell EG, Cheruvelil KS, et al (2015) Building a multi-scaled geospatial temporal ecology database from disparate data sources: Fostering open science and data reuse. Gigascience

Sousa-Silva R, Verbist B, Lomba Â, et al (2018) Adapting forest management to climate change in Europe: Linking perceptions to adaptive responses. For Policy Econ. https://doi.org/10.1016/j.forpol.2018.01.004

Suding KN, Lavorel S, Chapin FS, et al (2008) Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Glob Chang Biol. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Swenson NG, Weiser MD (2010) Plant geography upon the basis of functional traits: An example from eastern North American trees. Ecology. https://doi.org/10.1890/09-1743.1

Thornthwaite CW (1948) An Approach toward a Rational Classification of Climate. Geogr Rev. https://doi.org/10.2307/210739

Van Straalen NM (1998) Evaluation of bioindicator systems derived from soil arthropod communities. Appl Soil Ecol. https://doi.org/10.1016/S0929-1393(98)00101-2

Varela Z, López-Sánchez G, Yáñez M, et al (2018) Changes in epiphytic lichen diversity are associated with air particulate matter levels: The case study of urban areas in Chile. Ecol Indic. https://doi.org/10.1016/j.ecolind.2018.04.023

Vidiella B, Sardanyés J, Sole R (2018) Exploiting delayed transitions to sustain semiarid ecosystems after catastrophic shifts. J R Soc Interface. https://doi.org/10.1098/rsif.2018.0083

Violle C, Navas ML, Vile D, et al (2007) Let the concept of trait be functional! Oikos

Walker BH (1992) Biodiversity and Ecological Redundancy. Conserv Biol. https://doi.org/10.1046/j.1523-1739.1992.610018.x

Walz R (2000) Development of environmental indicator systems: Experiences from Germany. Environ Manage. https://doi.org/10.1007/s002670010048

Welsh AH, Cunningham RB, Donnelly CF, Lindenmayer DB (1996) Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecol Modell. https://doi.org/10.1016/0304-3800(95)00113-1

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr. https://doi.org/10.2307/1948435

Zuazo VHD, Pleguezuelo CRR (2009) Soil-erosion and runoff prevention by plant covers: A review. In: Sustainable Agriculture

Chapter 2

From species presences to abundances: using unevenly collected plant species presences to disclose the structure and functioning of a dryland ecosystem

Oliveira, A.C.P., Nunes, A., Pinho, P., Matos, P., Rodrigues, R.G. & Branquinho, C. (2020) From species presences to abundances: using unevenly collected plant species presences to disclose the structure and functioning of a dryland ecosystem. *Ecological Indicators*, 113, 106221.

2 From species presences to abundances: using unevenly collected plant species presences to disclose the structure and functioning of a dryland ecosystem

2.1 Abstract

Species abundance data is essential to understand ecosystems structure and functioning and to support species and habitat conservation. However, most regional to global databases provide only presence or presence/absence data. The main aim of this paper is to develop a methodology to estimate plant species abundances from a presence/absence database using as a case-study the largest and one of the most diverse tropical dry forest of the world – the understudied, Caatinga vegetation, that dominates in the drylands of Brazil. Plant data missed abundance estimations and derived from different sources, with uneven sampling efforts over space and time. Starting from the raw data, we considered only the presence records of terrestrial plant individuals identified to the species-level. Afterwards, we applied the re-sampling method to estimate species abundances thus obtaining database DB1. To deal with the uneven sampling effort along the study area and increase information reliability, we filtered DB1 in two ways: (i) we excluded re-sampling units with a lower sampling effort and produced the Database DB2; (ii) we excluded low occurrence species and build - Database DB3. The reliability of the databases was compared by calculating a measure of their completeness. DB1 had 789 species over 323 sampling units, DB2 retained 530 species distributed in 38 sampling units, and DB3 retained 48 species over 113 sampling units. In DB1 and DB2, despite the different number of species considered, the percentage of exotic (7%), endemism (14%), woody (44%), climber (12%), and herbaceous species (45%) was similar. DB3 included only native species (no exotic species) and displayed a higher percentage of endemism (29%) and woody species (79%), and a lower proportion of herbaceous species (21%) than DB1 and DB2. The databases obtained provide an important basis to improve Caatinga ecological knowledge and conservation: we suggest the use of DB2 to support conservation strategies, and of DB3 to support ecosystem structure and functioning studies. Moreover, the re-sampling methodology proposed to estimate plant abundances from presence data, dealing with uneven sampling efforts across large areas and over time, provides an important tool that may be used to obtain abundance data, often essential to the development of plant-based indicators of ecosystem structure and functioning, and to support conservation studies.

Keywords: Caatinga; Conservation; Ecosystem functioning; Regional plant database; Re-sampling; Uneven sampling effort.

2.2 Introduction

As more biodiversity-databases are available, the more we need to have tools to make most of them, in terms of conservation and ecosystem functioning. These datasets hold a lot of precious knowledge (Soranno et al. 2015) that needs to be worked out for different specific aims, to address the main societal challenges, from species conservation to ecosystem services provisioning. To evaluate trends in biodiversity change, species abundance is required (Mouillot et al. 2011; Maestre et al. 2012). Yet, for large datasets, species abundance data is often not available. For instance, the Global Biodiversity Information Facility (GBIF), which is a reference database in biological research has mainly occurrence data for a vast number of species. Thus, estimating abundance from presence-absence data is a crucial step to track biodiversity changes (Gleason, 1920; Conlisk et al. 2009) especially in the face of Earth global change (Cadotte et al. 2011).

Several methods toward this end were developed, such as (i) regression approaches, using a truncated Poisson or negative binominal distribution (Augustin et al. 1998; He & Gaston 2000; Pearce & Boyce 2006; Conlisk et al. 2009; Hwang & He 2011), (ii) methods based on the number of occupied cells of a rectangular grid (Gerrard & Chaing 1970; Kunin 1998; Joseph et al. 2006), (iii) the zero-inflated count model (Barry & Welsh 2002), and (iv) model count data, where a first model is fitted to account for occurrence, and then a second model follows to show abundance once presence is predicted (Welsh et al. 1996; Guisan & Kienast 1998). However, these methods have limitations. Most of them require knowledge on the average area occupied per individual of a species, but this information is rarely available and/or brings additional challenges. For instance, two species having the same total area of occupancy (i.e. number of occupied cells) can have different abundances (i.e. the number of individuals per area) (Gaston 1996; Gaston et al. 1998; Kunin 1998). Count data are difficult and expensive to collect in the case of techniques that deal with overdispersion as zero-inflated count model and models count data (Nielsen et al. 2005). Hence, estimating species abundances from presence data, particularly at wider scales, remains a challenge.

This challenge gains even greater importance for areas that have remarkably high biodiversity, as is the case of Neotropical seasonally dry forests. In these regions, limited by water availability, more than 4 600 species of woody plants have already been recorded together with a high number of endemic species and high floristic turnover (i.e. beta-diversity) (Banda et al. 2016). Additionally, several works have been arguing that 80% of the relative abundance of a community, usually the most abundant species, are able to capture the main effects of environmental drivers on key ecosystem processes, following the mass ratio hypothesis (Grime 1998; Lavorel & Garnier 2002; Hooper et al. 2005). Understanding the relation between environmental drivers and key ecosystem processes is essential in Neotropical seasonally dry forests because they (i) are among the most threatened tropical dry forest in the world (Miles et al. 2006); (ii) are highly fragmented with less than 10% of its original extent remaining in many countries (García Millán et al. 2014; Banda et al. 2016), (iii) have a population highly dependent on resources associated with its biodiversity, and (iv) suffer from the lack of scientific knowledge and public policies able the ensure a sustainable development in the region (IPCC 2011, 2014; Santos et al. 2011).

Caatinga is one of the most plant diverse of the Neotropical seasonally dry forest (Pennington et al. 2009; Portillo-Quintero & Sánchez-Azofeifa 2010; Banda et al., 2016) with more than 1 112 plant species (Banda et al., 2016) of which ca. 30% are endemic (Giulietti et al. 2002). This semi-arid ecosystem with peculiar flora within Neotropical seasonally dry forest is the most vulnerable one to climate change in Brazil (Sarmiento 1975; da Silva et al. 2018). In 2100 in Caatinga, temperature is expected to increase between 4ºC to 18ºC (IPCC, 2011), and rainfall is predicted to be reduced in 22% (Magrin et al. 2014) to 40% (Buriti & Barbosa 2018). Climate change together with anthropogenic activities may lead to a decrease in productivity in these ecosystems aggravating further land degradation. Furthermore, these factors can speed up the desertification process taking place in this ecosystem, which already affects more than 60% of the areas susceptible to desertification in Brazil (da Silva & Barbosa 2018). This will result in the loss of forest products (e.g., wood and forage) and ecosystem services (e.g., nutrient cycling, protection and restoration of soil fertility) that may affect 28.6 million people highly dependent on local natural resources

(Tabarelli et al. 2017). Taking into account the threats that this unique ecosystem faces in the near future, it is urgent to better understand Caatinga´s ecosystem structure and functioning, as an essential basis to develop strategies and policies for its conservation and restoration. For Caatinga, a database with information on about 1 000 plant species was collected since 2008 by *University of Vale do São Francisco* (UNIVASF) (data not published). Yet, this database is limited to species presence/absence data, lacking information on species abundances. Additionally, this database resulted from data derived from different sources, collected with different sampling methodologies and sampling efforts in space and over time.Thus, we need to develop tools to work out this data and transform species presence/absence data into estimations of species abundance, to support Caatinga's plant diversity conservation that needs to be put in place urgently, together with knowledge about its ecosystem structure and function. In this context, we make use of Caatinga's plant database to meet the following objectives: 1) develop and apply a re-sampling methodology to estimate species abundance from species presence/absence data; 2) improve and evaluate abundance data reliability for further ecological interpretation, by focusing on sites with a minimum sampling effort (minimum number of plant species recorded) and on plant species with a minimum number of occurrences along the study area; 3) compare the taxonomic diversity and composition of the databases obtained from the previous steps, including the proportion of endemism and exotic species, to evaluate their potential to support Caatinga´s plant conservation strategies and studies on ecosystem structure and functioning.

2.3 Methods

Study area

This study was carried out in Caatinga, a semi-arid seasonally dry tropical forest of Brazil. It covered a spatial area with 700 Km including four Brazilian states (Ceará, Paraíba, Pernambuco and Rio Grande do Norte) **(Figure 2.1).**

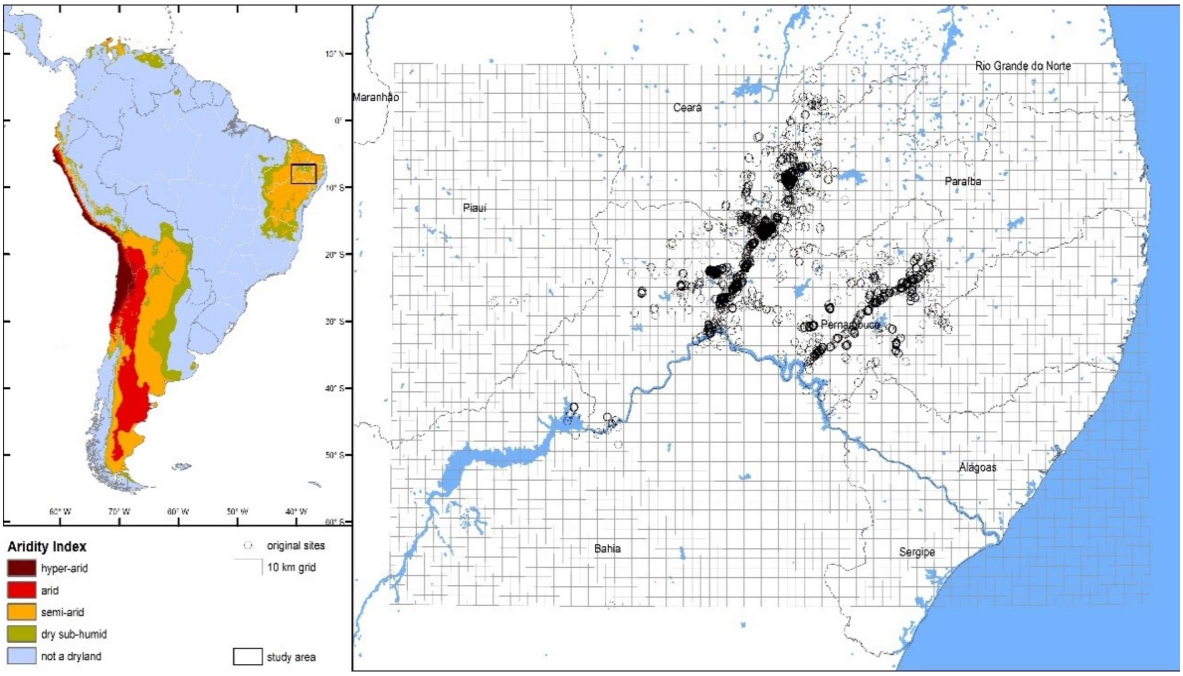


Figure 2.1. A) Location of the area in north-eastern Brazil surveyed by Centre for Ecology and Environmental Monitoring (NEMA), based at the University of Vale do São Francisco (Univasf), Petrolina, Pernambuco, Brazil (see legend colours for different aridity levels); B) Grid of 10 x 10 Km sampling units superimposed over the sampling sites (open dots) surveyed by NEMA.

Raw database description

The raw database used in the present study comes from a series of plant surveys led by the Centre for Ecology and Environmental Monitoring (NEMA) based at the University of Vale do São Francisco (UNIVASF), Petrolina, Pernambuco, Brazil. NEMA, under the impact assessment study of the São Francisco River Integration Project (PISF), is responsible for two environmental programs in the Caatinga ecosystem region: i) the conservation of flora and, ii) the restoration of degraded areas. In this sense, UNIVASF has been collecting information about Caatinga vegetation since 2008. This information comprises georeferenced individuals´ presence for aquatic and terrestrial flora, totalizing 24 317 individuals surveyed to date. The information is collected following a sampling scheme of 0,2° x 0,2° virtual grid squares corresponding to 22 x 22 Km squares, ensuring that all squares are visited **(Figure 2.1A)**. From all the data collected by UNIVASF, for this paper, we used the information collected in three different surveys. **Survey A) Presence of plant species from 2008-2012**. This survey followed a floristic inventory methodology, comprising 212 field expeditions with visits five times per week, 6-8h per day, walking randomly within the systematically defined grid squares described previously, in an area from 1 400 to 1 900 Km per week to register the presence of all woody and herbaceous plant species and record their GPS location. This survey represented ca. 82% of data collected by NEMA until 2012 (more information in Siqueira Filho, 2012); **Survey B) Presence of new plant species from 2012-2015.** The sampling methodology was like the formerly described, but here only new species that were not previously recorded within each grid squares were registered using the same method. This survey represented ca. 18% of the data collected for this paper; **Survey C) Abundance of plant species.** This survey was done in 135 permanent plots of 10 x 10 m located within the 22 x 22 Km grid squares. The abundance monitoring survey was done twice per year from January 2008 to July 2015, and all individuals were recorded and, species abundance estimated. However, in this case, contrary to what happened in the previous surveys, only shrub and tree species (woody species) were recorded.

Estimating plant abundance from presence/absence data

From the raw database, we excluded all the species classified as aquatic and semi-aquatic, since the focus of this paper was terrestrial plant diversity. The plant individuals not identified to the species-level were also excluded. This selection resulted in the first database called DB1, which only accounts for species presences.

Afterwards, a re-sampling methodology was applied to the DB1 database. This re-sampling methodology was intended to deal with possible problems resulting from data derived from different sources, with different sampling intensities over space and mostly missing abundance. To re-sample, a sampling unit of 10 x 10 Km **(Figure 2.2)** divided into 25 sampling quadrats of 2 x 2 Km side was superimposed on the study region. For each 10 Km sampling unit we calculated species abundance, using the presence of the species in the 25 2 x 2 Km sampling quadrats, weighted by the sampling effort within that sampling unit. For that, the following steps were taken.

Species presence in each small quadrat (2 x 2 Km) were considered as frequency. If a species was recorded more than once in a small sampling quadrat (2 x 2 Km), it counted only once. The sum of all frequencies of the 25 2 x 2 Km sampling quadrats in the larger 10 x 10 Km sampling unit corresponded to species abundance. Hence, the maximum abundance that a species can have within 10 x 10 Km sampling units is 25, if that species was present in all quadrats visited. We assumed that if in a sampling quadrat (2 x 2 Km), at least one species was registered, then all species were searched for in that quadrat. Thus, if a species was not registered in a sampling quadrat, then that species was considered absent, and thus with an abundance of zero. This assumption is reasonable because fieldwork was done through systematic visits to the region, assuring that all sampling quadrats were visited **(Figure 2.2).**

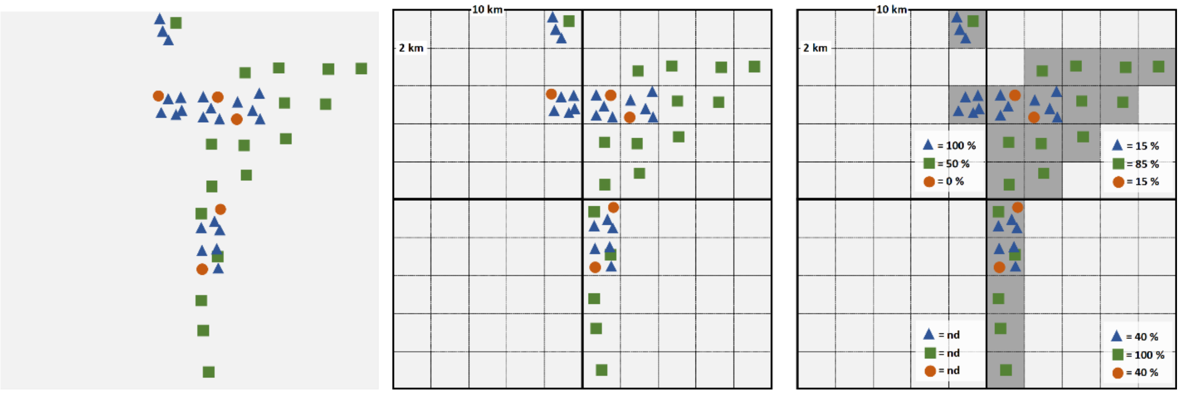


Figure 2.2. Re-sampling example. Left: the three coloured shapes represent species presences registered in a sampling region in grey; Centre: the 2 Km squares represent the sampling quadrats and the 10 Km squares the sampling units; Right: the grey represent the sampled quadrats, the number of quadrats occupied by each species within each sampling unit divided by the number of sampled quadrats represents species abundance, which is provided in percentage (%).

Improving abundance data reliability

As a measure of quality control, DB1 species richness was calculated for each sampling unit (data not shown). We found a strong positive correlation (Spearman correlation) between species richness and the number of sampling quadrats sampled (p-value < 0.001; data not shown).

To reduce the level of “uncertainty” in DB1 and consequently high the level of “completeness” due to unbalanced sampling efforts between sampling units, two databases were created from DB1. This was done, to i) ensure a minimum number of species per sampling unit, by removing under-sampled units (DB2); and ii) retain only species present in a minimum number of sampling units, removing rare species (DB3) **(see Figure 2.3).** DB2 was called “without undersampled sites” and resulted from the exclusion of sampling units (10 x 10 Km) with less than 35 species recorded. This threshold corresponded to the median value of species richness in DB1. DB3 was called “without rare species” and resulted from the exclusion of species with a very low occurrence, recorded in less than 5% of DB1 sampling units.

To assess the “reliability” of the database produced, we calculated a measure of sampling completeness for each one of the databases, to account for the uneven sampling effort between sampling units. This completeness measure corresponds to the number of quadrats visited divided by 25 (the maximum number of sampling quadrats within each sampling unit) and was mapped for all databases **(Figure 2.3).** The higher the number of quadrats sampled within each sampling unit, the higher its completeness.

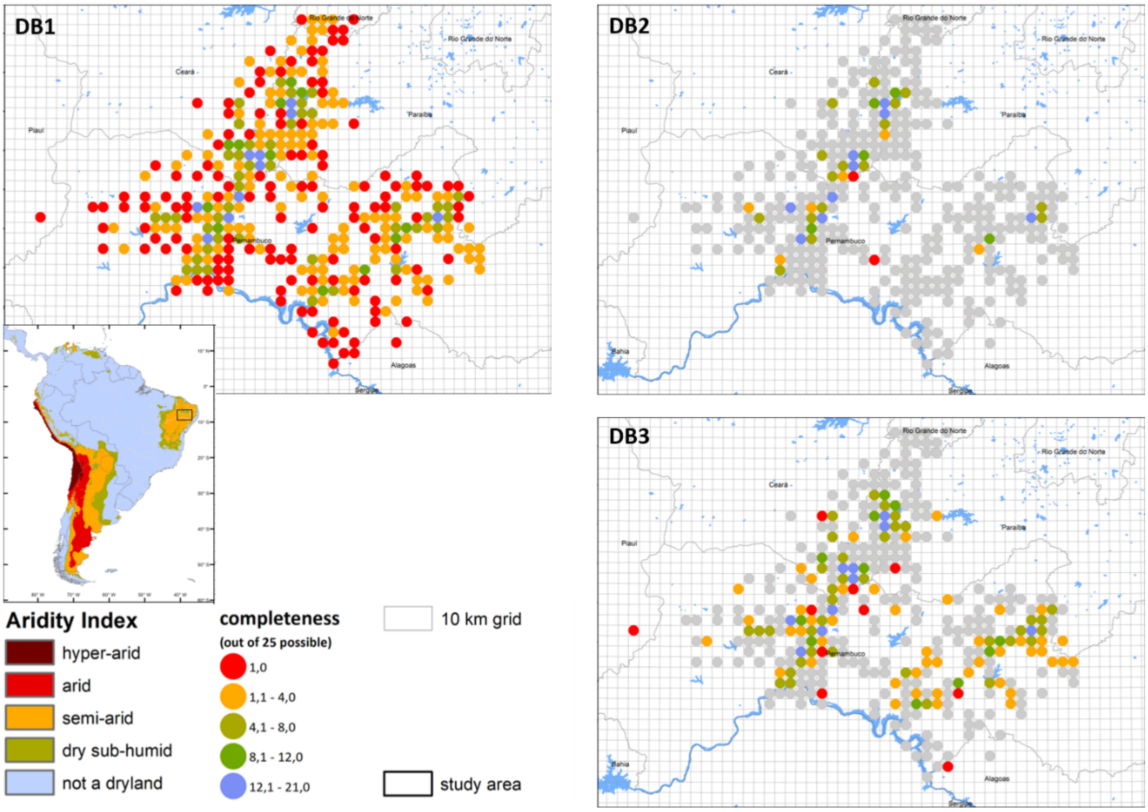


Figure 2.3. Map showing sampling completeness of DB1, DB2 and DB3. Sampling completeness corresponds to the number of sampling quadrats (2 x 2 km) visited per sampling unit (10 x 10 Km) out of the total number of possible quadrats (25). This information was superimposed to the sampling sites belonging to each database.

Data analysis

For each of the three databases, we compared the taxonomic diversity and composition to (i) understand the effects of excluding data from sampling sites or rare species and (ii) describe the potential of the abundance data of DB2 and DB3 for studying Caatinga ecosystem structure and functioning. For that, we calculated species richness, beta diversity and the partition of composition dissimilarity (beta diversity) into species turnover and nestedness (Baselga 2010). To calculate the partition of composition dissimilarity we used the method developed by Baselga and co-authors (2010, 2012). This method proposes that global beta diversity (βsor), calculated using the *Sorensen Index* (Sørensen 1948), can be mathematically decomposed into the dissimilarity index of Simpson – βsim and nestedness – βnes. The first represents the spatial substitution of species (turnover), and nestedness a new index of dissimilarity resulting from the sequential loss of species between samples. This was done using the “beta.multi-function” of the betapart package (Baselga et al. 2018) in R (R Core Team 2018).

In addition, we calculated the proportion of endemism, exotic species, species from the Fabaceae family and the community structure. Fabaceae was highlighted because of its importance to the functioning ecosystems by symbiotic nitrogen fixation (Dovrat & Sheffer 2019; Jaiswal & Dakora 2019). Community structure was here assessed as a proportion of each growth form in each database: trees, shrubs, climber and herbaceous species. These proportions correspond to the ratio of the number of species in each case divided by total species richness. Categorization into exotic species, endemism and growth form was done using bibliographical references (A. M. Giulietti et al. 2002; Moro et al. 2014, 2016) and the *Lista de Espécies da Flora do Brasil* (Flora do Brasil 2020 2018) that have information on geographical distribution, environment, growth form and pictures of about 41 000 Brazilian species.

2.4 Results

Plant abundance databases and their reliability

Three new abundance databases were produced from the raw presence database through the re-sampling methodology applied. The first database, DB1, showed more species, but less completeness and more rare species than both DB2 and DB3. DB1 contains 789 species corresponding ca. 85% of recorded in the raw database and distributed in 323 sampling units. The level of sampling completeness in DB1 was of 38% of the sampling units visited more than twice **(Figure 2.3 and 2.4).**

DB2 showed more species, more completeness and more rare species than DB3. Excluding sampling units with less than 35 species recorded, the DB2 retained 530 species corresponding to ca. 67% of the species recorded in DB1 and distributed in 38 sampling units. The level of sampling completeness in DB2 was 95% of the sampling units visited more than twice **(Figure 2.3 and 2.4).**

Excluding species recorded in less than 5% of sampling units, the database DB3 had fewer species than DB1 and DB2 that corresponded to ca. 6% (=48 species) of the species recorded in DB1, distributed in 113 sampling units. The level of sampling completeness in DB3 was 75% **(Figure 2.3 and 2.4).**

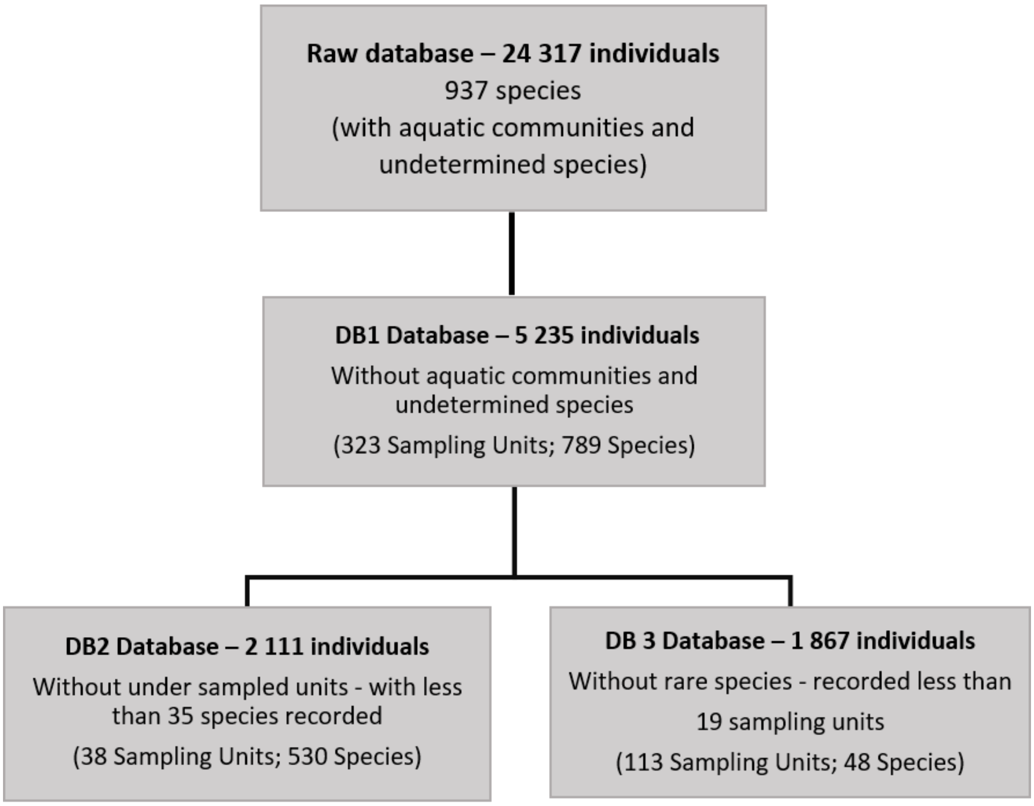


Figure 2.4. The workflow performed on the original Nema presence database (Center for Ecology and Environmental Monitoring, Federal University of Vale do São Francisco) to obtain the abundance databases that better allow the interpretation of the most important plant species for both conservation and the structure and functioning of the Caatinga's ecosystem. The number of sampling units, individuals and species included in each database are indicated. DB1, the base of the other two databases, was obtained after the exclusion of aquatic species and indeterminate individuals. DB2 was obtained after the exclusion of sampling units with less than 35 species recorded in DB1 ("without under sampled units"). DB3 was obtained after the exclusion of species recorded in less than 5% of the sampling units in DB1 ("without rare species").

Vegetation composition patterns obtained from abundance database

In DB1 and DB2, Fabaceae was the most represented family with 150 and 99 species, respectively, followed by Euphorbiaceae and Malvaceae (42 and 33 species respectively), Rubiaceae (33 and 20 species, respectively), and Asteraceae (32 and 20 species, respectively). In DB3, Fabaceae also was the most represented family (13 species) but followed by Cactaceae (8 species), Euphorbiaceae and Bromeliaceae (6 species each) and Anacardiaceae (3 species).

In DB1 and DB2, despite the different number of species considered, the percentage of exotic (7%), endemism (14%), woody (44%), climber (12%), and herbaceous species (45%) was similar **(Table 2.1).** DB3 included only native species and displayed a higher percentage of endemism (29%) and woody species (79%), a lower proportion of herbaceous species (21%) whereas climber species were absent **(Table 2.1).** The Fabaceae family showed the highest number of endemic species in all databases 25, 14 and 4 in DB1, DB2 and DB3, respectively **(Table 2.1).** In the three databases, the species turnover (Beta.Sim) at the regional scale was above 90%, whereas species nestedness (Beta.SNE) was lower than 0.1% **(Table 2.1).**

Table 2.1. Description of vegetation composition in DB1, DB2 and DB3 databases: number of individuals; species richness (number of species); number of genus, number of families; number and proportion of exotic species number and proportion of endemism; number and proportion of trees; number and proportion of shrubs; number and proportion of climbers; number and proportion of herbaceous species; beta diversity partitioning values (Beta.Sor = overall beta diversity; Beta.Sim = turnover; Beta.SNE = nestedness); proportion of Fabaceae family. The number of sampling units of each database are also given.

Database´s Description		**DB1**	**DB2**	**DB3**
Sampling units	Number of sampling units	323	38	113
Taxonomic composition and diversity	Number of individuals	5235	2111	1867
	Species richness	789	530	48
	Number of genus	453	350	43
	Number of families	102	89	17
Beta diversity partitioning	Beta.Sor (overall beta diversity)	0.993	0.948	0.97
	Beta.Sim (*turnover*)	0.986	0.928	0.950
	Beta.SNE (*nestedness*)	0.007	0.020	0.020
Community nativeness	Exotic species	53 (7%)	36 (7%)	0
	Endemism	108 (14%)	70 (13%)	14 (29%)
Community structure	Trees	172 (22%)	121 (23%)	26 (54%)
	Shrubs	164 (21%)	111 (21%)	12 (25%)
	Climber	98 (12%)	59 (11%)	0
	Herbaceous	357 (45%)	241 (45%)	10 (21%)
Fabaceae	Number of species from the Fabaceae	149 (19%)	99 (19%)	13 (27%)

2.5 Discussion

Improving abundance data reliability

In this paper, we were able to use species presence data collected over a large area and over time, by different observers to estimate plant species abundance. These new plant abundance databases obtained with the re-sampling methodology, provide an important basis to address the conservation of the unique dryland ecosystem of Caatinga regarding plant species. They are also essential to study the structure and functioning of the ecosystems which depend not only on the type of species present in the plant community but largely on their abundance.

The resulting dataset with plant species abundance showed different levels of confidence, depending on the sampling effort. Those sampling units with a higher sampling effort, i.e. where more quadrats were visited and/or visited more often, showed higher confidence in richness and abundance data, than the sampling units with a lower sampling effort. In order to improve data reliability overall, we produced the DB2 database by selecting only the units with a minimum number of species recorded (exclusion of under sampled units), resulting in higher species richness distributed in a lower number of sampling units than DB3. This dataset DB2 is optimized to be used for biodiversity conservation purposes since we can identify biodiversity hotspots in space and the presence of certain rare species.

Another point to consider is the role of chance in the detection of species during surveys performed by different observers and over large periods of time. In our case, sampling took place from 2008 to 2015, when a considerable inter and intra-annual climatic variability was observed. Ephemeral species, such as the majority of the herbaceous species in Caatinga, may be present at one date and not a few days or weeks after. This may create “false” dissimilarities between sampling units in species presence, just because they were sampled at different times and/or different seasonal conditions. Thus, to avoid this “stochastic” pattern, we removed the less abundant (rare) species and produced the DB3. Therefore, DB3 has a lower number of species (the most common) covering more sampling units than DB2.

The reliability of the databases derived from DB1, measured by their level of completeness, showed that this was improved considerably in DB2 and DB3 (95% and 75%, respectively) in relation to that of DB1 (38%)

Abundance data insights into vegetation composition patterns

In accordance with other studies in other dryland ecosystems (Banda et al. 2016), in this paper, we found high species turnover associated with DB2 and DB3 databases. Although both databases showed a high species turnover, we suggest that the factors behind this turnover are different in the two databases (DB2 and DB3). The turnover observed in DB2 could be mainly associated with the temporal dynamics of plant species, whereas the one associated with DB3 could be mainly associated with spatial heterogeneity. In fact, the plants in DB2 were only observed in 38 sampling units whereas the ones in DB3 were observed in 113 sampling units. In this way, DB3 covers a larger spatial area and consequently higher spatial range of environmental variation than DB2, justifying in this way the high turnover. Other authors also state that spatial heterogeneity in Caatinga results from the interplay between different environmental factors (Rizzini 1997; Andradre-Lima 1981; Araújo et al. 2005), such as temperature, precipitation, and soil type, which create gradients in resource availability (Borchert 1994), that are reflected in the mosaic of different physiognomies (Prado 2003; Andrade-Lima 1981). On the other hand, DB2 showed to have 45% of herbaceous plants. These plants have a small vegetative period, being present only in a small part of the year which could not match the sampling of the plants in field conditions. Additionally, the sampling period in the field occurred during several years (from 2008 to 2015), that is likely to have encompassed a considerable inter-annual meteorological variability that promoted different herbaceous plant species. According to other authors (Reis et al 2006; Silva et al. 2013), this climatic variability promotes changes in the structure and floristic composition of the herbaceous component over time, leading to higher diversity than that of the woody component (Moro et al. 2014). These facts support the idea that the high turnover observed in DB2 could be mainly associated with temporal dynamics of the plant community.

Abundance data insights into Caatinga conservation

DB1 contains more species than any of the others. Thus, whenever a complete species inventory is required this database should be used. This can be important in conservation studies when the aim is to provide conservation guidelines for as many species as possible. However, this higher number of species considered, comes at the expense of sampling completeness, implying lower reliability in abundance estimates.

Thus, suggesting costly conservation measures in a scenario of limited resources for species with high uncertainty in abundance estimates may be inadvisable. An alternative in such case is to use database DB2, which excluded under-sampled units and thus showed a lower level of uncertainty than DB1.

Besides taxonomic composition, the presence of endemism, native and exotic species and species turnover are essential to determine the plant patterns in neotropical dry forests (including the Caatinga), as well as in other biomes, and their conservation implication (Banda et al. 2016). In our study, taxonomic composition concerning the main botanical families followed the expected floristic patterns for Caatinga (Giulietti et al. 2004; Giulietti et al. 2006; Moro et al. 2014; Sampaio 1995). All databases can be used to describe Caatinga plant communities in terms of species composition, turnover, and endemism. The high proportion of endemism in the three databases reflects the uniqueness of Caatinga vascular plants, as previously described by Giulietti et al. (2002) and *Flora do Brasil* 2020 (2018).

Abundance data insights into Caatinga ecosystem structure and functioning

The DB3 database comprised the 48 most common and dominant perennial plant species in Caatinga. The diversity and abundance of dominant plants in a community are ecological surrogates of key ecosystem functions and ecosystem services (Martínez-Mena et al. 2002; Delgado-Baquerizo et al. 2013; Gaitán et al. 2014). Additionally, the contribution for the structure and functioning of Caatinga of perennial plant species, which are dominant in DB3, may be constant over time, particularly during the growing season when the vegetative and reproductive structures are present and fully developed. Contrastingly, for ephemeral plant species, present mostly in DB1 and DB2, the growing season may vary with time (Pérez-Harguindeguy et al. 2013). In this sense, the species included in the DB3 database can be considered as the ones contributing most to ensure the structure and functioning of Caatinga.

Finally, we acknowledge that the re-sampling methodology used in this paper to estimate species abundances from presence data was done at the expense of spatial resolution. Thus, it has limitations concerning the distribution of species at local spatial scales (under 10 Km), e.g. to understand the effect of local environmental factors such as altitude or aspect on the plant community (Príncipe et al. 2014, 2019). Nevertheless, it is an important tool for researchers focusing on the development of plant-based indicators of ecosystems structure and functioning in drylands, and on promoting their conservation since it can also be used for similar datasets collected over large areas where only plant species presence is available.

Concluding Remarks

In synthesis, we were able to estimate plant species abundance from presence/absence data, dealing with unevenly sampled large areas, to support in biodiversity conservation studies and evaluate ecosystem structure and functioning. We provide species abundance data for Brazilian Caatinga, one of the most threatened and understudied dryland ecosystems of the world. In this context, our paper gives a pivotal contribution to address this knowledge gap, providing a critical baseline for future and urgent studies on Caatinga conservation and ecological knowledge, on which depends the wellbeing of local population which is highly dependent on local natural resources. Moreover, the re-sampling methodology developed in this paper can be applied in other similar plant databases from large areas, built using different methodologies and sampling efforts, to estimate species abundance from presence data. Consequently, this re-sampling methodology is an important tool to support studies on ecosystems structure and functioning worldwide and promote their conservation.

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References

Andrade-Lima, D. 1981. “The Caatinga Dominium.” *Revista Brasileira de Botânica*

(4):149–53.

Araújo, E. L., K. A. Silva, E. M. N. Ferraz, E. V. S. B. Sampaio, and S. I. S. Silva. 2005. “Diversidade de Herbáceas Em Microhabitats Rochoso, Plano e Ciliar Em Uma Área de Caatinga, Caruaru, PE, Brasil.” *Acta Botanica Brasilica*.

Augustin, N. H., M. A. Mugglestone, and S. T. Buckland. 1998. “The Role of Simulation in Modelling Spatially Correlated Data.” *Environmetrics*.

Banda, K. R., et al. 2016. “Plant Diversity Patterns in Neotropical Dry Forests and Their Conservation Implications.” *Science*.

Barry, S. C. and A. H. Welsh. 2002. “Generalized Additive Modelling and Zero Inflated Count Data.” *Ecological Modelling*.

Baselga, A. 2010. “Partitioning the Turnover and Nestedness Components of Beta Diversity.” *Global Ecology and Biogeography*.

Baselga, A. 2012. “The Relationship between Species Replacement, Dissimilarity Derived from Nestedness, and Nestedness.” *Global Ecology and Biogeography*.

Baselga, A., et al., 2018. “Partitioning Beta Diversity into Turnover and Nestedness Components.” *R Package Version 1.5.1* 1–42.

Borchert, R. 1994. “Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees.” *Ecology*.

Buriti, C. O. and H. A. Barbosa. 2018. *Um Século de Secas: Por Que as Políticas Hídricas Não Transformaram o Semiárido Brasileiro?* edited by C. Editora.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. “Beyond Species: Functional Diversity and the Maintenance of Ecological Processes and Services.” *Journal of Applied Ecology*.

Conlisk, E., et al., 2009. “Improved Abundance Prediction from Presence-Absence Data.” *Global Ecology and Biogeography* 18(1):1–10.

Delgado-Baquerizo, M., et al. 2013. “Decoupling of Soil Nutrient Cycles as a Function of Aridity in Global Drylands.” *Nature*.

Dovrat, G. and E.Sheffer. 2019. “Symbiotic Dinitrogen Fixation Is Seasonal and Strongly Regulated in Water-limited Environments.” *New Phytologist* 221(4):1866–77.

Flora do Brasil 2020. 2018. “Flora Do Brasil 2020.” *Jardim Botânico Do Rio de Janeiro*.

Gaitán, J. J., et al., 2014. “Vegetation Structure Is as Important as Climate for

Explaining Ecosystem Function across Patagonian Rangelands." *Journal of Ecology*.

García Millán, V. E., A. Sánchez-Azofeifa, G. C. Málvarez García, and B. Rivard. 2014. "Quantifying Tropical Dry Forest Succession in the Americas Using CHRIS/PROBA." *Remote Sensing of Environment*.

Gaston, K. J. 1996. "Biodiversity. A Biology of Numbers and Difference." in *Blackwell Science*.

Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1998. "Aggregation and Interspecific Abundance-Occupancy Relationships." *Journal of Animal Ecology*.

Gerrard, D. J. and H. C. Chaing. 1970. "Density Estimation of Corn Rootworm Egg Populations Based upon Frequency of Occurrence." *Ecology* 51(2):237–45.

Giulietti, A.M., A. Conceição, and L. P. de Queiroz. 2006. "Diversidade e Caracterização Das Fenerógamas do Semi-Árido Brasileiro." in *Diversidade e caracterização das Fanerógamas do Semi-árido Brasileiro*.

Giulietti, A. M., et al., 2002. "Plantas Endêmicas Da Caatinga." Pp. 103–15 in *Vegetação e flora das caatingas*, edited by E. V. S. B. Sampaio et al. APNE / CNIP, Recife, PE.

Giulietti, A. M., et al., 2004. "Diagnóstico Da Vegetação Nativa Do Bioma Caatinga." in *Biodiversidade da caatinga: áreas e ações prioritárias para a conservação.*

Gleason, H. A. 1920. "Some Applications of the Quadrat Method." *Bulletin of the Torrey Botanical Club* 47(1):21–33.

Grime, J. P. 1998. "Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects." *Journal of Ecology*.

Guisan, A. and F. Kienast. 1998. "Predicting the Potential Distribution of Plant Species in an Alpine Environment." *Journal of Vegetation Science*.

He and Gaston. 2000. "Estimating Species Abundance from Occurrence." *The American Naturalist* 156(5):553–59.

Hooper, D. U., et al., 2005. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." *Ecological Monographs*.

Hwang, W. H. and F. He. 2011. "Estimating Abundance from Presence/Absence Maps." *Methods in Ecology and Evolution*.

IPCC. 2011. "Summary for Policymakers. In: IPCC Special Report on Renewable

Energy Sources and Climate Change Mitigation.” in *Cambridge University Press*.

IPCC. 2014. *2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*.

Jaiswal, S. K. and F. D. Dakora. 2019. “Widespread Distribution of Highly Adapted Bradyrhizobium Species Nodulating Diverse Legumes in Africa.” *Front Microbiol.* 10:1–16.

Joseph, L. N., S. A. Field, C. Wilcox, and H. P. Possingham. 2006. “Presence-Absence versus Abundance Data for Monitoring Threatened Species.” *Conservation Biology* 20(6):1679–87.

Kunin, W. E. 1998. “Extrapolating Species Abundance across Spatial Scales.” *Science*.

Lavorel, S. and E. Garnier. 2002. “Predicting Changes in Community Composition and Ecosystem Functioning from Plant Traits: Revisiting the Holy Grail.” *Functional Ecology*.

Maestre, F. T., et al., 2012. “Plant Species Richness and Ecosystem Multifunctionality in Global Drylands.” *Science*.

Magrin, G. O., et al., 2014. “Central and South America.” Pp. 1499–1566 in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovenmetal Panel on Climate Change*, edited by V. R. Barros et al. Cambridge University Press, Cambridge, United Kingdon and New York, NY, USA.

Martínez-Mena, M., J. Alvarez Rogel, V. Castillo, and J. Albaladejo. 2002. “Organic Carbon and Nitrogen Losses Influenced by Vegetation Removal in a Semiarid Mediterranean Soil.” *Biogeochemistry*.

Miles, L., et al., 2006. “A Global Overview of the Conservation Status of Tropical Dry Forests.” in *Journal of Biogeography*.

Moro, et al., 2014. “A Catalogue of the Vascular Plants of the Caatinga Phytogeographical Domain: A Synthesis of Floristic and Phytosociological Surveys.” *Phytotaxa*.

Moro, M. F., E. N. Lughadha, F. S. de Araújo, and F. R. Martins. 2016. “A Phytogeographical Metaanalysis of the Semiarid Caatinga Domain in Brazil.” *Botanical Review*.

Mouillot, D., S. Villéger, M. Scherer-Lorenzen, and N. W. H. Mason. 2011. “Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality.” *PLoS ONE*.

Nielsen, S. E., C. J. Johnson, D. C. Heard, and M. S. Boyce. 2005. “Can Models of Presence-Absence Be Used to Scale Abundance? Two Case Studies Considering Extremes in Life History.” *Ecography* 28(2):197–208.

Pearce, J. L., L. Jenine and M. S. Boyce. 2006. “Modelling Distribution and Abundance with Presence-Only Data.” *Journal of Applied Ecology* 43(3):405–12.

Pennington, R. T., M. Lavin, and A. Oliveira-Filho. 2009. “Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests.” *Annual Review of Ecology, Evolution, and Systematics*.

Pérez-Harguindeguy, N., et al., 2013. “New Handbook for Standardised Measurement of Plant Functional Traits Worldwide.” *Australian Journal of Botany*.

Portillo-Quintero, C. A. and G. A. Sánchez-Azofeifa. 2010. “Extent and Conservation of Tropical Dry Forests in the Americas.” *Biological Conservation*.

Prado, D. E. 2003. “As Caatingas Da América Do Sul.” in *Ecologia e Conservação da Caatinga*.

Príncipe, A., et al., 2014. “Modeling the Long-Term Natural Regeneration Potential of Woodlands in Semi-Arid Regions to Guide Restoration Efforts.” *European Journal of Forest Research*.

Príncipe, A., et al., 2019. "In Mediterranean drylands microclimate affects more tree seedlings than adult trees." *Ecological Indicators* 106:1-9.

Reis, A. M. S., E. L. Araújo, E. M. N. Ferraz, and A. N. Moura. 2006. “Inter-Annual Variations in the Floristic and Population Structure of an Herbaceous Community of ‘Caatinga’ Vegetation in Pernambuco, Brazil.” *Revista Brasileira de Botânica*.

Reynolds, J. F., et al., 2007. “Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences.” in *Terrestrial Ecosystems in a Changing World*.

Rizzini, C. M. 1997. “Prefácio Da 2ª Edição.” in *Tratade De Fitogeografia Do Brasil: Aspectos ecológicos; sociológicos e florísticos*.

Sampaio, E. V. S. B. 1995. “Overview of the Brazilian Caatinga.” in *Seasonally dry tropical forests*.

Santos, J. C., et al., 2011. “Caatinga: The Scientific Negligence Experienced by a Dry

Tropical Forest.” *Tropical Conservation Science*.

Sarmiento, G. 1975. "The dry plant formations of South America and their floristic connections"- Journal of Biogeography. 2:233-251.

da Silva, J. M. C. and L. C. F. Barbosa. 2018. “Impact of Human Activities on the Caatinga.” in *Caatinga: The Largest Tropical Dry Forest Region in South America*.

da Silva, J. M. C., L. C. F. Barbosa, I. R. Leal, and M. Tabarelli. 2018. “The Caatinga: Understanding the Challenges.” in *Caatinga: The Largest Tropical Dry Forest Region in South America*.

Silva, K. A., et al., 2013. “Spatial Variation in the Structure and Composition of the Herbaceous Community in a Semiarid Region of Northeastern Brazil.” *Brazilian Journal Biology* 73:135–48.

Soranno, P. A., et al., 2015. “Building a Multi-Scaled Geospatial Temporal Ecology Database from Disparate Data Sources: Fostering Open Science and Data Reuse.” *GigaScience*.

Sørensen, T. 1948. "A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons". K. Danske Videnske Selsk 5: 1-34.

Stocking, M. A. 2003. “Tropical Soils and Food Security: The Next 50 Years.” *Science*.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing.*

Welsh, A. H., R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 1996. “Modelling the Abundance of Rare Species: Statistical Models for Counts with Extra Zeros.” *Ecological Modelling*.

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Chapter 3

The response of plant functional traits to aridity in a Tropical dry forest

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3 The response of plant functional traits to aridity in a Tropical dry forest

3.1 Abstract

Drylands are experiencing an overall increase in aridity that is predicted to intensify in the future due to climate change. This may cause changes in the structure and functioning of dryland ecosystems, affecting ecosystem services and human well-being. Therefore, detecting early signs of ecosystem change before irreversible damage takes place is important. Thus, here we used a space-for-time substitution approach to study the response of the plant community to aridity in a Tropical dry forest (Caatinga, Brazil), and infer potential consequences of climate change. We assessed plant functional structure using the community weighted mean (CWM) and functional diversity, measured through functional dispersion (FDis), along a 700 km climatic gradient. We studied 13 functional traits, reflecting strategies associated with establishment, defense, regeneration, and dispersal of the most abundant 48 plant species in 113 sampling sites. Spearman correlations were used to test the relation between aridity and single-trait functional metrics. Aridity was a major environmental filter of the plant community functional structure. We found a higher abundance of species with deciduous leaves, zoochorous dispersal, fleshy fruits, chemical defense exudation and spinescence, and crassulacean acid metabolism towards more arid sites, at the expense of species with evergreen and thicker leaves, autochory dispersal, and shrub growth-form. The FDis of leaf type and thickness decreased with aridity, whereas FDis of fruit type, photosynthetic pathway, and defense strategies increased. Our findings provide functional indicators to early detect climate change impacts on Caatinga structure and functioning, to timely adopt preventive measures (e.g. conservation of forest remnants) and restoration actions (e.g. introduction of species with specific functional traits) in this threatened and unique ecosystem.

Keywords: Caatinga; climatic gradient; drylands; ecosystem functioning; functional diversity; space-for-time substitution

3.2 Introduction

Drylands cover almost 47% of terrestrial ecosystems with an expected expansion up to 56% until 2100 (Huang et al., 2016), due to a global increase in aridity associated with climate change (Pour, Wahab and Shahid, 2020). This increase in aridity will impact ecosystem structure and functioning, affecting the delivery of ecosystem services and human well-being of at least 39% of the world´s population currently living in drylands (Koutroulis, 2019). Therefore, it is essential to monitor changes in ecosystem structure and functioning due to climate, to timely adopt measures able to ensure the maintenance of key ecosystem services to population.

One way to monitor the structure and functioning of terrestrial ecosystems is by using plant biodiversity components as indicators of specific ecosystem functions (Branquinho *et al.*, 2019). The approaches based on plant functional traits have greatly improved the understanding of the effects of environmental change on biodiversity and ecosystem functioning (De Bello et al., 2010; Nunes *et al.*, 2017) since they are associated with plants´ adaptive strategies to respond to climate, soil resources, disturbance (e.g. competition and land use changes) and defense/protection needs (Pérez-Harguindeguy *et al.*, 2013). Hence, certain traits may be used to predict ecosystem changes in response to environmental factors (Lavorel and Garnier, 2002; Suding *et al.*, 2008).

There are several metrics based on functional traits that may be used to describe the functional structure of plant communities. Among them, the community weighted mean (CWM) (Garnier *et al.*, 2007) and functional diversity, are considered good predictors of ecosystem functioning (Valencia *et al.*, 2015). The community weighted mean reflects the dominant traits in a community (Garnier et al., 2007). Its importance derives from the "*mass ratio hypothesis*" proposed by Grime (1998), which assumes that ecosystem functioning is largely determined by the trait values of the dominant species (Ricotta and Moretti, 2011). Functional diversity reflects the degree of functional dissimilarity within the plant community (Laliberte and Legendre, 2010). A high functional diversity suggests high niche differentiation, i.e. the co-occurrence of species with different functional strategies that may lead to a more complete use of resources, enhancing ecosystem functioning (Mouchet et al., 2010). Previous studies showed that changes in both the CWM and in functional diversity, were good indicators of changes in major ecosystem processes; for example, the CWM of maximum plant height and functional diversity of specific leaf area were associated with primary productivity and decomposition rates, respectively (de Bello *et al.*, 2010; Valencia *et al.*, 2015; Le Bagousse-Pinguet *et al.*, 2019).

Aridity acts as a strong environmental filter in drylands (Berdugo et al. 2020), affecting the plant community. Studies showed that aridity may change the dominance of different growth-forms (e.g. shrubs, species with a prostrate habit) (Fay *et al.*, 2002) or of different plant sizes, e.g. selecting for smaller species (Gross et al., 2013). This may be because water stress increases the risk of cavitation, thus selecting for plants with lower stature. It may affect leaf traits, favouring stress-tolerant strategies e.g. evergreen leaves with low specific leaf area (SLA) (Wright *et al.*, 2004; Costa-Saura *et al.*, 2016). Yet, under extreme arid conditions these traits may be replaced by stress-avoidant species with semi-deciduous leaves and high SLA (Gross et al., 2013; Berdugo et al., 2020). Aridity may also determine the type of root system; e.g. more superficial roots may be advantageous to maximize acquisition during short peaks of resource availability (Schenk and Jackson, 2002). Fruit type and dispersal strategies may be also influenced by aridity, as it may select for e.g. short-distance dispersal strategies as a way to reach favourable conditions for growth restricted to small microsites in arid environments (van Rheede van Outdshoorn and van Rooyen, 1999; Pueyo *et al.*, 2008). The relative dominance of C3, C4 and crassulacean acid metabolism (CAM) plant photosynthetic pathways, closely linked to water and nutrient use efficiency, may also change in response to aridity. For instance, CAM plants are frequently found in semi-arid zones in tropical and sub-tropical regions (Medina, Olivares and Diaz, 1986). These studies highlight the importance of applying a trait-based approach to measure the response of plant communities to climate (Gross *et al.*, 2013; Valencia *et al.*, 2015; Nunes *et al.*, 2017).

Monitoring the response of the plant community to climate would be especially important for Brazilian dry forest locally called Caatinga where climate change, anthropogenic pressure and intensive and accelerated land-use intensification have been modifying substantially the natural landscape (da Silva and Barbosa, 2018; Sfair *et al.*, 2018). These pressures may cause irreversible shifts in ecosystem services which nowadays support 28.6 million people (da Silva, Leal and Tabarelli, 2018). For this reason, studies assessing responses of the plant community functional structure to increasing aridity in the Caatinga should be a priority. To monitor these effects over time, long time-series would be required, which are often not available or sufficiently detailed for the target region. To overcome this limitation, a space-for-time substitution approach is an alternative widely used in biodiversity modelling to infer past or future trajectories of ecological systems from spatial gradients (Matos *et al.*, 2017; Nunes *et al.*, 2017; Frasconi Wendt *et al.*, 2020).

The main objective of this study was to assess changes in plant functional structure along a wide regional climatic gradient in the Caatinga ecosystem, using a space-for-time substitution approach to infer potential consequences of climate change in these highly diverse and critically endangered areas. We addressed 13 functional traits related to plant strategies to deal with water limitations. We hypothesized that aridity is a strong environmental filter acting on the functional structure of plant communities in this tropical dry forest. We expect to find i) an increase in the relative abundance of drought-adapted traits towards stress-avoidant strategies (e.g., summer deciduousness) and ii) a reduction in functional diversity for most traits as a result of climatic filtering.

3.3 Material and methods

Site description and data sampling

This study was carried out in Caatinga, a semi-arid seasonally dry tropical forest in Brazil. It covered a spatial climatic gradient with 113 sampling sites (10 x 10 Km) including four Brazilian states (Alagoas, Ceará, Paraíba, Pernambuco, and Piauí) (Figure 3.1). Caatinga encompasses many vegetation types from open vegetation with rocky outcrops dominating in drier areas, to semi-deciduous forests dominating in richer and more humid soils (Fernandes and Queiroz, 2018). Along the study area mean annual precipitation was 680 mm (ranging from 440 to 1.098 mm), mean annual temperature 24 ºC (ranging from 21ºC to 26 ºC), altitude varied between 278 and 930 m, and the aridity index ranged from 0.27 to 0.69 (from more to less arid) (Hijmans *et al.*, 2005).

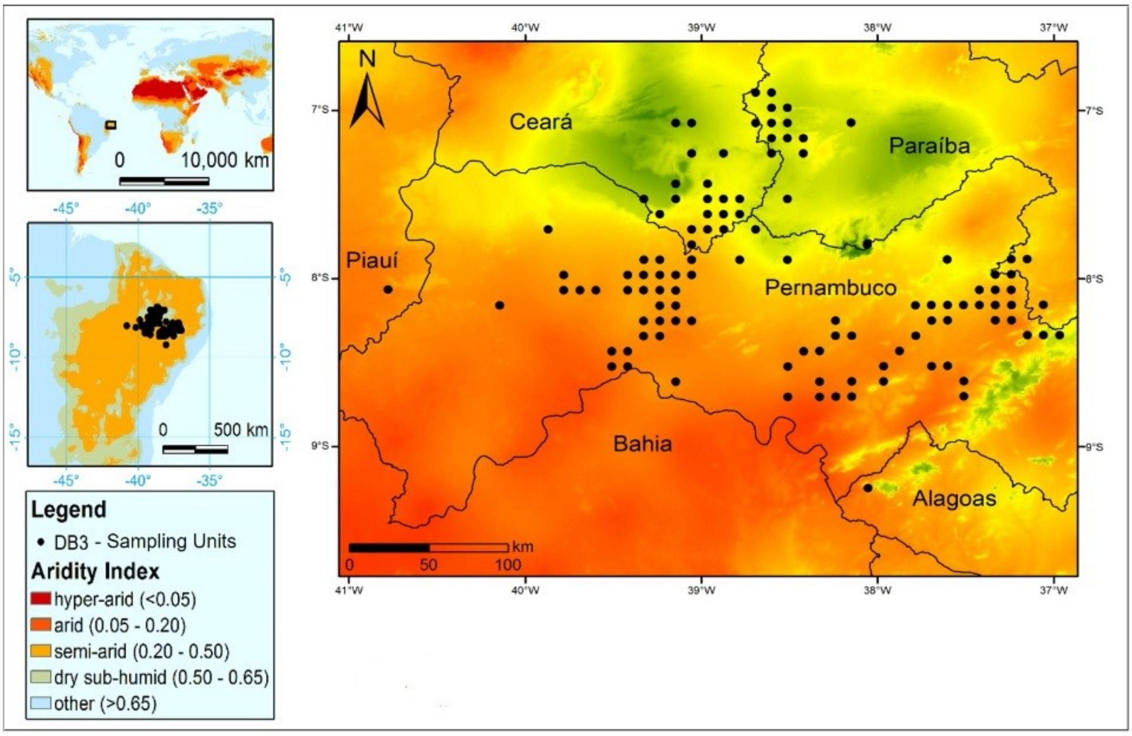


Figure 3.1. Location of the study area within global drylands (left), and of the 113 sampling sites (black circles) distributed along the regional climatic gradient based on the aridity index, in northeastern Brazil.

In this study, the list of the most abundant species was obtained by using a re-sampling methodology applied to a species presence database as described in Oliveira et al. (2020). Thus, we used species occurrence to obtain a proxy of their abundance. To obtain species abundances based on presence data we divided each of the 113 sampling units (10 x 10 Km) into 25 sampling quadrats of 2 x 2 Km. The abundance of each species was obtained by the sum of its presence at each small quadrat (2 x 2 Km), with each species counted only once in each small quadrat (even if recorded more than once). In this way, the maximum abundance at the sampling unit level was 25. This data allowed us to build an abundance database of the 80% most dominant species (48 species) distributed over 113 sampling units. For these 48 most abundant species **(Table S3.1)** we studied 13 functional traits: (1) growth form; (2) maximum plant height; (3) leaf phenology type; (4) leaf thickness; (5) specific leaf area (SLA); (6) root type; (7) dispersal strategy; (8) fruit type; (9) photosynthetic pathway; (10) spinescence presence; (11) presence of leaves arranged in a rosette; (12) chemical defense exudation; (13) rhytidome presence. These include continuous, categorical and binary traits reflecting plant strategies associated with their establishment, defense, regeneration, and dispersal (Lewinsohn and Vasconcellos-Neto, 2009; Pérez-Harguindeguy *et al.*, 2013). Trait data were obtained by direct field observations and measurements following standard protocols (Pérez-Harguindeguy *et al.*, 2013) (traits 1, 2, 4, 5, 10, 12 and 13), or from the botanical collection of Herbarium Vale do São Francisco (HVASF), Petrolina, Pernambuco, Brazil (traits 6 and 8), or from other bibliographic sources (traits 3, 7, 9 and 11 - e.g., Griz and Machado, 2001).

To assess changes in plant community functional structure along the climatic gradient, we used the community weighted mean (CWM) and functional diversity, using a single trait value (or category) per species. CWM represents the average trait value in a community weighted by the relative abundance of the species carrying each value (Garnier *et al.*, 2007). For continuous traits, CWM values correspond to the mean value of that trait in the community, while for the categoric and binary traits, we did the calculations so that CWM values represent the proportion of each category in the community. To assess functional diversity, we calculated functional dispersion (FDis) (Laliberte and Legendre, 2010), which measures the degree of functional dissimilarity within the plant community. FDis is calculated as the weighted mean distance of individual species from the weighted centroid of all species in a multidimensional trait space, where weights correspond to species relative abundances (Laliberte and Legendre, 2010). FDis was calculated individually for each trait, using the Gower distance to handle continuous, ordinal, and categorical variables, as well as missing values. All calculations were performed with dbFD function of the FD package (Laliberté, Legendre and Shipley, 2015) in R (The R Core Team, 2018).

We used the aridity index adopted by the United Nations as the main climate variable, retrieved from a global database (Trabucco *et al.*, 2008). It is calculated as the ratio between mean annual precipitation and annual potential evapotranspiration; thus, higher values of the aridity index correspond to less arid environments and vice-versa. Yet, to make it more intuitive to the reader, we use the term aridity (calculated as 1-the aridity index) in the description of the results and in the discussion section.

Data analysis

To analyze the response of the plant community functional structure along the climatic gradient, we tested for significant relationships between aridity (the aridity index) and single-trait functional metrics (CWM and FDis) using Spearman correlations, to account for possible non-linear relationships. Correlations were considered significant for $p < 0.05$. All statistical analyses were performed using R version 3.4 (The R Core Team, 2018).

3.4 Results

In general, the plant community in the study area was dominated by mostly deciduous trees with an average maximum plant height of 4 m (see CWM values in Table 3.1). Mean leaf thickness was 0.8 mm and mean specific leaf area (SLA) was 16 mm^2/mg (Table 1). Autochory dispersal was dominant in the plant community, followed by anemochory and zoochory, with 30% each (Table 3.1). In addition, the dominating root type was pivoting root. Fleshy fruits were present in 38% of the plants, crassulacean acid metabolism (CAM) in 18%, and spinescence in 28%, while 8% of the plants had leaves arranged in a rosette. Plants with chemical defense exudation and rhytidome presence represented 30% and 24% of the community, respectively (Table 3.1).

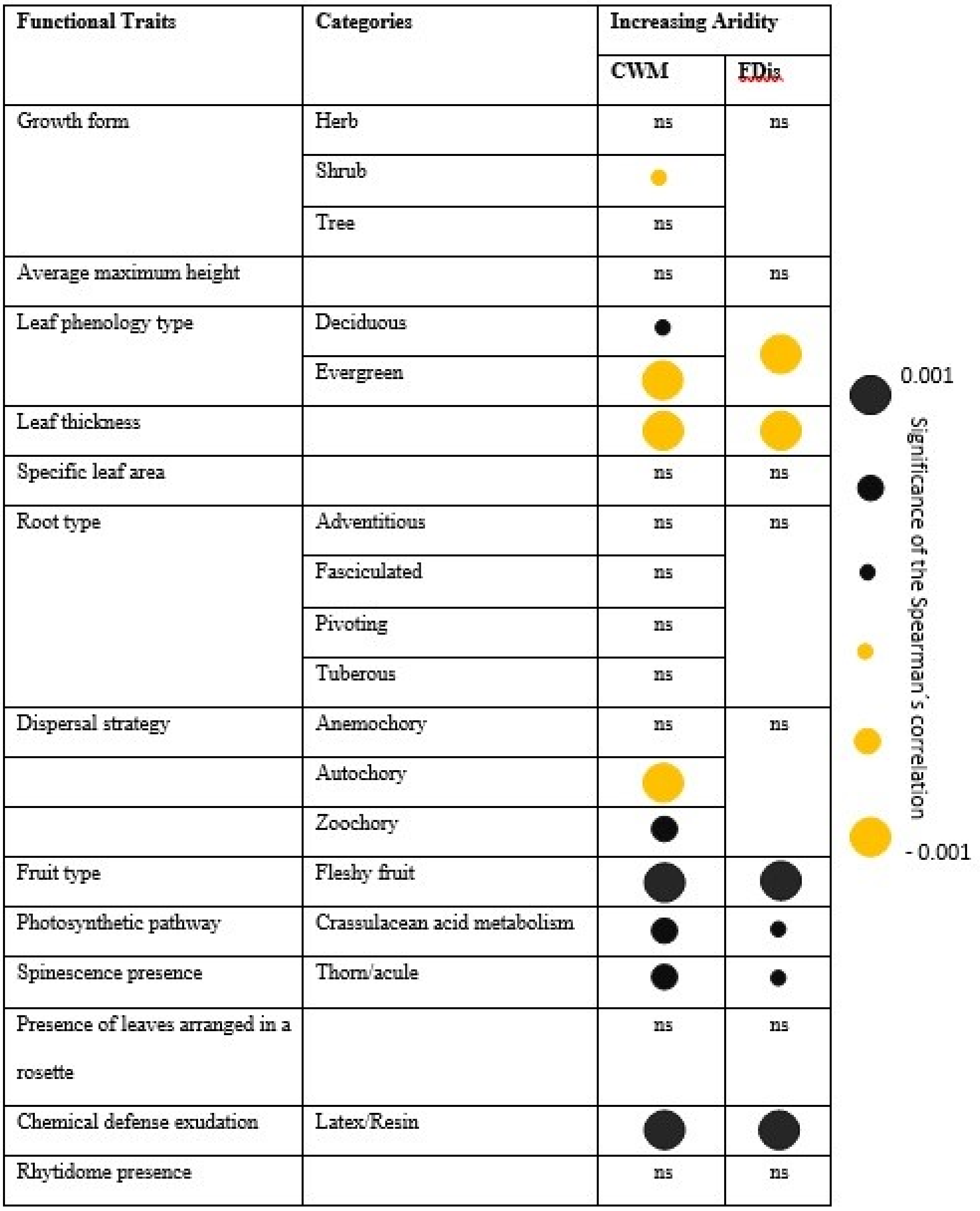
Table 3.1. Average community weighted mean (CWM) values (mean or percentage) for the 13 functional traits studied. The type of trait (categorical/continuous/binary) and their categories/units are indicated with their minimum and maximum values among plant communities. For categorical and binary traits, the minimum, maximum and mean values correspond to a percentage, while continuous traits values follow their units.

Functional Traits	Type	Categories/Units	Minimum	Maximum	Mean
Growth form	Categorical	Herb	0	87%	14%
		Shrub	0	33%	13.5 %
		Tree	0	100%	72.5 %
Average maximum height	Continuous	meters (m)	0.5	6	4
Leaf phenology type	Categorical	Deciduous	12%	100%	8%
		Evergreen	0	50%	8%
Leaf thickness	Continuous	millimetres (mm)	0.15	2.0	0.80
Specific leaf area	Continuous	mm2/mg	13	20	16
Root type	Categorical	Adventitious	0	50%	8.25 %
		Fasciculata	0	28%	8.25 %
		Pivoting	25%	100%	67%
		Tuberous	0	40%	16.5 %
Dispersal strategy	Categorical	Anemochory	10%	67%	30%
		Autochory	12%	78%	40%
		Zoochory	0	70%	30%
Fruit type	Binary	Presence Fleshy fruit	0	70%	38%
Photosynthetic pathways	Binary	Presence Crassulacean acid metabolism	0	75%	18%
Spinescence presence	Binary	Thorn/acule	0	86%	28%
Presence of leaves arranged in a	Binary		0	50%	8%

rosette					
Chemical defense exudation presence	Binary	Latex/Resin	0	69%	30%
Rhytidome presence	Binary		0	56%	24%

The CWMs of eight functional traits and FDis of six functional traits were significantly correlated with aridity (i.e. 1-the aridity index, to make the interpretation more intuitive; this term is used hereinafter) (Table 3.2), indicating a strong effect of aridity on the functional structure of the plant community. More arid sites showed a decreased abundance of evergreen leaf type, leaf thickness, autochory dispersal, and shrub growth-form, as evidenced by the negative correlation between CWMs and aridity (Table 3.2). In contrast, the presence of deciduous leaves, fleshy fruits, spinescence and chemical defense exudation increased towards drier sites, as well as zoochory dispersal and the abundance of CAM species (Table 3.2). More arid sites showed decreased functional dispersion for leaf phenology type and leaf thickness, and the opposite (higher FDis) for fruit type, photosynthetic pathway, spinescence presence and type of chemical defense exudation (Table 3.2). Five functional traits showed no consistent relationship with the aridity index, namely maximum plant height, specific leaf area, root type, presence of leaves arranged in a rosette and rhytidome presence.

Table 3.1. Significance of the spearman correlations between community weighted mean (CWM) and functional dispersion (FDis) values, with aridity (1- aridity index) for the 13 functional traits studied (n=113 sampling plots). Black circles represent positive correlations and yellow circles represent negative correlations. Circle dimensions represent the level of significance of the correlations: small circle ($p < 0.05$); medium circle ($p < 0.01$); large circle ($p < 0.001$). ns – no significant correlation.



Functional Traits	Categories	Increasing Aridity	
		CWM	FDis
Growth form	Herb	ns	ns
	Shrub	🟡	
	Tree	ns	
Average maximum height		ns	ns
Leaf phenology type	Deciduous	•	🟡
	Evergreen	🟡	
Leaf thickness		🟡	🟡
Specific leaf area		ns	ns
Root type	Adventitious	ns	ns
	Fasciculated	ns	
	Pivoting	ns	
	Tuberous	ns	
Dispersal strategy	Anemochory	ns	ns
	Autochory	🟡	
	Zoochory	●	
Fruit type	Fleshy fruit	⬤	⬤
Photosynthetic pathway	Crassulacean acid metabolism	●	•
Spinescence presence	Thorn/acule	●	•
Presence of leaves arranged in a rosette		ns	ns
Chemical defense exudation	Latex/Resin	⬤	⬤
Rhytidome presence		ns	ns

3.5 Discussion

In this work, we found a strong impact of aridity on Caatinga plant functional structure along a comprehensive aridity gradient, supporting our general working hypothesis. The plant community showed increased deciduousness and abundance of defense traits, more cacti and bromeliads, and lower shrub abundance towards drier sites. Some of these changes point to an increase in stress-avoidant strategies under more arid conditions, partly supporting our first hypothesis. We also hypothesized a reduction in functional diversity with increased aridity as a result of climatic filtering. This was true for leaf traits, but not for functional diversity of fruit type, photosynthetic pathway, and defense traits which increased with aridity, suggesting a higher niche complementarity in drier sites. Overall, the shifts found in functional structure in response to aridity may affect plant structural complexity, spatial distribution patterns and biotic interactions, able to negatively affect key ecosystem processes.

In addition, the effect of aridity was detected along our large climatic gradient, ranging from semi-arid to dry sub-humid areas, regardless of other environmental variations (e.g. soil, topography, land management) along the study area. This suggests that aridity acts as the main filter (hierarchically) at the regional scale, followed by the likely effects of other finer-scale local variables, and is in accordance with previous works showing that climate is a major driver of the floristic patterns of woody plant species in Caatinga (Silva and Souza, 2018).

Changes in vegetative traits

Higher aridity led to a decrease in functional diversity of leaf traits, coupled with an increase in the dominance of deciduous species with lower leaf thickness, a known plant stress-avoidant strategy to deal with water limitations, replacing the maintenance of more-costly thicker evergreen leaves characteristic of stress-tolerant ecological strategies (Lohbeck *et al.*, 2015). This is in accordance with our working hypotheses and with what other studies found for extremely arid and seasonal environments (Carvajal *et al.*, 2019; Berdugo *et al.*, 2020), where the classical prediction of transition from fast to slow resource acquisition strategies as aridity increases (Wright et al.

2014) may become disadvantageous because slow traits are costly to maintain (Carvajal et al. 2019).

Summer deciduousness leads to accumulation of litter on the soil surface. Previous studies show leaf fall may be responsible for 70% up to 80% of nutrient deposition in Caatinga (Santana and Souto, 2011; De Holanda *et al.*, 2017), as rapid decomposition may occur after precipitation events (Fredson *et al.*, 2009; Moura *et al.*, 2016). However, precipitation events are infrequent in Caatinga (Machado, Barros and Sampaio, 1997), and may become less and less frequent due to climate change, and that may reduce or even prevent leaf decomposition (Fredson *et al.*, 2009; Moura *et al.*, 2016), resulting in accumulated litter for a long period below deciduous plants, a very common image in Caatinga as in other drylands.

We also found a decrease in shrub growth form in drier sites suggesting that these areas have lower structural complexity, which may potentially affect habitat quality and biomass production, although we did not assess this. Contrastingly, the diversity of photosynthetic pathways increased towards drier conditions, probably due to an increase in the abundance of species with crassulacean acid metabolism (CAM), mainly cacti and bromeliads. This is a common strategy in arid environments, as CAM plants close their stomata during the day to avoid water losses and open them during the cooler more humid nighttime hours, allowing uptake of carbon dioxide (CO_2) for carbon fixation (Medina, Olivares and Diaz, 1986). Although CAM plants are able to store water e.g. in vacuoles, they are more inefficient than C3 plants at absorbing CO_2, and so they grow slowly (Medina, Olivares and Diaz, 1986). Thus, this change may affect biomass production.

In short, the shift found in plant community functional structure towards more arid conditions regarding the vegetative traits analyzed, particularly concerning changes in growth-form dominance and increased leaf deciduousness, is likely to affect key ecosystem processes in Caatinga, namely primary productivity, litter decomposition (Cornwell *et al.*, 2008) and carbon and nitrogen cycling (Milcu *et al.*, 2014).

Changes in reproductive and defense traits

Drier conditions led to an increase in the functional diversity of fruit types and in the abundance of fleshy fruited and zoochorous species, possibly affecting biotic interactions with seed-dispersing animals in drier sites (e.g. lizards, birds and bats) (Leal, Lopes and Machado, 2006). The increase of zoochory dispersion with aridity is in accordance with previous studies performed in Caatinga (e.g. Griz & Machado, 2001), and seems to be mostly due to the increase in the relative abundance of CAM species (cactus) in drier sites, many of them zoochorous (Griz & Machado, 2001). Many Cactaceae´s species (e.g. *Tacinga palmadora* (Britton & Rose) N.P. Taylor & Stuppy; recorded in our study area), flourish and bear fruit in the dry season (Locatelli and Machado, 1999) ensuring food resources to fauna that may be beneficial for pollination and dispersion (Griz and Machado, 2001; Leal, Lopes and Machado, 2006; Lima and Rodal, 2010). This may also be the reason why anemochory is not the predominant dispersion strategy in our case, as suggested by Howe and Smallwood (1982) for dry environments. However, these authors considered only species richness (i.e. the number of species with a particular dispersal strategy) while we are taking into account also species abundance (i.e. trait abundance).

However, the decrease in autochory dispersal in drier areas may affect plant spatial distribution in Caatinga, with potential negative effects on plant establishment. Autochory often originates a clustered distribution pattern (new plants clustered around the mother plant) providing “islands of fertility” with improved microclimate, facilitating seedling establishment, e.g. for cactus recruitment (Drezner, 2010; Landero and Valiente-Banuet, 2010).

Spinescence and chemical exudation (i.e., latex and resin) increased in drier areas. These strategies can protect plants against pathogens and herbivores (Olofsson et al., 2004; Lewinsohn and Vasconcellos-Neto, 2009). They affect plant palatability and thus the level of herbivory, which may in turn change the quantity and quality of litterfall, affecting nutrient cycling (Olofsson *et al.*, 2004). Yet, the presence of these traits may have fitness costs to plants (Gassmann and Futuyma, 2004), most probably reducing the growth rates (Belovsky *et al.*, 1991) and/or reducing the reproductive potential of plant populations in Caatinga under more arid conditions (Gómez and Zamora, 2002).

Concluding remarks

Overall, we found a strong impact of aridity on Caatinga plant functional structure, despite other environmental variations potentially acting at finer scales along the study area. The plant community in drier sites had increased deciduousness and abundance of defense traits, more cacti and bromeliads, and lower abundance of shrubs. This shift may influence plant structural complexity, spatial distribution patterns and biotic interactions, which may have potential negative consequences for key ecosystem processes. Some of the changes found point to an increase in stress-avoidant strategies under more arid conditions, partly supporting our initial hypothesis. Yet, contrary to our expectations, we did not find a reduction in functional diversity with increased aridity as a result of climatic filtering for most traits, except for leaf traits, and found the opposite trend (increase functional diversity) for fruit type, photosynthetic pathway, and defense traits, suggesting a higher niche complementarity in drier sites. Considering the predictions of increased aridity in the study area in the near future and assuming a space-for-time substitution, our results suggest that in the future we can use these functional traits to early warn us about the potential impacts of climate change on Caatinga. Additionally, this information about the response of plant functional traits along the aridity gradient may also contribute to guide preventive strategies (e.g. conservation of forest remnants) and/or corrective measures (e.g. include species with specific functional traits in restoration projects) to conserve this unique, remarkably diverse and highly threatened Caatinga ecosystem.

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References

Le Bagousse-Pinguet, Y. *et al.* (2019) ‘Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality’, *Proceedings of the National Academy of Sciences of the United States of America*. doi: 10.1073/pnas.1815727116.

de Bello, F. *et al.* (2010) ‘Towards an assessment of multiple ecosystem processes and services via functional traits’, *Biodiversity and Conservation*. doi: 10.1007/s10531-010-9850-9.

Belovsky, G. E. *et al.* (1991) ‘Effects of spines and thorns on Australian arid zone herbivores of different body masses’, *Oecologia*. doi: 10.1007/BF00317715.

Berdugo, M. *et al.* (2020) ‘Global ecosystem thresholds driven by aridity’, *Science*. doi: 10.1126/science.aay5958.

Branquinho, C. *et al.* (2019) ‘Essential Biodiversity Change Indicators for Evaluating the Effects of Anthropocene in Ecosystems at a Global Scale. In 201’, in. doi: 10.1007/978-3-030-10991-2_7.

Carvajal, D. E. *et al.* (2019) ‘A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies’, *Journal of Ecology*. doi: 10.1111/1365-2745.13092.

Cornwell, W. K. *et al.* (2008) ‘Plant species traits are the predominant control on litter decomposition rates within biomes worldwide’, *Ecology Letters*. doi: 10.1111/j.1461-0248.2008.01219.x.

Costa-Saura, J. M. *et al.* (2016) ‘Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species’, *Perspectives in Plant Ecology, Evolution and Systematics*. doi: 10.1016/j.ppees.2016.05.001.

Drezner, T. D. (2010) ‘Nurse tree canopy shape, the subcanopy distribution of cacti, and facilitation in the Sonoran Desert’, *The Journal of the Torrey Botanical Society*. doi: 10.3159/09-ra-069r1.1.

Fay, P. A. *et al.* (2002) ‘Altered rainfall patterns, gas exchange, and growth in grasses and forbs’, *International Journal of Plant Sciences*. doi: 10.1086/339718.

Fernandes, M. F. and Queiroz, L. P. de (2018) ‘Vegetação e flora da Caatinga.’, *Ciência e Cultura*, 70(4), pp. 51–56.

Frasconi Wendt, C. *et al.* (2020) ‘Using a space-for-time approach to select the best biodiversity-based indicators to assess the effects of aridity on Mediterranean drylands’, *Ecological Indicators*. doi: 10.1016/j.ecolind.2020.106250.

Fredson, J. *et al.* (2009) ‘Deposição e decomposição de serapilheira em área da

Caatinga.= Litter productivity and deposition in area of Caatinga.', *Revista Agro@mbiente On-line*.

Garnier, E. *et al.* (2007) 'Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites', *Annals of Botany*. doi: 10.1093/aob/mcl215.

Gassmann, A. J. and Futuyma, D. J. (2004) 'Consequence of herbivory for the fitness cost of herbicide resistance: photosynthetic variation in the context of plant-herbivore interactions', *Journal of Evolutionary Biology*. doi: 10.1111/j.1420-9101.2004.00819.x

Gómez, J. M. and Zamora, R. (2002) 'Thorns as induced mechanical defense in a long-lived shrub (Hormathophylla spinosa, Cruciferae)', *Ecology*. doi: 10.1890/0012-9658(2002)083[0885:TAIMDI]2.0.CO;2.

Grime, J. P. (1998) 'Benefits of plant diversity to ecosystems: Immediate, filter and founder effects', *Journal of Ecology*. doi: 10.1046/j.1365-2745.1998.00306.x.

Griz, L. M. S. and Machado, I. C. S. (2001) 'Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil', *Journal of Tropical Ecology*. doi: 10.1017/S0266467401001201.

Gross, N. *et al.* (2013) 'Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands', *Journal of Ecology*. Edited by S. Schwinning. John Wiley & Sons, Ltd (10.1111), 101(3), pp. 637–649. doi: 10.1111/1365-2745.12063.

Hijmans, R. J. *et al.* (2005) 'Very high resolution interpolated climate surfaces for global land areas', *International Journal of Climatology*. doi: 10.1002/joc.1276.

De Holanda, A. C. *et al.* (2017) 'Aporte de serapilheira e nutrientes em uma área de caatinga', *Ciencia Florestal*. doi: 10.5902/1980509827747.

Howe, F. and Smallwood, J. (1982) 'Ecology of seed dispersal.', *Annual review of ecology and systematics. Volume 13*.

Huang, J. *et al.* (2016) 'Accelerated dryland expansion under climate change', *Nature Climate Change*. doi: 10.1038/nclimate2837.

Koutroulis, A. G. (2019) 'Dryland changes under different levels of global warming', *Science of The Total Environment*. Elsevier, 655, pp. 482–511. doi: 10.1016/J.SCITOTENV.2018.11.215.

Laliberte, E. and Legendre, P. (2010) ‘ALaliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91(1), 299–305. http://doi.org/10.1890/08-2244.1 distance-based framework for measuring functional diversity from multiple ’, *Ecology*. doi: 10.1890/08-2244.1.

Laliberté, E., Legendre, P. and Shipley, B. (2015) ‘FD: measuring functional diversity from multiple traits, and other tools for functional ecology’, *R Package*. doi: http://cran.r-project.org/web/packages/FD/FD.pdf.

Landero, J. P. C. and Valiente-Banuet, A. (2010) ‘Species-specificity of nurse plants for the establishment, survivorship, and growth of a columnar cactus’, *American Journal of Botany*. doi: 10.3732/ajb.1000088.

Lavorel, S. and Garnier, E. (2002) ‘Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail’, *Functional Ecology*. doi: 10.1111/j.1399-0004.2006.00597.x.

Leal, F. C., Lopes, A. V. and Machado, I. C. (2006) ‘Polinização por beija-flores em uma área de caatinga no Município de Floresta, Pernambuco, Nordeste do Brasil’, *Revista Brasileira de Botanica*. doi: 10.1590/S0100-84042006000300005.

Lewinsohn, T. M. and Vasconcellos-Neto, J. (2009) ‘Como insetos sabotam defesas de plantas: o caso do latex', *Oecologia Brasiliensis*. doi: 10.4257/oeco.2000.0801.10.

Lima, A. L. A. and Rodal, M. J. N. (2010) ‘Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil’, *Journal of Arid Environments*. doi: 10.1016/j.jaridenv.2010.05.009.

Locatelli, E. and Machado, I. C. S. (1999) ‘ Comparative Study of the Floral Biology in Two Ornithophilous Species of Cactaceae: Melocactus zehntneri and Opuntia palmadora ’, *Bradleya*. doi: 10.25223/brad.n17.1999.a4.

Lohbeck, M. *et al.* (2015) ‘Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession’, *PLoS ONE*. doi: 10.1371/journal.pone.0123741.

Machado, I. C. S., Barros, L. M. and Sampaio, E. V. S. B. (1997) ‘Phenology of caatinga species at Serra Talhada, PE, Northeastern Brazil’, *Biotropica*. doi: 10.1111/j.1744-7429.1997.tb00006.x.

Matos, P. *et al.* (2017) ‘Tracking global change using lichen diversity: towards a global-scale ecological indicator’, *Methods in Ecology and Evolution*. doi: 10.1111/2041-210X.12712.

Medina, E., Olivares, E. and Diaz, M. (1986) ‘Water stress and light intensity effects on growth and nocturnal acid accumulation in a terrestrial CAM bromeliad (Bromelia humilis Jacq.) under natural conditions’, *Oecologia*. doi: 10.1007/BF00379509.

Milcu, A. *et al.* (2014) ‘Functional diversity of leaf nitrogen concentrations drives grassland carbon fluxes’, *Ecology Letters*. doi: 10.1111/ele.12243.

Mouchet, M. A. *et al.* (2010) ‘Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules’, *Functional Ecology*. doi: 10.1111/j.1365-2435.2010.01695.x.

Moura, M. M. S. *et al.* (2016) ‘Produção de serapilheira e suas frações em área da Caatinga no Semiárido Tropical’, *Revista Brasileira de Gestão Ambiental e Sustentabilidade*. doi: 10.21438/rbgas.030509.

Nunes, A. *et al.* (2017) ‘Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands’, *Agricultural and Forest Meteorology*. doi: 10.1016/j.agrformet.2017.03.007.

Oliveira, A. C. *et al.* (2020) ‘From species presences to abundances: Using unevenly collected plant species presences to disclose the structure and functioning of a dryland ecosystem’, *Ecological Indicators*. doi: 10.1016/j.ecolind.2020.106221.

Olofsson, J. *et al.* (2004) ‘Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone’, *Oikos*. doi: 10.1111/j.0030-1299.2004.13224.x.

Pérez-Harguindeguy, N. *et al.* (2013) ‘New handbook for standardised measurement of plant functional traits worldwide’, *Australian Journal of Botany*. doi: 10.1071/BT12225.

Pour, S. H., Wahab, A. K. A. and Shahid, S. (2020) ‘Spatiotemporal changes in aridity and the shift of drylands in Iran’, *Atmospheric Research*. doi: 10.1016/j.atmosres.2019.104704.

Pueyo, Y. *et al.* (2008) "Dispersal strategies and spatial organization of vegetation in arid ecosystems", *Oikos.* doi:10.1111/j.0030-1299.2008.16735.x

Ricotta, C. and Moretti, M. (2011) ‘CWM and Rao’s quadratic diversity: A unified framework for functional ecology’, *Oecologia*. doi: 10.1007/s00442-011-1965-5.

Santana, J. A. da S. and Souto, J. S. (2011) ‘Produção de serapilheira na Caatinga da região semi-árida do Rio Grande do Norte, Brasil’, *Idesia*. doi: 10.4067/s0718-34292011000200011.

Schenk, H. J. and Jackson, R. B. (2002) ‘Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems’, *Journal of Ecology*. doi: 10.1046/j.1365-2745.2002.00682.x.

Sfair, J. C. *et al.* (2018) ‘Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest’, *Environmental Research Letters*. doi: 10.1088/1748-9326/aa9f5e.

Silva, A. C. and Souza, A. F. (2018) ‘Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America’, *PLoS ONE*. doi: 10.1371/journal.pone.0196130.

da Silva, J. M. C. and Barbosa, L. C. F. (2018) ‘Impact of human activities on the Caatinga’, in *Caatinga: The Largest Tropical Dry Forest Region in South America*. doi: 10.1007/978-3-319-68339-3_13.

da Silva, J. M. C., Leal, I. R. and Tabarelli, M. (2018) *Caatinga: The largest tropical dry forest region in South America*, *Caatinga: The Largest Tropical Dry Forest Region in South America*. doi: 10.1007/978-3-319-68339-3.

Suding, K. N. *et al.* (2008) ‘Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants’, *Global Change Biology*. doi: 10.1111/j.1365-2486.2008.01557.x.

The R Core Team (2018) *R: A language and environment for statistical computing.*, *R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.* doi: 10.1038/sj.hdy.6800737.

Tilman, D. *et al.* (1997) ‘The influence of functional diversity and composition on ecosystem processes’, *Science*. doi: 10.1126/science.277.5330.1300.

Trabucco, A. *et al.* (2008) ‘Climate change mitigation through afforestation/reforestation: A global analysis of hydrologic impacts with four case studies’, *Agriculture, Ecosystems and Environment*. doi: 10.1016/j.agee.2008.01.015.

van Rheede van Oudtshoorn, K. and van Rooyen, M. W. (1999). Dispersal biology of desert plants. Springer.

Valencia, E. *et al.* (2015) ‘Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands’, *New Phytologist*. doi: 10.1111/nph.13268.

Wright, I.J., et al. (2004) "The worldwide leaf economics spectrum", *Nature* 12, 821–827.

Zhang, Q. *et al.* (2018) 'Comparative Analysis of Global Solar Radiation Models in Different Regions of China', *Advances in Meteorology*. doi: 10.1155/2018/3894831.

3.6 Supporting Information

Table S3.2 Lista of the 48 most abundant plant species from the Brazilian dry forest (Caatinga).

Family/Species	Author
ANACARDIACEAE	
Astronium urundeuva	(M.Allemão) Engl.
Schinopsis brasiliensis	Engl.
Spondias tuberosa	Arruda
APOCYNACEAE	
Aspidosperma pyrifolium	Mart. & Zucc.
BIGNONIACEAE	
Handroanthus impetiginosus	(Mart. ex DC) Mattos
BROMELIACEAE	
Bromelia laciniosa	Mart. ex Schult. & Schult.f.
Encholirium spectabile	Mart. ex Schult. & Schult.f.
Neoglaziovia variegata	(Arruda) Mez
Tillandsia loliacea	Mart. ex Schult. & Schult.f.
Tillandsia recurvata	(L.) L.
Tillandsia streptocarpa	Baker
BURSERACEAE	
Commiphora leptophloeos	(Mart.) J.B.Gillett
CACTACEAE	
Arrojadoa rhodantha	(Gürke) Britton & Rose
Cereus jamacaru	DC.
Harrisia adscendens	(Gürke) Britton & Rose
Melocactus zehntneri	(Britton & Rose) Luetzelb.
Xiquexique gounellei subsp. gounellei	(F.A.C.Weber) Lavor & Calvente
Pilosocereus pachycladus	F.Ritter
Tacinga inamoena	(K.Schum.) N.P.Taylor & Stuppy

Tacinga palmadora	(Britton & Rose) N.P.Taylor & Stuppy
CAPPARACEAE	
Cynophalla flexuosa	(L.) J.Presl
Neocalyptrocalyx longifolium	(Mart.) Cornejo & Iltis
CHRYSOBALANACEAE	
Microdesmia rigida	(Benth.) Sothers & Prance
EUPHORBIACEAE	
Cnidoscolus quercifolius	Pohl
Croton blanchetianus	Baill.
Jatropha mollissima	(Pohl) Baill.
Jatropha ribifolia	(Pohl) Baill.
Manihot carthagenensis	(Jacq.) Müll.Arg.
Sapium glandulosum	(L.) Morong
FABACEAE	
Amburana cearensis	(Allemão) A.C.Sm.
Anadenanthera colubrina	(Vell.) Brenan
Bauhinia cheilantha	(Bong.) Steud.
Cenostigma pyramidale	(Tul.) E.Gagnon & G.P.Lewis
Enterolobium contortisiliquum	(Vell.) Morong
Libidibia ferrea	(Mart.ex Tul.) L.P.Queiroz
Luetzelburgia auriculata	(Allemão) Ducke
Mimosa tenuiflora	(Willd.) Poir.
Parapiptadenia zehntneri	(Harms) M.P.Lima & H.C.Lima
Piptadenia retusa	P.G.Ribeiro, Seigler & Ebinger
Pityrocarpa moniliformis	(Benth.) Luckow & R.W.Jobson
Senna spectabilis	(DC.) H.S.Irwin & Barneby
Senna trachypus	(Benth.) H.S.Irwin & Barneby
MALVACEAE	
Pseudobombax marginatum	(A.St.-Hil., Juss. & Cambess.) A.Robyns
NYCTAGINACEAE	
Guapira noxia	(Netto) Lundell
RHAMNACEAE	
Sarcomphalus joazeiro	(Mart.) Hauenshild

SAPINDACEAE	
Sapindus saponaria	L.
SAPOTACEAE	
Sideroxylon obtusifolium	(Roem. & Schult.) T.D.Penn.
SELAGINELLACEAE	
Selaginella convoluta	(Arn.) Spring

Chapter 4

Using plant functional groups as ecological indicators to track the effects of aridity in dryland ecosystems

Oliveira, A.C.P., Nunes, A., Oliveira, M.A., Oliveira, R., Rodrigues, R.G. & Branquinho, C. (*in preparation*) Using plant functional groups as ecological indicators to track the effects of aridity in dryland ecosystems. Intended for submission to *Ecological Indicators*.

4 Using plant functional groups as ecological indicators to track the effects of aridity in dryland ecosystems

4.1 Abstract

Increasing aridity associated with climate change may lead to the crossing of critical ecosystem thresholds, changing its structure and negatively affecting the functioning of drylands. This may aggravate land degradation in drylands (i.e. desertification), affecting ecosystem services essential to human well-being. Thus, finding tools to early detect the effects of increasing aridity on ecosystems is extremely urgent to avoid irreversible damage. Here, we assessed changes in plant community functional structure along a spatial aridity gradient in a tropical dry forest, to select the more appropriate plant functional groups as ecological indicators to track the ecosystem trajectories in response to aridity over time. To do that, we identified the main functional groups of the dominant plant species based on multiple traits, such as growth form, chemical defense and crassulacean acid metabolism (CAM) photosynthetic pathway. We identified seven functional groups, whose relative abundances changed with increasing aridity, showing either increasing or decreasing trends, not always linear. Functional groups with chemical defense and CAM were those whose relative abundance increased most with increasing aridity. We suggest that these functional groups may be used as a tool to early detect aridity impacts on these drylands ecosystems. This information can also be used to assist in the elaboration of mitigation and restoration measures to combat future climate change impacts on tropical dry forest.

4.2 Introduction

There is growing scientific evidence that the increase in aridity due to climate change will cause shifts in ecological regimes (Berdugo et al. 2020). This is particularly important in drylands where water is the limiting factor to productivity. Thus, the increase in aridity is expected to impact considerably the structure and functioning of dryland ecosystems with consequences for the delivery of ecosystem services to the local populations (Nunes et al. 2017; Wendt et al. 2020; Oliveira et al., 2020a). In this regard, it is urgent to track the effects of climate change on ecosystems at an early stage, to delay or halt negative impacts on the ecosystem's functions and structure.

Plant diversity is a crucial component of the ecosystems, sensitive to changes over time and thus interesting to be monitored. Since the response of plant community to increasing aridity over time imply long-term studies requiring data that is often not available, we may study them thought short-term, spatial climatic gradients using a space for time approach, that may allow to select a few ecological indicators to track changes over time (Nunes et al. 2017; Wendt et al. 2020; Oliveira et al., 2020a). Ecological indicators based on plant functional traits are a reliable tool to measure the effects of increasing aridity on dryland ecosystems (Branquinho et al. 2019). This is because plant species ability to thrive under this context, will depend on the potential of their functional strategies to maintain their growth, reproduction, and survival. Functional traits metrics, in particular, have received increasing attention due to the link between plant functional traits and plants' adaptative strategies to respond to disturbance (Valencia et al. 2015; Nunes et al. 2017; Oliveira et al., 2020a). In drier environmental conditions, an increase of drought tolerance plant strategies (more conservative) may be expected (Wright et al. 2004). However, in extremely arid and simultaneously seasonal environments, several studies reported an increase in drought avoidance strategies, particularly regarding leaf traits, namely higher specific leaf area and increased leaf deciduousness (e.g. Carvajal et al. 2019; Berdugo et al. 2020). This may be because in these resource-poor environments thicker leaves are more costly to maintain, and traits for fast water acquisition and use may allow plants to take advantage of short and often unpredictable periods of water availability. Additionally, aridity may favor species with lower stature (Gross et al. 2013), CAM photosynthetic pathways (Oliveira et al., 2020a), and annual life cycle (Nunes et al., 2017). Yet, plant functional traits do not vary independently, but often co-vary, involving trade-offs or allometric relationships in biological functions like carbon gain, support, water uptake, and reproduction that are associated with different plant organs (Kleyer et al. 2019). This co-variation has been shown extensively by summarizing variation in plant traits in main axes of plant specialization, enabling to identify major plant ecological strategies associated with resource use (e.g. acquisitive *versus* conservative) and “tolerance” towards limiting factors (e.g. drought tolerance *versus* avoidance). Indeed, these are the underlying reasons for grouping “functionally” similar species into functional groups.

Aridity impact on the plant community is relatively less studied in tropical drylands (e.g. Ribeiro et al. 2019; Méndez-Toribio et al. 2020; Silva et al. 2020; Oliveira et al., 2020a) than in other drylands worldwide as the Mediterranean ones as well as grassland communities of other ecosystems (e.g. Frenette-Dussault et al. 2013; Gross et al. 2013; Valencia et al. 2015; Costa-Saura et al. 2016; Nunes et al. 2017). However, tropical drylands are home to the majority of the world´s dryland population and support ecosystem services to a million people (Mortimore et al. 2009). For instance, Brazilian dry forest, locally called Caatinga, shows a floristic diversity almost twice the highest species/area ratio of the Amazon rainforests (Fernandes et al. 2020) and support ecosystem services to 28.6 million people (da Silva et al. 2018b). It is crucial to study the effects of climate change on this ecosystem due to its ecological and social relevance and the fact that this ecosystem has been modified substantially due to climate change, anthropogenic pressure and accelerated land-use intensification (da Silva and Barbosa 2018; Sfair et al. 2018).

Then, our question is: can plant functional groups be used as ecological indicators to track the effect of aridity on the plant community, to early warn us about ecological regime shifts? To answer this question, we propose to assess changes in plant community functional structure along a spatial aridity gradient in Caatinga, by grouping plant species into functional groups based on multiple traits, such as growth form, chemical defense, and root type.

4.3 Methods

Study area

Our analysis used plant data from long-term sampling along a spatial climatic gradient over an area of 750 x 350 Km, across five Brazilian states (Alagoas, Ceará, Paraíba, Pernambuco and Piauí), covered by the Tropical dry forest locally called Caatinga **(Figure 4.1)**. Caatinga is one of the most plant diverse Neotropical seasonally dry forest (Pennington et al. 2009; Banda et al., 2016) and the most vulnerable one to climate change in Brazil (Sarmiento 1975; da Silva et al. 2018). This ecosystem encompasses many vegetation types from semi-deciduous forests dominating in richer and more humid soils, to open vegetation with rocky outcrops dominating in drier areas (Fernandes and Queiroz 2018). Along the study area mean annual temperature was 24 ºC (ranging from 21 to 26 ºC), average annual precipitation 680 mm (spanning from 440 to 1098 mm), altitude ranged between 214 and 930 m, and the aridity index varied from 0.27 to 0.69 (Oliveira et al., 2020a).

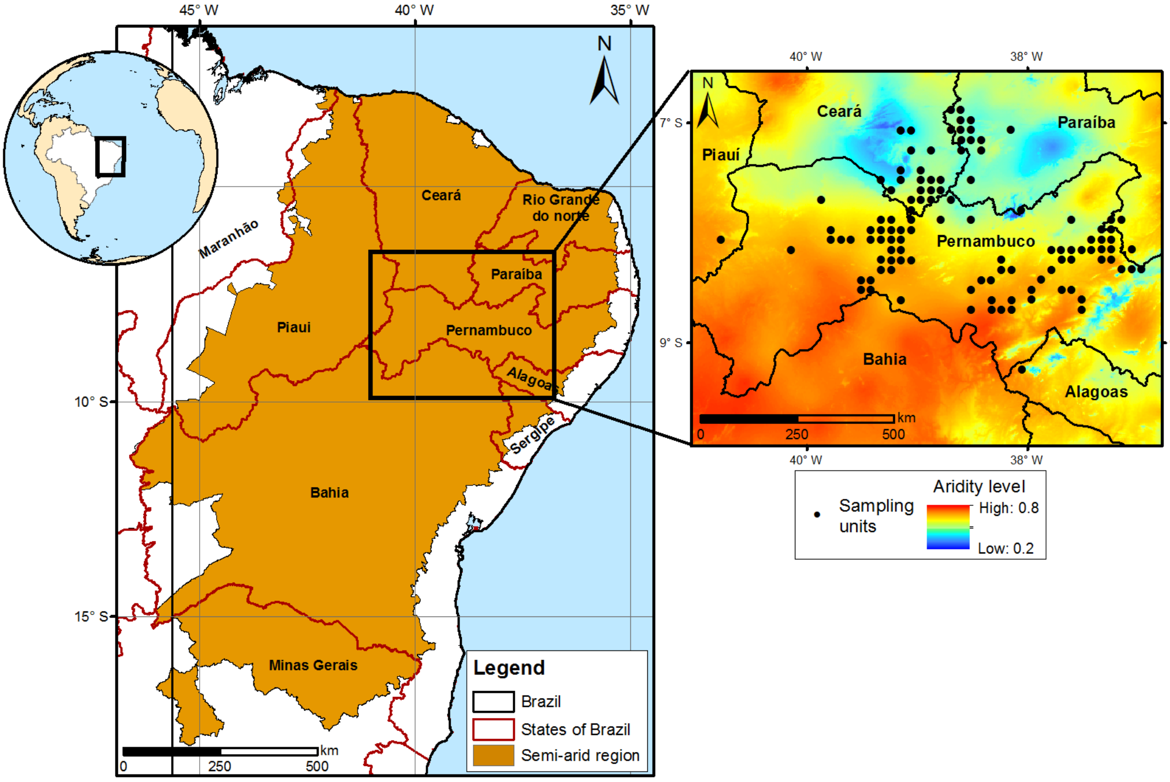

Figure 4.1 Location of the study area and the 113 sampling units (black circles) distributed along a regional aridity gradient.

Sampling

Species composition and structural attributes were evaluated in 113 sampling units (10 x 10 Km) along the spatial aridity gradient. Species abundance of the 48 most abundant Caatinga plant species was used to form our main database. Species abundances were obtained by using a re-sampling methodology applied to a species presence database (Oliveira et al. 2020b). Each of the 113 sampling units was divided into 25 sampling quadrats of 2 x 2 Km. The abundance of each species was obtained by the sum of its presence at each quadrat of 2 x 2 Km, with each species counted only once in each small quadrat (even if recorded more than once). Then, the maximum abundance at the sampling unit level was 25 (for more details see Oliveira et al., 2020b). For these 48 most abundant plant species, several functional traits were measured, namely: (1) chemical defense exudation mechanisms (hereafter chemical defense); (2) dispersal strategy; (3) fruit type; (4) growth form; (5) leaf phenology type; (6) leaf thickness; (7) maximum plant height; (8) photosynthetic pathway; (9) presence of leaves arranged in a rosette; (10) rhytidome presence; (11) root type; (12) specific leaf area (SLA); and (13) spinescence presence. These include continuous, categorical, and binary traits reflecting plant strategies associated with the establishment, defence, regeneration, and dispersal (Lewinsohn and Vasconcellos-Neto 2009; Pérez-Harguindeguy et al. 2016). Trait data were measured directly in the field following standard protocols (Pérez-Harguindeguy et al., 2016; traits 1, 2, 4, 5, 10, 12 and 13), extracted from other bibliographic sources (traits 3, 7, 9 and 11 - e.g., Griz and Machado 2001), or retrieved from the botanical collection of Herbarium Vale do São Francisco (HVASF), Petrolina, Pernambuco, Brazil (traits 6 and 8).

We used the aridity index adopted by the United Nations as the main climate variable, retrieved from a global database (Trabucco et al. 2008). It is calculated as the ratio between mean annual precipitation and annual potential evapotranspiration; thus, higher values of the aridity index correspond to less arid environments and vice-versa. Yet, to make it more intuitive to the reader, we use the term aridity (calculated as 1-the aridity index) in the discussion section.

Considering that functional traits is an “universal approach”, in the sense that they can be studied in any type of community, we elaborated a dichotomous key to identify the functional groups *in loco* in the Caatinga and in different tropical dry forest.

Data analysis

The data were grouped into separate functional groups using hierarchical, agglomerative cluster analysis with Euclidean distances and Ward linkage method - function dbFD of package FD - (Murphy, 2004) and followed by visual inspection of the resulting dendrogram and consistency in the separation of the various traits that characterize the species. The classification was based on functional traits (13 traits). Categorical traits were coded as binary or ordinal values. The abundance of the resulting functional groups was correlated with the aridity index using Spearman correlations (correlations were considered significant for $P < 0.05$). In addition, the effect of aridity on the abundance of functional groups was analysed using generalized linear models (GLM). Given that the response of the plant community to aridity is not necessarily linear, a quadratic term for aridity was also included and tested in all cases. Response variables were log-transformed whenever necessary to meet model assumptions. All statistical analyses were performed using R software version 3.4 (The R Core Team 2018).

4.4 Results

The 48 most abundant plant species in Caatinga and your traits were aggregated into seven functional groups (FG) (**Figure 4.2**; Table 1 - supplementary material). These seven formed functional groups were represented by: shrubs or herbs without leaves arranged in a rosette and without CAM photosynthetic pathway (FG1) (hereafter CAM); trees with tuberous roots but without chemical defense (latex/resin) (FG2); deciduous trees with pivoting root but without chemical defense (FG3); evergreen trees with pivoting root but without chemical defense (FG4); trees with chemical defense (FG5); CAM plants without leaves arranged in a rosette (FG6); plants with leaves arranged in a rosette (FG7) (**Figure 4.2**; see dichotomous key).

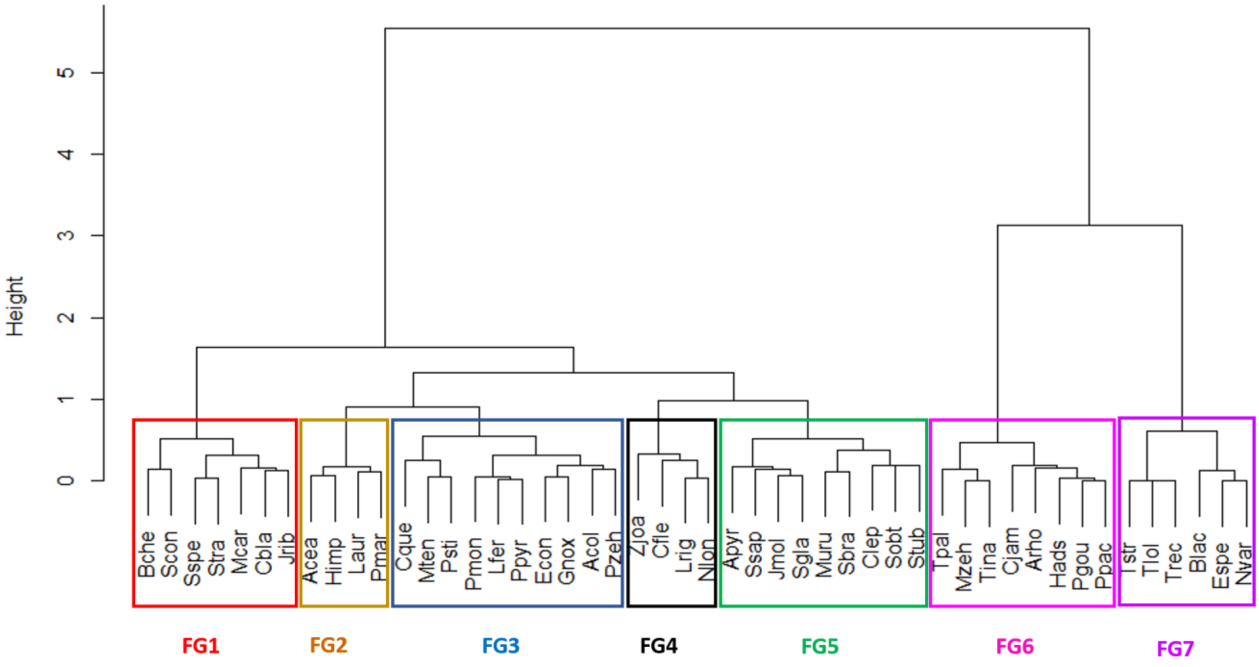

Figure 4.2 Identification of functional groups through a cluster dendrogram of species based on the functional traits of the 48 most abundant species, using the clustering method by Ward.D2 (Murphy, 2004). FG1 - shrubs or herbs without leaves arranged in a rosette and without CAM photosynthetic pathway; FG2 - trees with tuberous roots but without chemical defense (latex/resin); FG3 - deciduous trees with pivoting root but without chemical defense; FG4 - evergreen trees with pivoting root but without chemical defense; FG5 - trees with chemical defense; FG6 - CAM plants without leaves arranged in a rosette, and; FG7 - plants with leaves arranged in a rosette. Abbreviated species names: Bche (*Bauhinia cheilantha*), Scon (*Selaginella convoluta*), Sspe (*Senna spectabilis*), Stra (*Senna trachypus*), Mcar (*Manihot carthagenensis*), Cbla (*Croton blanchetianus*), Jrib (*Jatropha ribifolia*), Acea (*Amburana cearensis*), Himp (*Handroanthus impetiginosus*), Laur (*Luetzelburgia auriculata*), Pmar (*Pseudobombax marginatum*), Cque (*Cnidoscolus quercifolius*), Mten (*Mimosa tenuiflora*), Psti (*Piptadenia stipulacea*), Pmon (*Pityrocarpa moniliformis*), Lfer (*Libidibia ferrea*), Ppyr (*Cenostigma pyramidale* var. *pyramidale*), Econ (*Enterolobium contortisiliquum*), Gnox (*Guapira noxia*), Acol (*Anadenanthera colubrina*), Pzeh (*Parapiptadenia zehntneri*), Zjoa (*Sarcomphalus joazeiro*), Cfle (*Cynophalla flexuosa*), Lrig (*Microdesmia rigida*), Nlon (*Neocalyptrocalyx longifolium*), Apyr (*Aspidosperma pyrifolium*), Ssap (*Sapindus saponaria*), Jmol (*Jatropha mollissima*), Sgla (*Sapium glandulosum*), Muru (*Astronium urundeuva*), Sbra (*Schinopsis brasiliensis*), Clep (*Commiphora leptophloeos*), Sobt (*Sideroxylon obtusifolium*), Stub (*Spondias tuberosa*), Tpal (*Tacinga palmadora*), Mzeh (*Melocactus zehntneri*), Tina (*Tacinga inamoena*), Cjam (*Cereus jamacaru*), Arho (*Arrojadoa rhodantha*), Hads (*Harrisia adscendens*), Pgou (*Xiquexique gounellei subsp. gounellei),* Ppac (*Pilosocereus pachycladus*), Tstr (*Tillandsia streptocarpa*), Tlol (*Tillandsia loliacea*), Trec (*Tillandsia recurvata*), Blac (*Bromelia laciniosa*), Espe (*Encholirium spectabile*), Nvar (*Neoglaziovia variegata*).

Dichotomous key for the identification of the functional groups for Tropical dry forest based on plant functional traits of the Caatinga

1. Herb or shrub ……………………………………………………….………..……. 2
    2. No CAM or leaves in rosete plants ………………………..…...………. **FG1**
    2´. CAM or plants with leaves in rosette …………………………....…....…. 3
        3. CAM plants ……….………………………………..……………….. **FG6**
        3´. Plants with leaves in rosette ………………….…..……….….…. **FG7**
1´. Trees ………...………………………..………………………..……………. 4
    4. With chemical defense …………………..………………….……….…. **FG5**
    4´. Without chemical defense ……………………………..……………..…. 5
        5. Tuberous roots ……………………...…………………..…………. **FG2**
        5´. Pivoting roots ……………………………………………………..……. 6
6. Deciduous plants ………………………………...……………………. **FG3**
6´. Evergreen plants ……………………………………………………..……. **FG4**

Functional groups exhibited either a linear (FG1, FG2, FG4, FG5, and FG7) or non-linear (FG3 and FG6) response to increasing aridity **(Figure 4.3)**. The relative abundance of FG1, FG2, and FG4 decreased linearly with increasing aridity, while the abundance of FG5 and FG7 increased. The slope of FG5 relationship with aridity was more pronounced than that of other functional groups, indicating higher rates of change in the relative abundance with changing aridity. There is an abrupt change in the response of the abundance of FG3 and FG6 to aridity index around 0.4. FG3 abundance decreases linearly until 0.4, and it begins to increase after this threshold towards higher aridity, while FG6 shows the opposite trend **(Figure 4.3)**.

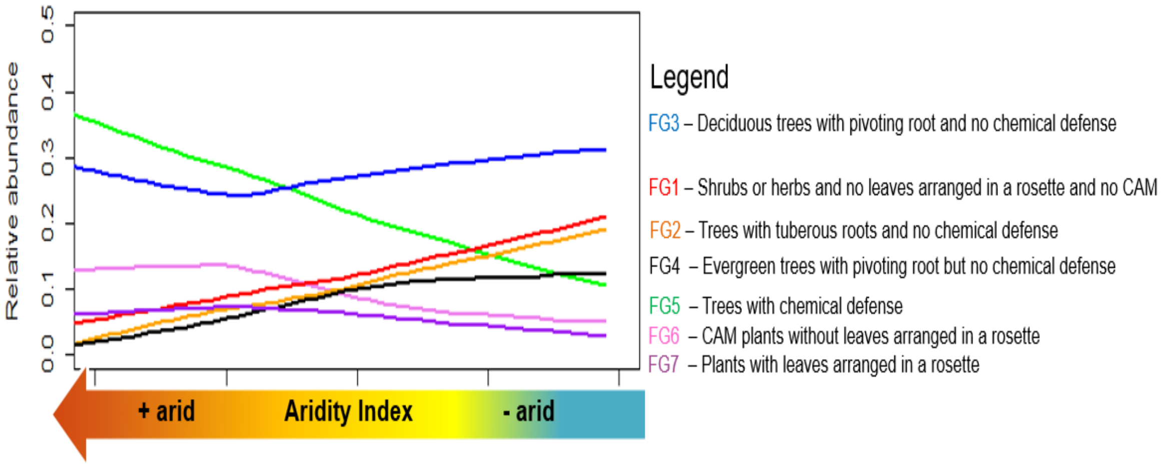

Figure 4.3 Relationships between the relative abundance of seven functional groups and aridity modelled through generalized linear models (GLM). FG1 - shrubs or herbs without leaves arranged in a rosette and without CAM photosynthetic pathway; FG2 - trees with tuberous roots but without chemical defense (latex/resin); FG3 - deciduous trees with pivoting root but without chemical defense; FG4 - evergreen trees with pivoting root but without chemical defense; FG5 - trees with chemical defense; FG6 - CAM plants without leaves arranged in a rosette, and; FG7 - plants with leaves arranged in a rosette.

4.5 Discussion

In this work, we identified seven plant functional groups which aggregate species based on various functional traits (e.g. roots, leaves and form of growth) and reflected co-variation between different traits. All of the seven functional groups responded to aridity but the groups with chemical defense and CAM photosynthetic pathway apparatus were the dominating ones in terms of relative abundance. This and the fact that they considerably change with aridity suggests that both functional groups (plants with chemical defenses and plant with CAM photosynthesis pathway) which are based on the existence of chemical defenses and the type of photosynthesis traits were the best ones to be used over time to track the effect of aridity on the tropical dry forest of Caatinga. Within this context and responding to our main question, plant functional groups may be used as ecological indicators to track the effect of aridity over time in tropical dry forests and to early warn us about ecological regime shifts.

Chemical defense is strongly associated with plant protection towards herbivory and pathogens (Gómez and Zamora 2002; Olofsson et al. 2004; Lewinsohn and

Vasconcellos-Neto 2009), and only a few studies indicate their link with the regulation of water balance (Sen and Chawan 1972; Parkin 1990 apud Farrell et al. 1991)(Sen and Chawan 1972; Farrell et al. 1991) or with other abiotic factors (e.g. aridity) (Oliveira et al., 2020a). Due to its role as a defense mechanism against herbivory attacks (e.g. pathogens, insects and mammals), its presence can represent an indirect way to control nutrient fluxes and, consequently its influence on productivity, biomass, and species composition of plant communities (Hunter 2001; Frank et al. 2002; Olofsson et al. 2002). Thus, in environments with strong herbivory pressure, plants with protection against these predators have an advantage in relation to plants without this defense strategy. Plants without chemical defenses are more easily predated (Ribeiro et al., 1999) and tend to decrease in abundance as herbivores pressure increases. In Caatinga, goats are important herbivores, as they can eat all parts of the palatable plants, from the flower to the litter (Leal et al. 2003). In 2017, nine million goats were estimated to live in Caatinga, and their pressure represents a threat to the composition, dynamics, and functioning of this ecosystem (Guimarães Filho and Goes, 1998). Having this in mind, under increasing aridity, the increase of the functional group represented by trees with chemical defense (FG5), may be more directly associated with the herbivory pressure of the environment, and only indirectly with water limitations.

In terms of the photosynthetic pathway, CAM is a common strategy found in arid environments in which plants close their stomata during the day to prevent water losses and open them during the night to allow the uptake of carbon dioxide (CO_2) for carbon fixation (Medina et al. 1986). In Caatinga, as well as, in other dryland ecosystems (e.g. America and Africa) this trait is present in succulent plants such as the emblematic Cactaceae that were the only representatives of FG6. Along the spatial climate gradient, the abundance of this functional group was relatively constant increasing above 0.5 of aridity index. They are easy to identify and given that their relative proportion increases with aridity, their abundance can be used as an ecological indicator to identify the trajectory to more arid environments.

Meanwhile in less arid environments, shrubs and herbs without CAM and leaves not arranged in a rosette (FG1) tend to decrease its relative abundance with aridity. Shrubs as woody plants with shorter stature compared to trees, may minimize the hydraulic failure that occurs when water transport is disrupted in many embolized vessels (cavitation) due to water limitations (Urli et al. 2013; Gong et al. 2020). The presence of this strategy is important since it translates into resistance to drought-induced xylem embolism (Gong et al. 2020). Although this strategy could be associated with environments with water limitation (but nor only), this functional group decreases with aridity and is replaced by plants of the FG6 and FG7, which have CAM photosynthetic pathway and leaves arranged in a rosette, respectively. Then, these latter traits seems to be more advantageous to deal with the lack of water and its seasonality in more arid areas.

Trees with pivoting roots but no chemical defenses, whether they are deciduous or evergreen (FG3 and FG4), tolerate less aridity than trees with chemical defenses. The root system of trees with tuberous roots has specific organs to store water and nutrients in response to water deficit stress (Mertens et al. 2017). Deciduous and evergreen leaf phenology types are associated with plants that drop their leaves during dry seasons (drought avoidance) and plants that retain their leaves throughout the year (drought tolerance), respectively. These leaf phenology types, together with other leaf traits (e.g. thickness), support photosynthesis and transpiration rates to avoid or conserve water during dry periods (Ackerly 2004; Markesteijn and Poorter 2009). Although the trees of the FG3 and FG4 have traits considered specific to deal with water limitation namely tuberous roots and leaf phenology type deciduous and evergreen they do not tolerate so much aridity as compared to the ones with chemical defenses. This result suggests that the limiting factor for survival and reproduction in the more arid area of the gradient is more directly related to herbivory than with the lack of water.

The plants with leaves arranged in a rosette (FG7) have mechanisms to avoid water loss through traits that allow a decrease in the evaporative surface area and also that reduce the amount of the absorbed radiation from external to internal leaves (Neuner et al. 1999). The relative abundance of this functional group did not show substantial changes along the aridity gradient indicating that this functional group (FG7) is not the most appropriate to track the effects of aridity in tropical drylands.

Concluding remarks

Overall, our results showed that the two functional groups of plants with chemical defense and plants with CAM photosynthetic pathway may be appropriate ecological indicators to track the effects of aridity on the ecosystem in tropical drylands such as the Caatinga. In this context, more arid environments will be dominated by trees with chemical defense. While in less arid environment deciduous with pivoting root but without chemical defense will tend to be dominant.

Thus, the use of functional groups as ecological indicators can be a good tool to track the effects of aridity. This may be used to early warn about some thresholds that are expected to occur in drylands (Berdugo et al. 2020). Additionally, decision-makers can use these results as well as the dichotomous key for the identification of the functional groups, to delay or stop the reaching of thresholds that may cause a permanent change in the ecosystems. This means that restoration projects should include plants which prioritize not only the number of traits adequate for each aridity level but also the proportion of those traits. In this way it is expected to restore both traits diversity and the functionality of the ecosystem, thus ensuring essential ecosystem services for human well-being.

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References

Ackerly D (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol Monogr. https://doi.org/10.1890/03-4022

Berdugo M, Delgado-Baquerizo M, Soliveres S, et al (2020) Global ecosystem thresholds driven by aridity. Science (80-). https://doi.org/10.1126/science.aay5958

Branquinho C, Serrano HC, Nunes A, et al (2019) Essential Biodiversity Change Indicators for Evaluating the Effects of Anthr1. Branquinho C, Serrano HC, Nunes

A, Pinho P, Matos P. Essential Biodiversity Change Indicators for Evaluating the Effects of Anthropocene in Ecosystems at a Global Scale. In 201

Carvajal DE, Loayza AP, Rios RS, et al (2019) A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. J Ecol. https://doi.org/10.1111/1365-2745.13092

Costa-Saura JM, Martínez-Vilalta J, Trabucco A, et al (2016) Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species. Perspect Plant Ecol Evol Syst. https://doi.org/10.1016/j.ppees.2016.05.001

da Silva JMC, Barbosa LCF (2018) Impact of human activities on the Caatinga. In: Caatinga: The Largest Tropical Dry Forest Region in South America

da Silva JMC, Barbosa LCF, Leal IR, Tabarelli M (2018a) The Caatinga: Understanding the challenges. In: Caatinga: The Largest Tropical Dry Forest Region in South America

da Silva JMC, Leal IR, Tabarelli M (2018b) Caatinga: The largest tropical dry forest region in South America

Farrell BD, Dussourd DE, Mitter C (1991) Escalation of plant defense: do latex and resin canals spur plant diversification? Am Nat. https://doi.org/10.1086/285258

Fernandes MF, Cardoso D, de Queiroz LP (2020) An updated plant checklist of the Brazilian Caatinga seasonally dry forests and woodlands reveals high species richness and endemism. J Arid Environ. https://doi.org/10.1016/j.jaridenv.2019.104079

Fernandes MF, Queiroz LP de (2018) Vegetação e flora da Caatinga. Cienc Cult 70:51–56

Frank DA, Kuns MM, Guido DR (2002) Consumer control of grassland plant production. Ecology. https://doi.org/10.1890/0012-9658(2002)083[0602:CCOGPP]2.0.CO;2

Frasconi Wendt C, Nunes A, Verble R, et al (2020) Using a space-for-time approach to select the best biodiversity-based indicators to assess the effects of aridity on Mediterranean drylands. Ecol Indic. https://doi.org/10.1016/j.ecolind.2020.106250

Frenette-Dussault C, Shipley B, Meziane D, Hingrat Y (2013) Trait-based climate change predictions of plant community structure in arid steppes. J Ecol.

https://doi.org/10.1111/1365-2745.12040

Guimarães Filho C, Góes JG. (1998) Desempenho reprodutivo de caprinos na Caatinga sob diferentes taxas de lotação. Pesquisa Agropecuária Brasileira, 23:309-314.

Gómez JM, Zamora R (2002) Thorns as induced mechanical defense in a long-lived shrub (Hormathophylla spinosa, Cruciferae). Ecology. https://doi.org/10.1890/0012-9658(2002)083[0885:TAIMDI]2.0.CO;2

Gong XW, Guo JJ, Jiang DM, et al (2020) Contrasts in xylem hydraulics and water use underlie the sorting of different sand-fixing shrub species to early and late stages of dune stabilization. For Ecol Manage. https://doi.org/10.1016/j.foreco.2019.117705

Griz LMS, Machado ICS (2001) Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. J Trop Ecol. https://doi.org/10.1017/S0266467401001201

Gross N, Börger L, Soriano-Morales SI, et al (2013) Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. J Ecol 101:637–649. https://doi.org/10.1111/1365-2745.12063

Hunter MD (2001) Insect population dynamics meets ecosystem ecology: Effects of herbivory on soil nutrient dynamics. Agric. For. Entomol.

Kleyer M, Trinogga J, Cebrián-Piqueras MA, et al (2019) Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. J Ecol. https://doi.org/10.1111/1365-2745.13066

Leal IR, Tabarelli M, Silva JMC (2003) Ecologia e Conservação da Caatinga. Ecol e Conserv da Caatinga Recife Ed Univ da UFPE. https://doi.org/10.1016/j.rec.2015.02.025

Lewinsohn TM, Vasconcellos-Neto J (2009) Como insetos sabotam defesas de plantas: o caso do latex. Oecologia Bras. https://doi.org/10.4257/oeco.2000.0801.10

Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. J Ecol. https://doi.org/10.1111/j.1365-2745.2008.01466.x

Medina E, Olivares E, Diaz M (1986) Water stress and light intensity effects on growth and nocturnal acid accumulation in a terrestrial CAM bromeliad (Bromelia humilis

Jacq.) under natural conditions. Oecologia. https://doi.org/10.1007/BF00379509

Méndez-Toribio M, Ibarra-Manríquez G, Paz H, Lebrija-Trejos E (2020) Atmospheric and soil drought risks combined shape community assembly of trees in a tropical dry forest. J Ecol. https://doi.org/10.1111/1365-2745.13355

Mertens J, Germer S, Germer J, Sauerborn J (2017) Comparison of soil amendments for reforestation with a native multipurpose tree under semiarid climate: Root and root tuber response of Spondias tuberosa. For Ecol Manage. https://doi.org/10.1016/j.foreco.2017.04.010

Mortimore M, Anderson S, Cotula L et al. (2009) Dryland opportunities: a new paradigm for people, ecosystem and development, IUCN, Gland, Switzerland; IIED, London, UK and UNDP/DDC, Nairobi, Kenya. X + 86p. ISBN: 978-2-8317-1183-6

Murphy AP (2004). The cult of personality: how personality tests are leading us to miseducate our children, mismanage our companies, and misunderstand ourselves. New York: Free Press.

Neuner G, Braun V, Buchner O, et al (1999) Leaf rosette closure in the alpine rock species Saxifraga paniculata Mill.: Significance for survival of drought and heat under high irradiation. Plant, Cell Environ. https://doi.org/10.1046/j.1365-3040.1999.00508.x

Nunes A, Köbel M, Pinho P, et al (2017) Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. Agric For Meteorol. https://doi.org/10.1016/j.agrformet.2017.03.007

Oliveira ACP, Nunes A, Rodrigues RG, et al (2020a) The response of plant functional traits to aridity in a Tropical dry forest. Science of the Total Environment https://doi.org/10.1016/j.scitotenv.2020.141177

Oliveira ACP, Nunes A, Pinho P, et al (2020b) From species presences to abundances: Using unevenly collected plant species presences to disclose the structure and functioning of a dryland ecosystem. Ecol Indic. https://doi.org/10.1016/j.ecolind.2020.106221

Olofsson J, Hulme PE, Oksanen L, Suominen O (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. Oikos. https://doi.org/10.1111/j.0030-1299.2004.13224.x

Olofsson J, Moen J, Oksanen L (2002) Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. Oikos.

https://doi.org/10.1034/j.1600-0706.2002.960208.x

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. Annu Rev Ecol Evol Syst. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2016) Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot. https://doi.org/10.1071/bt12225_co

Portillo-Quintero CA, Sánchez-Azofeifa GA (2010) Extent and conservation of tropical dry forests in the Americas. Biol Conserv. https://doi.org/10.1016/j.biocon.2009.09.020

Ribeiro EMS, Lohbeck M, Santos BA, et al (2019) Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J Ecol. https://doi.org/10.1111/1365-2745.13177

Ribeiro JELS et al. (1999) Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central. INPA, DFID Editora Manaus.

Sen DN, Chawan DD (1972) Leafless euphorbia on Rajasthan (India) rocks. Vegetatio. https://doi.org/10.1007/bf02387396

Sfair JC, De Bello F, De Frana TQ, et al (2018) Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. Environ Res Lett. https://doi.org/10.1088/1748-9326/aa9f5e

Silva JLS, Cruz-Neto O, Rito KF, et al (2020) Divergent responses of plant reproductive strategies to chronic anthropogenic disturbance and aridity in the Caatinga dry forest. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2019.135240

The R Core Team (2018) R: A language and environment for statistical computing.

Trabucco A, Zomer RJ, Bossio DA, et al (2008) Climate change mitigation through afforestation/reforestation: A global analysis of hydrologic impacts with four case studies. Agric Ecosyst Environ. https://doi.org/10.1016/j.agee.2008.01.015

Urli M, Porté AJ, Cochard H, et al (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. Tree Physiol. https://doi.org/10.1093/treephys/tpt030

Valencia E, Maestre FT, Le Bagousse-Pinguet Y, et al (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in

Mediterranean drylands. New Phytol. https://doi.org/10.1111/nph.13268

Wright IJ, Reich PB, Westoby M, et al (2004) The worldwide leaf economics spectrum. Nature. https://doi.org/10.1038/nature02403

Supporting Information

Table S4.1 Characterization of the seven functional groups identified according to the proportion of each of the 13 functional traits. For continuous traits values correspond to a range, while for categorical and binary traits values correspond to a percentage. FG1 - shrubs or herbs without leaves arranged in a rosette and without CAM photosynthetic pathway; FG2 - trees with tuberous roots but without chemical defense (latex/resin); FG3 - deciduous trees with pivoting root but without chemical defense; FG4 - evergreen trees with pivoting root but without chemical defense; FG5 - trees with chemical defense; FG6 - CAM plants without leaves arranged in a rosette, and; FG7 - plants with leaves arranged in a rosette.

Functional Groups/Units	Categories	FG1	FG2	FG3	FG4	FG5	FG6	FG7
Growth form (%)	Herbs	14	0	0	0	0	0	100
	Shrubs	86	0	0	0	0	0	0
	Trees	0	100	100	100	100	0	0
Height (m - range)		0.2 - 5.4	3.0 - 5.5	3.5 - 8.0	2.0 - 6.0	2.0 - 8.0	0.4 - 3.5	0.2 -1.0
Leaf thickness (mm - range)		0.15 - 0.84	0.9 - 2.0	0.41 - 1.55	0.58 - 0.89	0.60 - 0.92	NA	NA
Specific leaf area (mm2/mg - range)		13 - 22	16 - 18	13 - 23	51 - 21	83 - 24	NA	NA
Leaf phenology type (%)	Deciduous	86	75	100	0	100	NA	0
	Evergreen	14	25	0	100	0	NA	100
Leaves arranged in a rosette (%)	With	0	0	0	0	0	0	100
	Without	100	100	100	100	100	100	0
CAM (%)	With	0	0	0	0	0	100	50
	Without	100	100	100	100	100	0	50
Root type (%)	Adventitious	0	0	0	0	0	0	100
	Fasciculated	43	0	0	0	0	40	0
	Pivoting	43	0	90	100	90	60	0
	Tuberous	14	100	10	0	10	0	0
Fleshy fruit (%)	With	0	0	0	75	70	100	0
	Without	100	100	100	25	30	0	100
Dispersion (%)	Anemochory	0	100	10	0	33.3	0	90
	Autochory	100	0	70	25	33.3	0	10
	Zoochory	0	0	20	75	33.3	100	0
Spinescence (%)	With	0	0	30	25	10	100	50

	Without	100	100	70	75	90	0	50
Chemical defense (%)	With	43	0	10	0	100	0	0
	Without	57	100	90	100	0	100	100
Rhytidome (%)	With	0	75	30	25	10	0	0
	Without	100	25	70	75	90	100	100

Chapter 5

How do taxonomic and functional diversity metrics change along an aridity gradient in Tropical dry forest?

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5 How do taxonomic and functional diversity metrics change along an aridity gradient in Tropical dry forest?

5.1 Abstract

It is a consensus that anthropogenic threats and climate change can lead to ecosystem degradation and loss of ecosystem services that safeguard human well-being. These negative expectations provide strong motivation to evaluate biodiversity loss or change in response to climate, to anticipate them and timely adopt mitigation or restoration actions. Here, we study the response of complementary plant taxonomic and functional diversity metrics along a spatial aridity gradient in a Tropical dry forest, to infer about potential impacts of climate change over time. We found diferent responses of taxonomic (species richness and Simpson index) and functional metrics (diversity and redundancy) to aridity. While species diversity showed a hump-shaped curve in response to aridity, functional diversity and redundancy showed a positive and a negative linear relation with increasing aridity, respectively. Thus, despite the increase in functional diversity of the plant community found towards drier sites, these are composed of a low number of species with unique functions and low functional redundancy. Our results suggest a high vulnerability (low redundancy) of this tropical dry forest to the increase in aridity predicted by climate change, since the potential loss of (even a few) species can lead to the loss of key ecosystem functions. We also show that the integration of complementary taxonomic and functional diversity metrics, despite the individual response of each one, is essential for reliably tracking the impacts of climate change in drylands in space and over time.

Keywords: Caatinga; climatic gradient; functional redundancy; hump-shaped curve; space-for-time substitution.

5.2 Introduction

Anthropogenic activities, climate change, and invasive alien species have led to a global biodiversity crisis, encompassing not only biodiversity loss but also biodiversity change (Jackson and Sax 2010; Dornelas et al. 2014; Branquinho et al. 2019). These losses and changes can affect ecosystem services and consequently human well-being (Díaz et al. 2006). Thus, it is urgent to know the integrated response of biodiversity to global change drivers to anticipate irreversible damage and timely adopt adequate actions to mitigate impacts and, if possible, restore damaged ecosystems. This knowledge can avoid the crossing of tipping points (Dakos et al. 2019) and reduce mitigation and restoration costs, by implementing a proactive rather than a reactive approach (Walls 2018).

Species richness, i.e., the total number of species, is traditionally and widely used as a proxy of taxonomic metrics for biodiversity assessments (Cadotte et al. 2011). Previous studies showed plant species richness is positively related to the ability of ecosystems to maintain multiple functions, such as productivity and carbon storage, suggesting that conservation of plant diversity is crucial to minimize the negative effects of environmental change, particularly in drylands (Maestre et al. 2012). Yet, species richness provides rough information about a biological community, given that it does not consider species abundance, their representativeness nor their traits (Magurran 2004). Abundance and equitability of each species can also be included in taxonomic metrics (Ricotta 2005), such as the Simpson diversity index, which measures the probability of two random individuals in a community to belong to the same species (Ricotta 2005). Overall, taxonomic diversity metrics provide strong evidence that diversity promotes ecosystem stability and functioning, contributing significantly to many ecosystem services (Loreau 2000; Maestre et al. 2012; Mori et al. 2018). Even so, taxonomic metrics consider all species and individuals as equivalents, (Magurran 2004; Cianciaruso et al. 2009), disregarding e.g. their functional role and how they affect ecosystem functioning (Naeem and Wright 2003).

The study of species functional traits allows to overcome this limitation, providing a more mechanistic link between species and multiple ecosystem functions, such as primary productivity and nutrient cycling, as species influence these functions via their traits (Mason and De Bello 2013). Hence, functional diversity metrics have been increasingly used in addition to taxonomic metrics, as indicators of mechanisms driving changes in biological communities and as predictors of ecosystem functioning

(Petchey and Gaston 2006; Matos et al. 2017; Nunes et al. 2017; Sfair et al. 2018). Functional traits encompass morphological, behavioral and ecological differences among the individuals and species that can interfere with species growth, reproduction and survival (Violle et al. 2007).

Despite the success of the use of functional diversity *per se* or jointly with taxonomic metrics in ecological studies, these alone do not reflect the ability of communities to ensure the maintenance of ecosystem functions in face of environmental changes (De Bello et al. 2007). In this context, the concept of functional redundancy was proposed by Walker (1992), corresponding to a measure of how much a community is functionally saturated by different species represented by analogous traits. In this regard, functional redundancy can be used as a measure of detecting potential loss of species that carry out unique roles in important ecosystem processes as well as reorganization and renovation of the ecosystem after the disturbance (resilience), which can significantly affect and change ecosystem functioning (Walker 1992; Fonseca & Ganade, 2001; Hooper et al. 2005; de Bello et al., 2007; Pillar et al., 2013). Due to the peculiarity and at the same time the complementary character of these metrics, it is important to evaluate how they change along environmental gradients, and how can we interpret the observed patterns to better anticipate changes in the structure and functioning of the ecosystems to be studied over time.

Studying biodiversity changes along climatic gradients in space has become an important tool to understand potential changes over time due to climate change and has allowed to follow and anticipate abrupt changes in ecosystem structure and functioning. Dryland systems (composed of hyper-arid, arid, semi-arid and dry sub-humid areas) are characterized by a combination of high evaporation, low rainfall, and human activities such as livestock grazing, the collection of wood and non-wood forest products, fire use, and soil cultivation (Pennington et al. 2009). These characteristics make drylands highly vulnerable to climate and environmental changes (Maestre et al. 2012). Additionally, global dryland areas are expected to expand due to climate change (Dai 2011; Feng and Fu 2013; IPCC 2019; Koutroulis 2019). The global land surface occupied by drylands currently exceeds 47% and may increase an additional 7% by 2100 (Koutroulis 2019).

This study is focused on the vegetation of Caatinga, a Tropical dry forest with peculiar flora covering the semi-arid region of Brazil, and showing the highest vulnerability to climate change in that country (Sarmiento 1975; da Silva et al. 2018). A rise in temperature and a decrease in rainfall are expected to occur up to 2100 in Caatinga (IPCC 2011; Magrin et al. 2014; Buriti and Barbosa 2018). Climate change, together with anthropogenic activities, may lead to a decrease of primary production in these ecosystems, further aggravating land degradation and affecting 28.6 million people highly dependent on local natural resources (da Silva et al. 2018b). In this context, the main objective of this study is to assess changes in plant taxonomic and functional diversity metrics along a spatial aridity gradient in the Caatinga ecosystem, assuming that these can give indications about climate change impacts over time. We hypothesized that complementary diversity metrics will respond differently to aridity in this tropical dry forest, namely that with increasing aridity we will find: (i) a decrease in species richness to only those highly adapted to drought (e.g., Maestre et al., 2012); (ii) a decrease in functional diversity due to environmental filtering (e.g., Nunes et al., 2017); (iii) an increase in functional redundancy between species sharing the same drought-adapted traits (e.g., Fonseca and Ganade 2001; De Bello et al. 2007; Pillar et al. 2013).

5.3 Methods

Study area

The present study was carried out along a regional aridity gradient over an area of 11 300 km^2 covering four Brazilian states, namely Alagoas, Ceará, Paraíba, Pernambuco and Piauí **(Figure 5.1)**. This gradient overlaps the Caatinga Phytogeographic Domain which has many vegetation types ranging from semi-deciduous forests to open vegetation, located in rocky outcrops in driest areas (Fernandes and Queiroz 2018). The study area has a mean annual temperature of 24 ºC (ranging from 21 ºC to 26 ºC), average annual precipitation of 680 mm (spanning from 440 to 1098 mm), and an altitude between 278 m and 930 m (Oliveira et al., 2020a). The aridity index varies from 0.27 to 0.69 including mostly semi-arid and humid (Oliveira et al., 2020a).

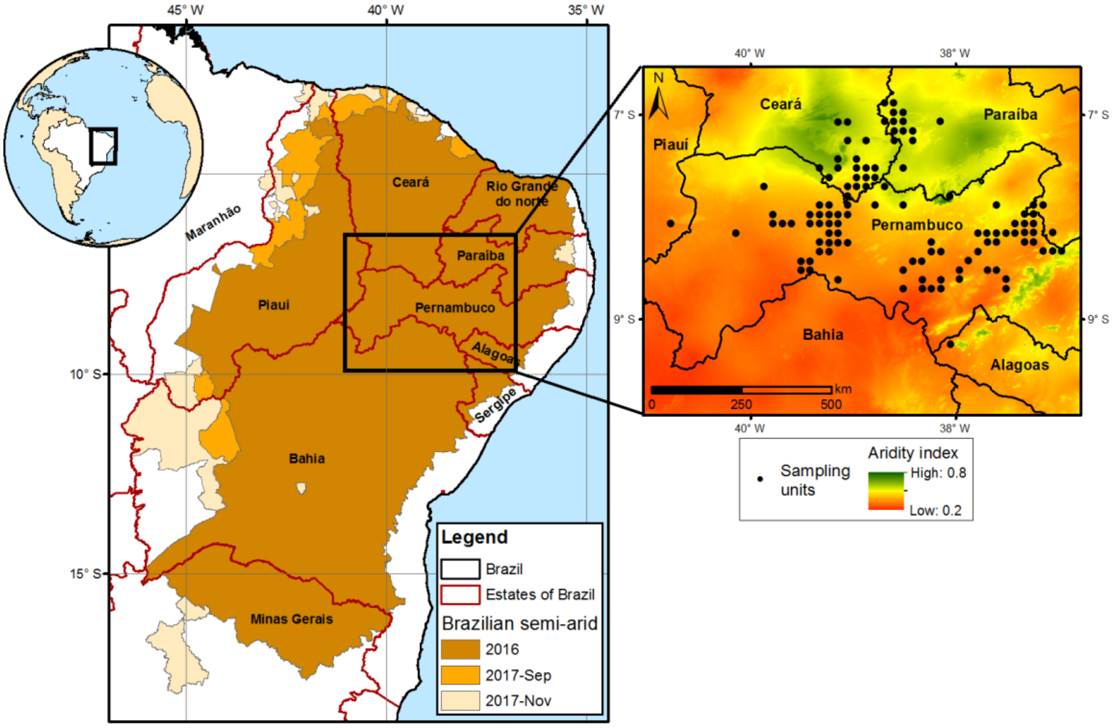

Figure 5.1. Map with the location of the study area (Adapted from Laboratório de Análise e Processamento de Imagens de Satélites – LAPIS) and the 113 sampling units (black dots) distributed along a regional aridity gradient.

Data Sampling

The database used in this work comprises the most abundant plant species from the Brazilian dry forest extracted from an initial database with presence records of 937 plant species, collected between 2008 and 2015 within 32.300 Km^2. To estimate species abundances based on presence data for these 937 plant species we divided each of the 113 sampling units (10 x 10 Km) into 25 sampling quadrats of 2 x 2 Km (for more details see Oliveira et al. 2020a). The sum of the presence records of each species at each small quadrat (2 x 2 Km) was considered a proxy of its abundance, with each species, counted only once in each quadrat (even if recorded more than once). Thus, the maximum abundance at the sampling unit level was 25. With these data we built an abundance database and selected the most dominant species comprising 80% of species relative abundance, obtaining 48 species distributed in 17 families and 42 genera. Fabaceae was the most frequent family (13 species), followed by Cactaceae (eight species), Euphorbiaceae and Bromeliaceae (six species each) and Anacardiaceae (four species).

Then, we used this database to calculate taxonomic and functional diversity metrics for each sampling unit to assess the response of plant communities to climate along an aridity gradient. Taxonomic diversity was calculated as total species richness (i.e., number of different taxa found) and the Simpson diversity index (Simpson 1949). To compute community functional metrics, we selected 13 functional traits, namely: (1) growth form; (2) maximum plant height; (3) leaf phenology type; (4) leaf thickness; (5) specific leaf area (SLA); (6) root type; (7) dispersal strategy; (8) fruit type; (9) photosynthetic pathway; (10) spinescence presence; (11) presence of leaves arranged in a rosette; (12) chemical defence exudation mechanisms; and (13) rhytidome presence. These comprise continuous, categorical and binary traits reflecting plant strategies associated with plant establishment, defence, regeneration, and dispersal (Lewinsohn and Vasconcellos-Neto 2009; Pérez-Harguindeguy et al. 2016). Trait data for the 48 most abundant species were measured directly in the field following standard protocols (Pérez-Harguindeguy et al., 2016; for traits 1, 2, 4, 5, 10, 12 and 13), retrieved from the botanical collection of Herbarium Vale do São Francisco (HVASF), Petrolina, Pernambuco, Brazil (for traits 6 and 8), or from other bibliographic sources (for traits 3, 7, 9 and 11). We then calculated functional diversity (Rao's quadratic entropy) and functional redundancy (De Bello et al. 2007; Pillar et al. 2013) for the plant community. Rao's quadratic entropy (Rao's hereinafter) is influenced by species abundance and diversity in their traits (Botta-Dukat 2005). In this index, the dissimilarity among species abundance range from 0 to 1 and is based on a set of functional traits (Botta-Dukat, 2005). All calculations were performed with the statistical software R (The R Core Team 2018), using the dbFD function of the FD package (Laliberté et al. 2015). Functional Redundancy (FR), a feature related to the stability, resistance and resilience of ecosystems to environmental changes (Hooper et al. 2005; Guillemot et al. 2011), was also determined. Functional redundancy was obtained for each sampling unit through the differences between taxonomic diversity (using the Simpson diversity index) and functional diversity (using Rao´s quadratic entropy) (De Bello et al. 2007; Pillar et al. 2013).

To characterize the climatic gradient, we used the aridity index adopted by the United Nations, whose values were retrieved from a global database (Trabucco et al. 2008). The aridity index is calculated as the ratio between mean annual precipitation and annual potential evapotranspiration. Thus, lower values correspond to more arid environments, and vice-versa.

Data Analysis

To evaluate the response of the plant community to aridity, we used the aridity index as a predictor to explain changes in community taxonomic and functional metrics (species richness, Simpson diversity index, Rao´s, and functional redundancy). The relationships between the aridity index and taxonomic and functional metrics were tested using general linear models, except for species richness (counts), which was analysed using generalized linear models (GLM) with Poisson distribution, accounting for overdispersion. For all models we included and tested a quadratic term for aridity, as the response of the plant community to aridity is not necessarily linear. Response variables were log transformed whenever necessary to meet model assumptions. All statistical analyses were performed using R software version 3.4 (R Core Team, 2018).

5.4 Results

Within the 113 sampling units distributed along the aridity gradient, species richness ranged between 8 and 45 of a maximum of 48 species **(Figure 5.2 A).** Simpson diversity index ranged from 0.87 to 0.98 **(Figure 5.2 B).** Functional diversity, represented by Rao's, ranged from 0.03 to 0.15 and functional redundancy spanned from 0.57 to 0.71 **(Figure 5.2 C and D,** respectively**)**.

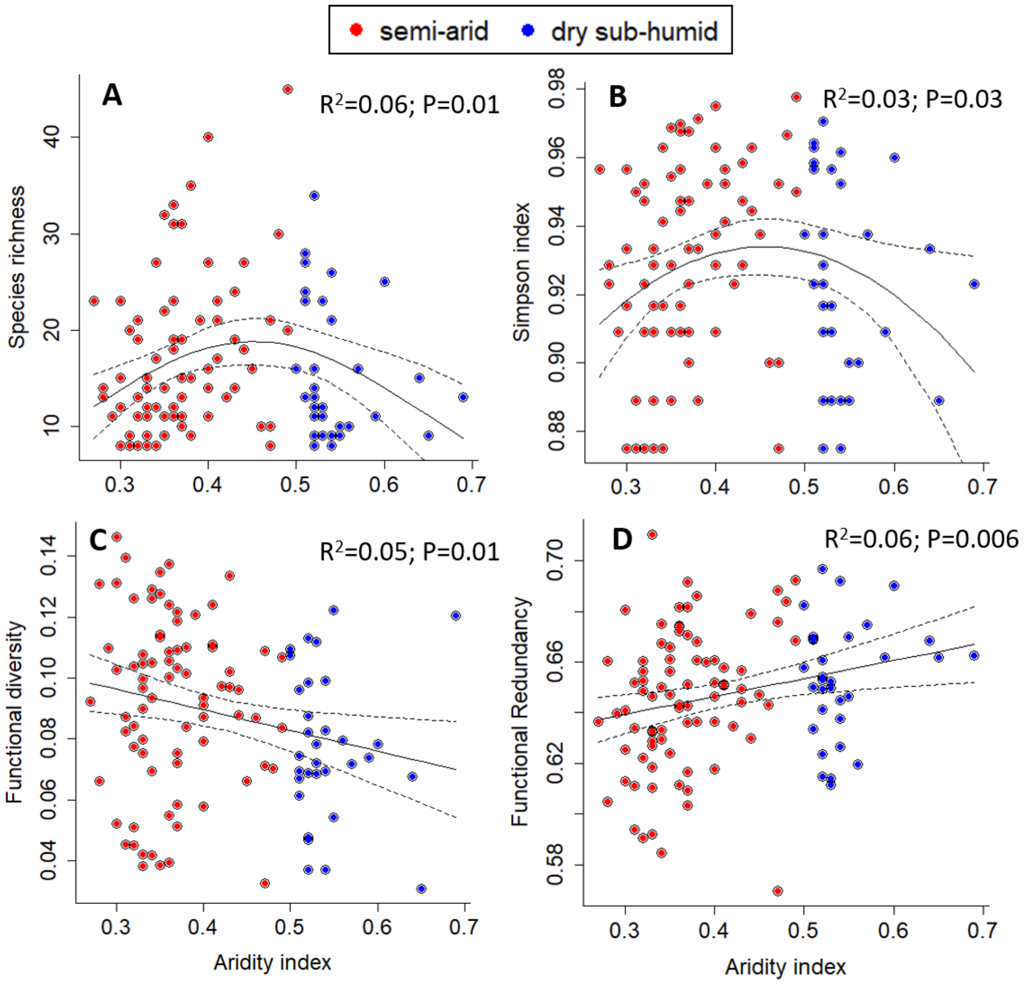

Figure 5.2. Relationships between the aridity index and: (A) species richness; (B) Simpson diversity index; (C) functional diversity; and (D) functional redundancy. Solid and dashed lines represent the fitted linear or quadratic regression and 95% confidence intervals, respectively. Adjusted R^2 and associated p-values are also shown.

Taxonomic metrics, namely species richness and the Simpson diversity index, showed a significant hump-shaped relationship with the aridity index (lower value of the aridity index corresponds to higher aridity, and vice-versa), peaking at intermediate aridity levels, despite the considerable dispersion of values between sites **(Figure 5.2 A, B)**. This is supported by the best fit of the quadratic regression between taxonomic metrics and the predictor variable **(Figure 5.2 A, B).** Plant communities with a larger number of species were found within an aridity index ranging from 0.34 to 0.52. Most species showed a widespread distribution along the studied gradient **(Figure 5.3).** Yet, we found species with a more restricted distribution occurring in a minimum of 17% of sampled plant communities along the climatic gradient, while species with a higher distribution range occurred in a maximum of 70%. Despite many species are present along the gradient (e.g., *Anadenanthera colubrina* (Vell.) Brenan, Fabaceae), although, with different abundances, there are also species of more restricted distribution, associated mainly with the most arid places (e.g, *Cnidosculus quercifolius* Pohl, Euphorbiaceae) and others to less arid ones (e.g., *Microdesmia rigida* (Benth.) Sothers & Prance, Chrysobalanaceae) **(Figure 5.3).**

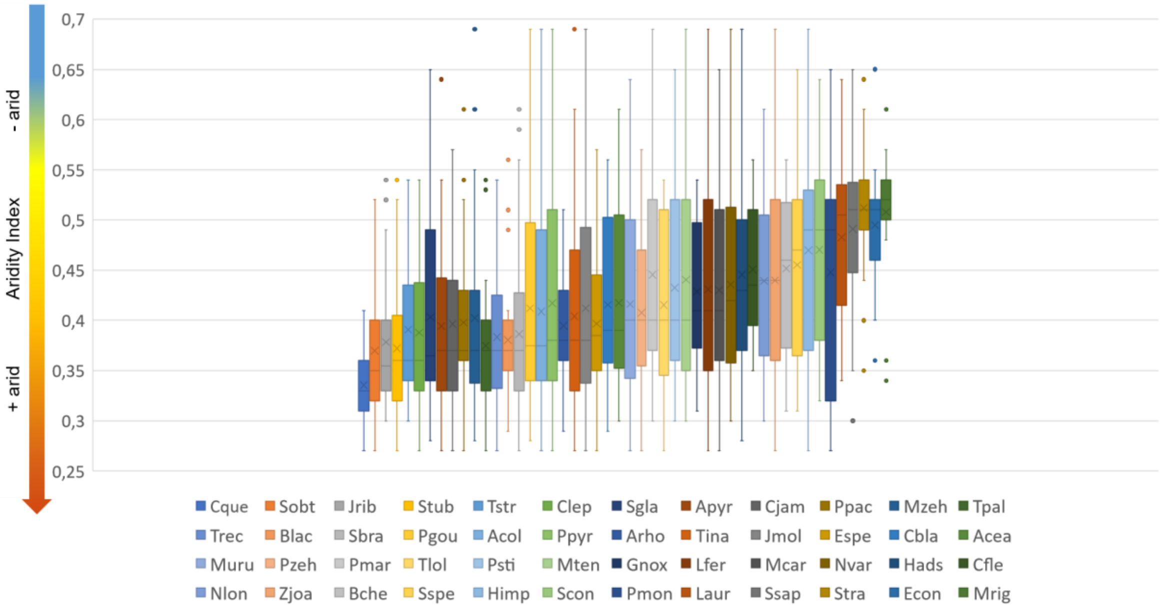

Figure 5.3. Boxplots showing the distribution of species' presence along the aridity gradient ranked by median values. Abbreviated species´ names: Cque (*Cnidoscolus quercifolius*), Sobt (*Sideroxylon obtusifolium*), Jrib (*Jatropha ribifolia*), Stub (*Spondias tuberosa*), Tstr (*Tillandsia streptocarpa*), Clep (*Commiphora leptophloeos*), Sgla (*Sapium glandulosum*), Apyr (*Aspidosperma pyrifolium*), Cjam (*Cereus jamacaru*), Ppac (*Pilosocereus pachycladus*), Mzeh (*Melocactus zehntneri*), Tpal (*Tacinga palmadora*), Trec (*Tillandsia recurvata*), Blac (*Bromelia laciniosa*), Sbra (*Schinopsis brasiliensis*), Pgou (*Xiquexique gounellei subsp. gounellei*), Acol (*Anadenanthera colubrina*), Ppyr (*Cenostigma pyramidale* var. *pyramidale*), Arho (*Arrojadoa rhodantha*), Tina (*Tacinga inamoena*), Jmol (*Jatropha mollissima*), Espe (*Encholirium spectabile*), Cbla (*Croton blanchetianus*), Acea (*Amburana cearensis*), Muru (*Astronium urundeuva*), Pzeh (*Parapiptadenia zehntneri*), Pmar (*Pseudobombax marginatum*), Tlol (*Tillandsia loliacea*), Psti (*Piptadenia stipulacea*), Mten (*Mimosa tenuiflora*), Gnox (*Guapira noxia*), Lfer (*Libidibia ferrea*), Mcar (*Manihot carthagenensis*), Nvar (*Neoglaziovia variegata*), Hads (*Harrisia adscendens*), Cfle (*Cynophalla flexuosa*), Nlon (*Neocalyptrocalyx longifolium*), Zjoa (*Sarcomphalus joazeiro*), Bche (*Bauhinia cheilantha*), Sspe (*Senna spectabilis*), Himp (*Handroanthus impetiginosus*), Scon (*Selaginella convoluta*), Pmon (*Pityrocarpa moniliformis*), Laur (*Luetzelburgia auriculata*), Ssap (*Sapindus saponaria*), Stra (*Senna trachypus*), Econ (*Enterolobium contortisiliquum*), Lrig (*Microdesmia rigida*).

In contrast with taxonomic metrics, functional metrics, namely functional diversity and functional redundancy, showed a linear trend along the aridity gradient **(Figure 5.2 C and D**, respectively**)**. Functional diversity increased towards more arid sites, displaying its highest values within an aridity index below 0.4 **(Figure 5.2 C).**

Functional redundancy showed the opposite trend, increasing towards less arid conditions **(Figure 5.2 D).**

5.5 Discussion

In this study, we found different responses of taxonomic and functional diversity to the aridity gradient, highlighting the importance of using complementary metrics to better understand the response of the plant community to changes in climate. The hump-shaped curve displayed by species diversity (i.e. species richness and Simpson diversity index) found in our study, peaking at intermediate levels of aridity, was contrary to our first hypothesis. However, other authors also found similar curves to the one found in this work in other studies (Wilkinson 1999; Chawla et al. 2008; Soliveres et al., 2014).

In our case, sites with intermediate aridity levels can be interpreted as an ecotone between semi-arid and more mesic sites, where most species, both from drier and more mesic environments, may co-exist, still finding adequate environmental conditions to survive (Gross et al. 2000; Mittelbach et al. 2001; Suding et al. 2005), at least in some sites. The co-existence of different species along this ecotone, can be related to a high environmental heterogeneity characteristic of Tropical dry forest (Moro et al. 2014; Oliveira et al. 2020b). For example, the typical intra and interannual irregularities in the distribution of precipitation in these regions (Moro et al. 2014; Oliveira et al. 2020b), either in space or over time, can lead to a heterogeneous distribution of vegetation, leading to high niche diversity allowing multiple species to coexist (Richerson and Lum 1980; Orians 1982; Pausas and Austin 2001).

Even so, these conditions may vary greatly along space and over time depending on interannual climatic fluctuations and their legacies on the plant community over the years, and this may be the main reason for the high variation in species diversity among sites at intermediate aridity levels, displaying both very high and very low species diversity. This variation is much lower in the extremes of the gradient, where the consistently lower species diversity suggests that plants dominating in the two extremes have different ecological strategies to cope with water availability, the main limiting factor for plants in drylands. Species dominating in more arid conditions need traits that allow them to withstand long periods of drought, as is the case of e.g. Bromeliaceae species, which have leaves arranged in a rosette, that function as “storage tanks” of water and facilitate the acquisition of nutrients (Takahashi et al. 2007). These strategies are different from the ones dominating in more mesic sites, where we found e.g. more evergreen trees such as *Cynophalla flexuosa* (L.) J. Presl (Capparaceae). Thus, species ability to persist and dominate in the plant community is a result of the environmental filtering of their traits (to deal with water and nutrient availability), and also of species interactions, e.g. their competitive ability under particular ecological conditions (competitors or stress tolerators, sensu Grime 1977) (Lloyd et al. 2000; Walker et al. 2003).

The dominance of different plant ecological strategies in the extremes of the gradient is also supported by the results of functional diversity. The tendency for higher functional diversity in drier sites, suggests that higher aridity selects for particular drought-adapted species with diverse functional traits that allow them to avoid or tolerate those stressful conditions. An example is the coexistence of species with distinct photosynthetic pathways in drier sites, including the crassulacean acid metabolism (CAM) of Cactaceae species. Again, this may be related with a higher heterogeneity in resource distribution (higher niche differentiation) in drier sites, leading to the coexistence of species with dissimilar resource acquisition strategies (Adler et al. 2001; Stubbs and Wilson 2004; De Bello et al. 2006). Yet, these findings contradict our expectations of finding a lower functional diversity in the more arid sites, as a result of environmental filtering, as was found for other (Mediterranean) drylands (e.g., Nunes et al., 2017). This contrasting result may be because our study (i) analysed different functional traits (e.g. chemical defense exudation, photosynthetic pathways and leaves arranged in a rosette), (ii) encompassed a greater geographic coverage (ca. 700 km), and (iii) considered a wider aridity range (aridity index from 0.27 to 0.69), compared to the one performed in Mediterranean drylands.

The higher functional diversity found in drier sites, coupled with low species richness, led to a lower functional redundancy, contradicting our expectations (third hypothesis). This means that drier sites have few species with different functional traits and resource acquisition strategies, to cope with high niche differentiation in a heterogeneous environment where resources are scarce, thus avoiding competing for the same resources. Hence, as aridity increases, ecosystem functioning in this tropical dry forest is largely assured by only a few species with unique functions, displaying low functional redundancy. Within this context, the loss of species with key functions, or set of species that exhibited similar ecological functions, can compromise the stability, resistance and resilience and further increase the susceptibility (Fonseca and Ganade 2001; Bellwood et al. 2003) of this ecosystem to changes in aridity. This statement is supported by the importance of: (i) species diversity in controlling the stability of ecosystems and communities (e.g., Lawton and Brown 1994; Ehrlich and Walker 1998); (ii) functional diversity in improving the resistance of dryland ecosystems to aridity (e.g., Díaz and Cabido 2001; Volaire et al. 2014); (iii) species redundancy in ensuring ecosystem resilience to disturbance (e.g., McCann 2000).

Concluding remarks

Our results observed along a spatial climatic gradient are a proxy of what might happen with climate change over time and have alarming implications for the future of these drylands. Caatinga´s Tropical dry forests are among the most diverse drylands. Yet, despite its high plant functional diversity, our findings regarding low functional redundancy suggest a high susceptibility of this ecosystem to an increase in aridity due to climate change. In what concerns the management of Caatinga, the knowledge acquired in this work can be used as an early warning, to timely adopt strategies to improve its stability, resistance and resilience to future environmental changes. This is particularly relevant given that this ecosystem has already experienced an increase and rapid anthropic derived degradation (Sfair et al. 2018; Ribeiro et al. 2019). Extra negative impacts due to an increase in temperature and reduced precipitation associated with climate change, may lead to the loss of species with key traits, compromising the functioning of this ecosystem. Furthermore, these negative impacts can accelerate desertification processes, which will affect 28.6 million people highly dependent on local natural resources (da Silva et al. 2018).

To sum up, the responses of complementary diversity metrics to aridity and the interdependence between them shown in this work, contribute to a better understanding of the susceptibility of this ecosystem to climate change, and may help to define strategies to improve the stability, resilience, and resistance to ongoing and future global changes in drylands.

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References

Adler P, Raff D, Lauenroth W (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia

Aguetoni Cambuí C, Gaspar ML, Mercier H (2009) Detection of urease in the cell wall and membranes from leaf tissues of bromeliad species. Physiol Plant. https://doi.org/10.1111/j.1399-3054.2009.01217.x

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. Ecol Lett. https://doi.org/10.1046/j.1461-0248.2003.00432.x

Botta-Dukát Z (2005) Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. J Veg Sci. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Branquinho C, Serrano HC, Nunes A, et al (2019) Essential Biodiversity Change Indicators for Evaluating the Effects of Anthr1. Branquinho C, Serrano HC, Nunes A, Pinho P, Matos P. Essential Biodiversity Change Indicators for Evaluating the Effects of Anthropocene in Ecosystems at a Global Scale. In 201

Buriti CO, Barbosa HA (2018) Um século de secas: por que as políticas hídricas não transformaram o semiárido brasileiro?

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol.

Chawla A, Rajkumar S, Singh KN, et al (2008) Plant species diversity along an altitudinal gradient of Bhabha Valley in western Himalaya. J Mt Sci. https://doi.org/10.1007/s11629-008-0079-y

Cianciaruso M V., Batalha MA, Gaston KJ, Petchey OL (2009) Including intraspecific variability in functional diversity. Ecology. https://doi.org/10.1890/07-1864.1

da Silva JMC, Leal IR, Tabarelli M (2018) Caatinga: The largest tropical dry forest region in South America

Dai A (2011) Drought under global warming: A review. Wiley Interdiscip. Rev. Clim. Chang.

Dakos V, Matthews B, Hendry AP, et al (2019) Ecosystem tipping points in an evolving world. Nat Ecol Evol. https://doi.org/10.1038/s41559-019-0797-2

De Bello F, Lepš J, Lavorel S, Moretti M (2007) Importance of species abundance for assessment of trait composition: An example based on pollinator communities. Community Ecol. https://doi.org/10.1556/ComEc.8.2007.2.3

De Bello F, Lepš J, Sebastià MT (2006) Variations in species and functional plant diversity along climatic and grazing gradients. Ecography (Cop). https://doi.org/10.1111/j.2006.0906-7590.04683.x

Díaz S, Cabido M (2001) Vive la différence: Plant functional diversity matters to ecosystem processes. Trends Ecol. Evol.

Díaz S, Fargione J, Chapin FS, Tilman D (2006) Biodiversity loss threatens human well-being. PLoS Biol.

Dornelas M, Gotelli NJ, McGill B, et al (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science (80-). https://doi.org/10.1126/science.1248484

Ehrlich P, Walker B (1998) Rivets and Redundancy. Bioscience. https://doi.org/10.2307/1313377

Feng S, Fu Q (2013) Expansion of global drylands under a warming climate. Atmos Chem Phys. https://doi.org/10.5194/acp-13-10081-2013

Fernandes MF, Queiroz LP de (2018) Vegetação e flora da Caatinga. Cienc Cult 70:51–56

Fonseca CR, Ganade G (2001) Species functional redundancy, random extinctions and the\nstability of ecosystems - Fonseca - 2001 - Journal of Ecology -\nWiley Online Library. J Ecol

Grime JP (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. Am Nat. https://doi.org/10.1086/283244

Griz LMS, Machado ICS (2001) Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. J Trop Ecol. https://doi.org/10.1017/S0266467401001201

Gross KL, Willig MR, Gough L, et al (2000) Patterns of species density and productivity at different spatial scales in herbaceous plant communities. Oikos. https://doi.org/10.1034/j.1600-0706.2000.890301.x

Guillemot N, Kulbicki M, Chabanet P, Vigliola L (2011) Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. PLoS One. https://doi.org/10.1371/journal.pone.0026735

Hooper DU, Chapin III FS, Hector A, et al (2005) Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. Ecol Monogr. https://doi.org/10.1890/04-0922

IPCC (2019) IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse gas fluxes in Terrestrial Ecosystems

IPCC (2011) Summary for Policymakers. In: IPCC Special Report on Renewable Energy Sources and Climate Change Mitigation. In: Cambridge University Press

Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends Ecol. Evol.

Koutroulis AG (2019) Dryland changes under different levels of global warming. Sci Total Environ 655:482–511. https://doi.org/10.1016/J.SCITOTENV.2018.11.215

Laliberté E, Legendre P, Shipley B (2015) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Packag. https://doi.org/http://cran.r-project.org/web/packages/FD/FD.pdf

Lawton JH, Brown VK (1994) Redundancy in Ecosystems. In: Biodiversity and Ecosystem Function

Lewinsohn TM, Vasconcellos-Neto J (2009) Como insetos sabotam defesas de plantas: o caso do latex. Oecologia Bras. https://doi.org/10.4257/oeco.2000.0801.10

Lloyd KM, McQueen AAM, Lee BJ, et al (2000) Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. J Veg Sci.

https://doi.org/10.2307/3236560

Loreau M (2000) Biodiversity and ecosystem functioning: Recent theoretical advances. Oikos

Maestre FT, Quero JL, Gotelli NJ, et al (2012) Plant species richness and ecosystem multifunctionality in global drylands. Science (80-). https://doi.org/10.1126/science.1215442

Magrin GO, Marengo JA, Boulanger J-P, et al (2014) Central and South America. In: Barros VR, Field CB, Dokken DJ, et al. (eds) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovenmetal Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdon and New York, NY, USA, pp 1499–1566

Magurran AE (2004) Measuring of Biological Diversity

Mason NWH, De Bello F (2013) Functional diversity: A tool for answering challenging ecological questions. J Veg Sci. https://doi.org/10.1111/jvs.12097

Matos P, Geiser L, Hardman A, et al (2017) Tracking global change using lichen diversity: towards a global-scale ecological indicator. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.12712

McCann KS (2000) The diversity-stability debate. Nature

Mittelbach GG, Steiner CF, Scheiner SM, et al (2001) What Is the Observed Relationship between Species Richness and Productivity? Ecology. https://doi.org/10.2307/2679922

Mori AS, Isbell F, Seidl R (2018) β-Diversity, Community Assembly, and Ecosystem Functioning. Trends Ecol. Evol.

Moro MF, Lughadha EN, Filer DL, et al (2014) A catalogue of the vascular plants of the Caatinga Phytogeographical Domain: A synthesis of floristic and phytosociological surveys. Phytotaxa. https://doi.org/10.11646/phytotaxa.160.1.1

Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. Ecol. Lett.

Nunes A, Köbel M, Pinho P, et al (2017) Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. Agric For Meteorol. https://doi.org/10.1016/j.agrformet.2017.03.007

Oliveira ACP, Nunes A, Rodrigues RG, et al (2020a) The response of plant functional traits to aridity in a Tropical dry forest. Science of the Total Environment https://doi.org/10.1016/j.scitotenv.2020.141177

Oliveira ACP, Nunes A, Pinho P, et al (2020b) From species presences to abundances: Using unevenly collected plant species presences to disclose the structure and functioning of a dryland ecosystem. Ecol Indic. https://doi.org/10.1016/j.ecolind.2020.106221

Orians GH (1982) The influence of tree falls in tropical forests in tree species richness. Tropical Ecology

Pausas JG, Austin MP (2001) Patterns of plant species richness in relation to different environments: An appraisal. J Veg Sci. https://doi.org/10.2307/3236601

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests. Annu Rev Ecol Evol Syst. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2016) Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot. https://doi.org/10.1071/bt12225_co

Petchey OL, Gaston KJ (2006) Functional diversity: Back to basics and looking forward. Ecol. Lett.

Pillar VD, Blanco CC, Müller SC, et al (2013) Functional redundancy and stability in plant communities. J Veg Sci. https://doi.org/10.1111/jvs.12047

Ribeiro EMS, Lohbeck M, Santos BA, et al (2019) Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J Ecol. https://doi.org/10.1111/1365-2745.13177

Richerson PJ, Lum K (1980) Patterns of Plant Species Diversity in California: Relation to Weather and Topography. Am Nat. https://doi.org/10.1086/283645

Ricotta C (2005) Through the jungle of biological diversity. Acta Biotheor.

Sarmiento G (1975) The Dry Plant Formations of South America and Their Floristic Connections. J Biogeogr. https://doi.org/10.2307/3037998

Sfair JC, De Bello F, De Frana TQ, et al (2018) Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. Environ Res Lett. https://doi.org/10.1088/1748-9326/aa9f5e

Simpson EH (1949) Measurement of diversity [16]. Nature

Soliveres S, Maestre FT, Bowker MA, et al (2014) Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands. Perspect Plant Ecol Evol Syst. https://doi.org/10.1016/j.ppees.2014.05.001

Stubbs WJ, Wilson JB (2004) Evidence for limiting similarity in a sand dune community. J Ecol. https://doi.org/10.1111/j.0022-0477.2004.00898.x

Suding KN, Collins SL, Gough L, et al (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proc Natl Acad Sci U S A. https://doi.org/10.1073/pnas.0408648102

Takahashi CA, Ceccantini GCT, Mercier H (2007) Differential capacity of nitrogen assimilation between apical and basal leaf portions of a tank epiphytic bromeliad. Brazilian J Plant Physiol. https://doi.org/10.1590/S1677-04202007000200004

The R Core Team (2018) R: A language and environment for statistical computing.

Trabucco A, Zomer RJ, Bossio DA, et al (2008) Climate change mitigation through afforestation/reforestation: A global analysis of hydrologic impacts with four case studies. Agric Ecosyst Environ. https://doi.org/10.1016/j.agee.2008.01.015

Violle C, Navas ML, Vile D, et al (2007) Let the concept of trait be functional! Oikos

Volaire F, Barkaoui K, Norton M (2014) Designing resilient and sustainable grasslands for a drier future: Adaptive strategies, functional traits and biotic interactions. Eur. J. Agron.

Walker BH (1992) Biodiversity and Ecological Redundancy. Conserv Biol. https://doi.org/10.1046/j.1523-1739.1992.610018.x

Walker S, Wilson JB, Steel JB, et al (2003) Properties of ecotones: Evidence from five ecotones objectively determined from a coastal vegetation gradient. J Veg Sci. https://doi.org/10.1111/j.1654-1103.2003.tb02185.x

Walls SC (2018) Coping with constraints: Achieving effective conservation with limited resources. Front Ecol Evol. https://doi.org/10.3389/fevo.2018.00024

Wilkinson DM (1999) The Disturbing History of Intermediate Disturbance. Oikos. https://doi.org/10.2307/3546874

Chapter 6

General Discussion

6 General Discussion

6.1 Main conclusions

The main objective of this thesis was to identify potential ecological indicators, based on both taxonomic and functional plant diversity, which can be used as tools to monitor the effects of climate change on tropical dry forests. The motivation for this thesis was mainly based on the existence of: (i) a global problem, such as the impacts of climate change on ecosystems, (ii) a susceptible region – drylands - that cover approximately 47% of all terrestrial ecosystems and are home to 39% of the world's population (Koutroulis 2019) and, (iii) a threatened ecosystem – the Tropical dry forest (Caatinga), where climate change coupled with other anthropogenic pressures, such as accelerated land-use intensification, have been substantially modifying the natural landscape (da Silva and Barbosa 2018; Sfair et al. 2018).

Our results showed that: (i) it is possible to estimate plant species abundance from presence-absence data, even when data collection regarding plant species presence was uneven over time or space, (ii) aridity was the main environmental filter shaping plant community composition, as well as its functional structure, (iv) abundance of functional groups can be adequate tools to track changes in the structure and functioning of ecosystems, and (v) the complementary responses of taxonomic and functional diversity to aridity and their interdependence contribute to better understand the susceptibility of this ecosystem to climate change.

These findings support the use of plant functional traits as ecological indicators in the context of the Tropical dry forest ecosystem and contribute to the understanding of how plant species and trait diversity respond to aridity. Furthermore, these results highlight the importance of using complementary diversity metrics to track the effects of increasing aridity on biodiversity. This knowledge is paramount to forecast shifts in plant communities as a response to climate change and give an important contribution to the development of measures/strategies to combat desertification and land degradation, providing science-based information to guide ecological restoration plans where ecosystem degradation could not be avoided. The conclusions of this thesis resulted from a work plan involving different steps.

In **Chapter 2** the abundance of the dominant plant species was estimated from presence/absence data obtained through an uneven sampling effort over large areas, using a resampling method. Estimating abundance from presence-absence data is a crucial step, considering abundance data is essential to track biodiversity changes. In this chapter, we calculated the abundances of the most dominant plant species considering that they capture the main effects of environmental drivers (e.g. human activities and climate change) on key ecosystem processes (Grime 1998; Lavorel and Garnier 2002; Hooper et al. 2005). The resulting databases will be made publicly available (*in press*) and may now support biodiversity conservation studies and/or be used to study ecosystem structure and functioning. Additionally, the resampling methodology developed in this study may apply to other databases with similar characteristics.

The approach presented in this study added value to the pre-existing plant species databases for Caatinga, expanding the baseline knowledge for studies concerning the biodiversity of this ecosystem at a local, regional, and global scales. At a local and regional scale, this contribution provides other information (e.g., percentage of endemism) beyond abundance data, reducing the knowledge gap about Caatinga, one of the most threatened and understudied dryland ecosystems of the world. At a global scale, the new database can contribute to the study of the impacts of climate change on the global loss and change of biological diversity in drylands. The availability of new databases is of great relevance, especially at a time when the challenge for the scientific community is to expand the network of shared knowledge.

Based on the database of the most abundant species in the Caatinga distributed along a spatial aridity gradient, we found aridity was a major environmental filter of the plant community functional structure, affecting functional trait composition and diversity **(Chapter 3)**. The results presented in chapter 3 show an increase in functional diversity with increasing aridity for fruit type, photosynthetic pathway, and defense traits, likely related to a higher niche complementarity in drier sites. The opposite trend was found for leaf traits (decreasing functional diversity), suggesting that an increase in aridity can result in climatic filtering for these traits. The concept of environmental filter predicts that some of the species or traits present at a regional scale, may be reduced or filtered out of the community on a local scale, because the range of successful strategies necessary to overcome the environmental filter is reduced, and thus species tend to have similar characteristics (Cornwell et al. 2006). These results suggest that functional traits can be used to predict the effects of climate change over time on Tropical dry forest. As functional traits are considered a “universal approach”, in the sense that they can be studied in any type of community, independently of the species identity, this approach can be replicated and expanded to other worldwide drylands. The application of this method to other drylands does not imply the use of the same traits (e.g. crassulacean acid metabolism photosynthetic pathway) but can be based on other traits that, in a given community and ecosystem, respond to an increase in aridity. The extension of this study to other drylands is crucial considering the expected response of ecosystems to ongoing climate change, entailing abrupt changes in ecosystem structural and functional attributes, causing soil disruption, identified as one of the causes of critical threshold of change in drylands across the globe (Berdugo et al. 2020).

In **Chapter 4** we identified seven functional groups based on multiple functional traits. Functional groups with chemical defense and CAM photosynthetic pathway were those whose relative abundance increased most with increasing aridity. The more arid environments were dominated by trees with chemical defense, a higher proportion of cacti (with CAM) and bromeliads (with leaves arranged in a rosette). While in less arid environment trees without chemical defense, and shrubs or herbs without CAM were the dominant strategies. These changes observed along an aridity gradient can be the expected future scenario with increasing aridity in Tropical dry forest. Thus, monitoring the increase or reduction of functional groups' abundance used as ecological indicators, may warn about the ongoing impacts of aridity on plant communities in the Caatinga. This finding can be extended as an early warning method for drylands on a global scale, for which there is evidence of critical thresholds reached in ecosystems caused by an increase in aridity (Berdugo et al. 2020). Therefore, expanding this on-site vegetation-focused approach can be an effective tool (ecological indicator) for monitoring, tracking, diagnosing, and, consequently, providing an early warning of the impacts of aridity on the structure and functioning of each dryland. In addition, the on-site vegetation-focused approach will allow to formulate mitigation and restoration actions tailored specifically for each dryland and thereby ensure the success of the actions on a local scale.

In **Chapter 5**, the importance of using complementary metrics (taxonomic and functional) to better understand the response of the plant community to changes in climate are highlighted. Moreover, the response of functional redundancy, which is a metric that aggregates taxonomic and functional metrics was used. Functional redundancy can be used as a proxy of ecosystem stability, resistance, and resilience to disturbance. A low functional redundancy means that a few species with particular traits carry out unique roles in ecosystem processes. Thus, their potential loss as a consequence of environmental changes can dictate the loss of these functions, negativellly affecting ecosystem functioning, as there are no other 'functionally similar' species that can continue to ensure them. Hence, it is an important informative metric to assess ecosystem vulnerability to environmental changes.This integrated knowledge of the response of compementary diversity metrics can be used to anticipate irreversible damage on ecosystem services, affecting human well-being (Díaz et al. 2006). Also, based on the results shown in Chapter 5, it is possible to indicate priority areas for conservation and restoration in the Caatinga.

As all drylands, tropical dry forests are highly vulnerable to climate change. Expanding the use of complementary diversity metrics to predict/determine the impacts of climate change on ecosystems and deepen the approach to assess functional redundancy, can be used to increase the stability, resilience, and resistance of dryland ecosystems, tropical or not, in the face of an aridity increase.

6.2 Recommendations

Based on the response of tropical dry forest plant diversity metrics to climate changes (i.e. aridity) **(Chapter 3, 4 and 5)**, it is clear that the conservation of its remarckable biodiversity and plant communities, and associated ecosystem functions, is key to guarantee the resilience and functioning of this ecosystem in the face of global change pressures (e.g. climatic and anthropogenic). In agreement, the main recommendations based on the results of this work are:

(a) **To prioritise conservation areas**, considering the response of plant diversity to climate change. The abundance of the dominant plant species, as well as, of rare, endemic, and endangered species, may be used as a basis for delimitation or creation of new conservation areas. Additionally, the abundance of the dominant plant species may be used to adapt management strategies (e.g. regarding grazing pressure). This is supported by the results presented, given that the use of the 48 most abundant plant species provided a strong and robust understanding of the response of biodiversity and ecosystem functioning to aridity: drier sites showed a higher functional diversity supported by few species with unique functions, which in turn may increase vulnerability and compromise ecosystem stability, resistance, and resilience. Ensuring the conservation of these most abundant species and their traits in semi-arid environments can minimize future shifts of the environment as a result of an aridity increase, especially at values below 0.36 of the aridity index.

(b) **To select indicators** that better track the effects on ecosystems, **to anticipate and prevent a regime shift in dryland ecosystems**. The desertification process is a typical process of shifts towards increased land degradation from a less to a more arid environment, with ecological as well as socio-economic dramatic consequences. Currently, about 1/3 of the Caatinga is turning into a desertified territory and almost 95% of the region, where this ecosystem is the main vegetation cover, shows moderate to high desertification risk (Vieira et al. 2015). Thus, another implication of our results would be to anticipate the impacts of aridity, but also, to combat the advance of the desertification process in the tropical dry forest.

(c) **To prioritise restoration areas** and to integrate trait-based ecology, to ensure ecosystem functioning and resilience in face of climate change. By prioritising restoration areas, additional socioeconomic gains will also be obtained, because, without the conservation of the ecosystem and the prevention of possible shifts from the current to a ‘poorer’ alternative ecosystem stable state, the well-being of thousands of people will be affected. Consequently, post-degradation interventions, which are usually more costly in the short term than preventive measures, will have to be deployed. Interventive actions include the restoration of ecosystems´ composition and functions. Furthermore, our results suggest that the inclusion of a functional approach, e.g. exploring native aridity-resistant species, is a necessary tool in restoration ecology.

These recommendations, which include biodiversity conservation, prevention of desertification, and restoration, require the development of a new paradigm in the region: the inclusion of scientific knowledge and effective political actions is a necessity for the survival and maintenance of this region. Especially, if we aim to deliver sustainable ecosystem services, to promote well-being to citizens, while simultaneously protecting biodiversity and maintaining a healthy and productive ecosystem.

6.3 Future challenges

This work contributed to advance the knowledge on plant functional response to aridity and to understand its variation in space to be able to measure its trends over time. This is especially true for tropical drylands, where this approach is less studied/researched (e.g. Ribeiro et al. 2019; Méndez-Toribio et al. 2020; Silva et al. 2020) when compared to other drylands worldwide, such as Mediterranean drylands and grassland communities of other ecosystems (e.g. Frenette-Dussault et al. 2013;

Gross et al. 2013; Valencia et al. 2015; Costa-Saura et al. 2016; Nunes et al. 2017). Based on the knowledge gathered, several future research lines can be drawn, such as:

> (a) **To extend and validate the trait-based indicators** of aridity impacts in other Tropical dry forests around the world (e.g., America and Africa). This is essential to confirm if the relationship found between functional structure and aridity for the analysed plant traits is representative of different geographic locations and taxonomic composition.
>
> (b) **To combine phylogeny** and plant functional traits. The phylogenetic information of communities contributes with the role of evolution in the assembly of communities and can help to predict the properties of ecosystems and provide responses to environmental changes (Webb et al. 2002; Cavender-Bares et al. 2006).
>
> (c) **To include the intraspecific variation in functional traits**. Differences between individuals of the same species are important for community processes (e.g., functioning). For this reason, we hypothesize that the intraspecific variability can relate organisms present in the community more efficiently to ecological processes and environmental variables (Pachepsky et al. 2007).

References

Berdugo M, Delgado-Baquerizo M, Soliveres S, et al (2020) Global ecosystem thresholds driven by aridity. Science (80-). https://doi.org/10.1126/science.aay5958

Cavender-Bares J, Keen A, Miles B (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology. https://doi.org/10.1890/0012-9658(2006)87[109:psofpc]2.0.co;2

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: Convex hull volume. Ecology. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Costa-Saura JM, Martínez-Vilalta J, Trabucco A, et al (2016) Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species. Perspect Plant Ecol Evol Syst.

https://doi.org/10.1016/j.ppees.2016.05.001

da Silva JMC, Barbosa LCF (2018) Impact of human activities on the Caatinga. In: Caatinga: The Largest Tropical Dry Forest Region in South America

Díaz S, Fargione J, Chapin FS, Tilman D (2006) Biodiversity loss threatens human well-being. PLoS Biol.

Frenette-Dussault C, Shipley B, Meziane D, Hingrat Y (2013) Trait-based climate change predictions of plant community structure in arid steppes. J Ecol. https://doi.org/10.1111/1365-2745.12040

Grime JP (1998) Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. J. Ecol.

Gross N, Börger L, Soriano-Morales SI, et al (2013) Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. J Ecol 101:637–649. https://doi.org/10.1111/1365-2745.12063

Hooper DU, Chapin FS, Ewel JJ, et al (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr. https://doi.org/10.1890/04-0922

Koutroulis AG (2019) Dryland changes under different levels of global warming. Sci Total Environ 655:482–511. https://doi.org/10.1016/J.SCITOTENV.2018.11.215

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct. Ecol.

Maestre FT, Quero JL, Gotelli NJ, et al (2012) Plant species richness and ecosystem multifunctionality in global drylands. Science (80-). https://doi.org/10.1126/science.1215442

Méndez-Toribio M, Ibarra-Manríquez G, Paz H, Lebrija-Trejos E (2020) Atmospheric and soil drought risks combined shape community assembly of trees in a tropical dry forest. J Ecol. https://doi.org/10.1111/1365-2745.13355

Nunes A, Köbel M, Pinho P, et al (2017) Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. Agric For Meteorol. https://doi.org/10.1016/j.agrformet.2017.03.007

Pachepsky E, Bown JL, Eberst A, et al (2007) Consequences of intraspecific variation for the structure and function of ecological communities Part 2: Linking diversity and function. Ecol Modell. https://doi.org/10.1016/j.ecolmodel.2007.05.005

Ribeiro EMS, Lohbeck M, Santos BA, et al (2019) Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J Ecol. https://doi.org/10.1111/1365-2745.13177

Sfair JC, De Bello F, De Frana TQ, et al (2018) Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. Environ Res Lett. https://doi.org/10.1088/1748-9326/aa9f5e

Silva JLS, Cruz-Neto O, Rito KF, et al (2020) Divergent responses of plant reproductive strategies to chronic anthropogenic disturbance and aridity in the Caatinga dry forest. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2019.135240

Valencia E, Maestre FT, Le Bagousse-Pinguet Y, et al (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. New Phytol. https://doi.org/10.1111/nph.13268

Vieira RMSP, Tomasella J, Alvalá RCS, et al (2015) Identifying areas susceptible to desertification in the Brazilian northeast. Solid Earth. https://doi.org/10.5194/se-6-347-2015

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu. Rev. Ecol. Syst.