Title: The response of plant functional structure and diversity to aridity in Caatinga dryland: implications for climate change

Ana Cláudia Pereira de Oliveira[1], Alice Nunes [1*], Renato Garcia Rodrigues[2], Cristina Branquinho[1]

[1] Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal

[2] Núcleo de Ecologia e Monitoramento Ambiental, Universidade Federal do Vale do São Francisco, Petrolina, Pernambuco, Brazil.

* Corresponding author: amanunes@fc.ul.pt
Campo Grande, Bloco C2, 6º Piso D
1749-016 – Lisboa, Portugal

Abstract

Drylands cover almost 47% of terrestrial ecosystems with an expected expansion up to 56% until 2100 associated with the increase in aridity due to climate change. This may affect dryland ecosystems´ structure and functioning, undermining ecosystem services and human well-being. Therefore, it is extremely important to detect early signs of ecosystem changes due to climate change, to avoid irreversible damage. Functional traits proved to be good indicators of ecosystems´ responses to environmental changes. Here, we studied the response of the plant community to aridity in a dryland ecosystem. We assessed plant functional structure (CWM) and functional diversity (FDis) along a 700 km climatic gradient, using a space-for-time substitution approach to infer potential consequences of climate change on Caatinga dryland in Brazil - a unique, highly diverse and critically endangered ecosystem. 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. 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 thick 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. These changes may negatively impact key processes in Caatinga such as primary productivity and nutrient cycling and affect plant spatial distribution patterns and biotic interactions. 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: Brazil; climatic gradient; dry tropical forest; ecosystem functioning; functional traits; semi-arid ecosystem; space-for-time substitution;

1.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 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 understand how ecosystems are being impacted by environmental factors in interaction with climate change to ensure that the ecosystem services needed for maintaining this population are conserved. This involves tracking changes in ecosystem structure and functioning by using the most appropriate ecological indicators (Branquinho *et al.*, 2019).

One way to monitor the structure and functioning of terrestrial ecosystems is by using plant biodiversity components as indicators of specific ecosystem functions (Cadotte, Carscadden and Mirotchnick, 2011; Branquinho *et al.*, 2019), for instance, through the use of a approach (De Bello *et al.*, 2010). Plant functional traits have greatly improved the understanding of the effects of environmental change on biodiversity and ecosystem functioning (Petchey and Gaston, 2006; 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 (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2016). Hence, certain traits may be used to predict the 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. *Seed dispersal mode* determines the distance species can cover (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013, 2016).

Functional structure (i.e., the community weighted mean – CWM) (Garnier *et al.*, 2007) and functional diversity (FDis) are two functional metrics considered good predictors of ecosystem functioning (Cardinale *et al.*, 2007; Valencia *et al.*, 2015).

The importance of functional structure derives from the "*mass ratio hypothesis"* proposed by Grime (1998), which implies that ecosystem functioning is largely determined by the trait values of the dominant species (Ricotta and Moretti, 2011). Regarding functional diversity the "diversity hypothesis" postulates that traits´ diversity within a community can affect ecosystem processes (Tilman *et al.*, 1997). A high functional diversity may allow for a more complete use of resources in space or time among species (co-occurrence of different functional strategies and niches) enhancing ecosystem functioning (Díaz and Cabido, 2001; Mouchet *et al.*, 2010).

Substituting space-for-time 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). For example, a recent study developed along a spatial aridity gradient indicates that the functional structure and diversity of plant community in Mediterranean drylands may change with increasing aridity (Nunes *et al.*, 2017).

In drylands, recent studies have highlighted the importance of applying a trait-based approach to measure the response of plant communities to environmental and climatic impacts (Gross *et al.*, 2013; Valencia *et al.*, 2015; Nunes *et al.*, 2017). However, although some of these studies cover considerable geographic areas, to the best of our knowledge, there are few studies addressing this issue in Brazilian Caatinga (e.g., address Sfair et al., 2018; Pinho et al., 2019; Ribeiro et al., 2019; Silva et al., 2019), the most plant diverse ecosystem among drylands (Pennington, Lavin and Oliveira-Filho, 2009; Portillo-Quintero and Sánchez-Azofeifa, 2010). Moreover, climate change, anthropogenic pressure and intensive and accelerated land-use have been modifying its natural landscape (da Silva and Barbosa, 2018; Sfair *et al.*, 2018). These pressures may cause an irreversible shift 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 and diversity to climate change in the Caatinga should be a priority.

In this context, the main objective of this study was to assess changes in plant functional structure and diversity along a wide climatic gradient in the Caatinga ecosystem, using a space-for-time substitution approach to infer potential consequences of future climate change in these highly diverse and critically endangered areas. We addressed several functional traits related to plant strategies to deal with water limitations. We hypothesized that functional metrics for most of the analysed plant traits would change along the climatic gradient, given that changes in some of these traits in response to aridity were already reported for other ecosystems in other parts of the world (e.g. Valencia et al., 2015; Nunes et al., 2017). We suggest these changes indicate potential impacts of climate change on dryland ecosystems in the future, and that biodiversity components changing with climate along space might be used as ecological indicators to track climate change impacts over time.

2. Materials and methods

2.1 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 including four Brazilian states (Ceará, Paraíba, Pernambuco, and Rio Grande do Norte) (Fig. 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 ^{o}C (ranging from 21^{o}C to 26 ^{o}C), 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).

The plant community was sampled in 113 sampling units (10 x 10 km) distributed along the climatic gradient. The presence and abundance of plant species were registered, and 13 functional traits of the 48 most abundant plant species were measured. The following traits were considered: (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 the establishment, defense, regeneration, and dispersal (Lewinsohn and Vasconcellos-Neto, 2009; Pérez-Harguindeguy *et al.*, 2013). Trait data were obtained by direct field measurements following standard protocols (Pérez-Harguindeguy *et al.*, 2013) (traits 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 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 7 and 9 - e.g., Griz and Machado, 2001; Meiado *et al*, 2012).

To assess changes in plant community functional structure along the climatic gradient, the community weighted mean (CWM) was determined. This functional metric 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, CWM values represent the proportion of each category in the community.

To assess changes in plant community functional diversity along the climatic gradient, functional dispersion (FDis) was computed for each trait (single-trait FDis). This index measures the degree of functional dissimilarity within the plant community (Laliberte and Legendre, 2010). 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 and can be calculated for single traits and for multiple traits (Laliberte and Legendre, 2010). We used Gower distance to determine FDis 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).

2.2 Climatic variables

We used 19 climatic variables retrieved from the global climate database (http://www.worldclim.org.br) (Hijmans *et al.*, 2005). We also used the aridity index adopted by the United Nations, retrieved from a global database (Trabucco *et al.*, 2008) (Table 1). 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.

2.3 Data analysis

First, to detect main changes in plant community composition along the climatic gradient, a non-metric multidimensional scaling ordination (NMDS) was performed, based on species relative abundance, using *metaMDS* function from the vegan package (The R Core Team, 2018; Oksanen *et al.*, 2019). The Bray-Curtis distance was chosen, and ordination goodness of fit was assessed through the *stress* statistic. Secondly, to analyze which climatic variables were driving plant community composition, all variables were superimposed over NMDS ordination, and the significance of the correlations between climatic variables and the ordination axes were determined using Spearman correlations, to account for possible nonlinear relationships. We also explored the correlation among the climatic variables to avoid redundancy among them and used only variables with a correlation coefficient < 0.7 among them (Table S1). The aridity index was selected as a predictor given that it correlated well with five climatic variables (further explained in the Results section).

Finally, to study the response of plant community functional structure and diversity along the gradient, we used Spearman correlations to check for the relationship between aridity (the aridity index) and single-trait functional metrics (CWM and FDis). Correlations were considered significant for $p < 0.05$. All statistical analyses were performed using in R version 3.4 (The R Core Team, 2018).

3. Results

3.1 Plant community composition gradients

The results from the multivariate analysis displayed 3 axes but we show only results for the first two axes, as they accounted for most of the variance (50.6%) (Fig. 2).

The aridity index (ranging from 0.27 to 0.69) was significantly correlated with NMDS axis 1, 2 and 3 (Table 2) while altitude (from 214 to 930 m) was significantly correlated with NMDS 1 axis (Table 2).

Additionally, the aridity index was also significantly correlated with 12 of the 19 climatic variables while altitude was correlated with 13 of the 19 climatic variables (Table S1). The aridity index was chosen as the best descriptor of vegetation patterns given that it reflected major macroclimatic conditions. It showed a strong correlation with seven climatic variables that correlated with NMDS1 and with six climatic variables that better described main changes in plant community composition along the climatic gradient, namely: (1) annual precipitation (Spearman´s r=0.97, P<0.001), (2) precipitation of wettest month (Spearman´s r=0.84, P<0.001), (3) precipitation of wettest quarter (Spearman´s r=0.91, P<0.001), (4) isothermality (Spearman´s r= 0.39, P<0.001), (5) temperature seasonality (Spearman´s r= -0,51, P<0.001), and (6) mean temperature of wettest quarter (Spearman´s r= -0,39, P<0.001) (Table S1).

3.2 Plant community functional structure

In the study area, the plant community was dominated by trees (72.5%) (Table 3). The average maximum plant height was 4 m (ranging from 0.5 to 6 m), and most of the plants were deciduous (68%) (Table 3). Mean leaf thickness was 76 mm (ranging from 48 to 95 mm) and mean specific leaf area (SLA) was 16 mm^2/mg (ranging from 13 to 20 mm^2/mg). Root type was dominated by pivoting root (67%). Autochory dispersal strategy was present in 40% of the plant community, followed by anemochory and zoochory, with 30% each (Table 3). 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).

3.3 Functional structure (CWM) and functional diversity (FDis) changes along the spatial aridity gradient

The CWMs of eight functional traits and the FDis of six functional traits were significantly correlated association with aridity (Table 4). We found a negative correlation between aridity and evergreen leaf type ($p < 0.001$), leaf thickness ($p < 0.001$), autochory dispersal ($p < 0.001$), and shrub growth-form ($p < 0.05$) (Table 4). Aridity was positively correlated with fleshy fruit presence ($p < 0.001$), chemical defense exudation ($p < 0.001$), spinescence presence ($p < 0.01$), zoochory dispersal ($p < 0.01$), crassulacean acid metabolism photosynthesis ($p < 0.01$), and deciduous leaf type ($p < 0.05$) (Table 4).

Aridity was negatively correlated with functional diversity (FDis) for leaf phenology type and leaf thickness ($p < 0.001$), and positively correlated for fruit type ($p < 0.001$), photosynthetic pathway ($p < 0.01$), spinescence presence ($p < 0.01$) and type of chemical defense exudation ($p < 0.001$) (Table 4).

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.

4. Discussion

Aridity was the main environmental filter shaping plant community composition, as well as its functional structure and diversity along the spatial gradient. This is in accordance with previous works showing that climatic variables (e.g. aridity, precipitation and temperature) are major drivers of the floristic patterns of woody plant species in Caatinga (Silva and Souza, 2018). Aridity, which takes into account both precipitation and temperature, can be seen as an integrated measure, as demonstrated by its strong correlation with most of the climatic variables studied. Local environmental variations e.g. in topography, soil characteristics or land management may also influence plant community characteristics, as showed in previous studies in water-limited ecosystems (Chozas *et al.*, 2015; Nunes *et al.*, 2019). However, these works addressed less comprehensive climate gradients (shorter range) than ours. Our work encompassed a larger climatic gradient including arid, semi-arid, and dry sub-humid areas, where local environmental factors are likely to play a weaker relative role in shaping plant community. In addition, along our study area, the variations in orography were limited to a few small plateaus, and plant sampling tried to capture, as much as possible, areas less influenced by human activities.

The traits that dominate with aridity

Along the gradient, we found a decrease in functional diversity of leaf traits towards more arid sites, along with a decrease in the abundance of plants with evergreen and thicker leaves. Thus, plant functional structure in drier sites was characterized by a higher dominance of non-shrub deciduous species with lower leaf thickness. Summer deciduousness i.e. leaf loss during drier periods, is a known plant adaptation strategy to avoid water losses. According to our findings, this strategy tends to dominate towards more arid conditions in Caatinga, replacing the maintenance of more-costly thicker evergreen leaves (Lohbeck *et al.*, 2015). Consequently, a larger amount of litter accumulates on the soil surface in drier areas during dry periods.

The higher leaf deposition on the soil surface could protect it from direct solar radiation and minimize rainwater erosive impact and increase nutrient deposition (i.e. carbon and nitrogen). 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 extremely infrequent in Caatinga, and leaf fall usually occurs during the drier period (Machado, Barros and Sampaio, 1997) that may reduce or even prevent leaf decomposition (Fredson *et al.*, 2009; Moura *et al.*, 2016), resulting in accumulated litter for a long time below deciduous plants, a very common image in Caatinga as in other drylands.

Also, plant´s leaves are fundamental to photosynthetic performance in semiarid regions (Zhang *et al.*, 2018). Yet, in what concerns leaf quantify and phenology, after leaf fall at the first signs of water shortage, deciduous plants remain leafless until the next precipitation period (Correia and Andrade, 1999). We also found an increase in the diversity of photosynthetic pathways 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 (CO2) 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 CO2, and so they grow slower (Medina, Olivares and Diaz, 1986).

Additionally, the decrease in shrub growth form in drier sites suggests a lower habitat structural complexity, which may reduce ecosystem´s ability to house particular species (e.g. animal species) and may also contribute to decrease biomass production.

In short, the shift in plant community functional structure and diversity towards more arid conditions regarding the vegetative traits analyzed, is likely to affect key ecosystem processes in Caatinga, namely primary productivity, hydric balance, litter decomposition (Cornwell *et al.*, 2008) and carbon and nitrogen cycling (Milcu *et al.*, 2014).

Changes in dispersion strategies and fruit type with aridity

Drier conditions led to an increase in the diversity of fruit types along with an increase in the abundance of fleshy fruited and zoochorous species, suggesting more interactions with seed-dispersing animals in drier sites (e.g. lizards, birds and bats) (Leal, Lopes and Machado, 2006; Quirino and Machado, 2014). This response may be partially associated with increased abundance of Cactaceae´s species, half of which have zoochorous dispersion (8 of the 16 species) displaying as a specialized dispersal strategy (Silva *et al*., 2019) e.g. by bats in Caatinga (Machado and Lopes, 2004).

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) whereas for the majority Caatinga´s plants this happens at the beginning of the rainy season (Machado, Barros and Sampaio, 1997; Lima and Rodal, 2010). This strategy ensures food resources to fauna which by its turn guarantee pollination and dispersion during drier periods (Griz and Machado, 2001; Leal, Lopes and Machado, 2006; Lima and Rodal, 2010). Yet, despite the positive aspects of increased zoochory for plant dispersal during drier periods, the decrease in autochory dispersal in drier areas may affect species spatial distribution in Caatinga. Autochory is the most common dispersal mode for the majority of the species from Fabaceae and Euphorbiaceae families (Lima, 2008) which are dominant in Caatinga (Moro et al., 2014; Fernandes; Queiroz, 2018). These species disperse seeds nearby the mother plant, originating a clustered distribution pattern. These patches may work as “islands of fertility” providing favorable microclimatic niches facilitating seedling establishment, e.g. for cactus recruitment (Drezner, 2010; Munguía-Rosas and Sosa, 2008; Landero and Valiente-Banuet, 2010). Hence, a decrease in autochory dispersal mode may lead to more scattered plant distribution, thus affecting the typical structure of Caatinga.

Changes in plant defense strategies with aridity

Plant defense strategies such as spinescence and chemical exudation (i.e., latex and resin) increased in drier arid areas. These strategies can protect plants against pathogens and herbivores as reported in many studies (Gómez and Zamora, 2002; Lewinsohn and Vasconcellos-Neto, 2009). The persistence or increase in these traits is essential for Caatinga plants (Olofsson, Moen, Oksanen, 2002). First, because they affect plant palatability and thus the level of herbivory, which may in turn change the quantity and quality of litterfall, affecting nutrient cycling (Ritchik, Tilman and Knops, 1998; Olofsson *et al.*, 2004). Additionally, pathogen attacks (Liu and He, 2019) and goats´ herbivory greatly impact natural regeneration, namely seedling establishment (Moles and Westoby, 2004). Yet, the presence of these traits may have fitness costs to plants (Strauss, Conner and Rush, 1996; Koricheva, 2002; Gassmann and Futuyma, 2005), affecting growth (Belovsky *et al.*, 1991) and the reproductive potential of plant populations in Caatinga (Gómez and Zamora, 2002).

Implications for climate change

We found a strong impact of aridity on Caatinga plant functional structure and diversity along a comprehensive aridity gradient. The plant community showed increased deciduousness, more cacti and bromeliads and plants with defense traits, and lower shrub and abundance towards drier sites. This shift indicates likely changes in plant structural complexity, spatial distribution patterns and biotic interactions, able to negatively affect key ecosystem processes such as primary productivity, litter decomposition and carbon and nitrogen cycling, and consequently the wellbeing of about 28.6 million people depending on Caatinga. Climate models predict an increase in aridity up to 2100 in this region (IPCC, 2014, 2019), which is already facing extremely long drought periods e.g. between 2010 and 2016 (Marengo Orsini *et al.*, 2018). Thus, assuming a space-for-time substitution, our results suggest a strong impact of climate change on Caatinga.

Our results may also contribute to guide preventive strategies (e.g. conservation of forest remnants) and corrective measures (e.g. include species with specific functional traits in restoration projects) in the unique, remarkably diverse and highly threatened Caatinga ecosystem.

Acknowledgements

The authors acknowledge the Centre for Ecology and Environmental Monitoring (NEMA) for all field work logistics and Maria Alexandra S.G.C. de Oliveira for the help in reviewing English. This work was funded by Fundação para a Ciência e a Tecnologia/Ministério da Educação e Ciência (FCT/MEC - PTDC/AAG-GLO/0045/2014) and partially supported by Conselho National de Desenvolvimento Científico e Tecnológico - CNPq (grant number: 206444/2014-1).

References

Agrawal, A. A., Strauss, S. Y. and Stout, M. J., 1999. Costs of Induced Responses and Tolerance to Herbivory in Male and Female Fitness Components of Wild Radish, *Evolution*. doi: 10.2307/2640814.

Alvalá, R. C. S. *et al.*, 2017. Drought monitoring in the Brazilian Semiarid region. *Anais da Academia Brasileira de Ciencias*, pp. 1–15. doi: http://dx.doi.org/10.1590/0001-3765201720170209.

Augustine, D. J. and McNaughton, S. J., 1998. Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance, *The Journal of Wildlife Management*. doi: 10.2307/3801981.

De Bello, F. *et al.*, 2010. The partitioning of diversity: Showing Theseus a way out of the labyrinth, *Journal of Vegetation Science*. doi: 10.1111/j.1654-1103.2010.01195.x.

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.

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

Buriti, C. O. and Barbosa, H. A., 2018. *Um século de secas: por que as políticas hídricas não transformaram o semiárido brasileiro?* Edited by C. Editora.

Cadotte, M. W., Carscadden, K. and Mirotchnick, N., 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services, *Journal of Applied Ecology*. doi: 10.1111/j.1365-2664.2011.02048.x.

Cardinale, B. J. *et al.*, 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity', *Proceedings of the National Academy of Sciences*. doi: 10.1073/pnas.0709069104.

Chozas, S. *et al.*, 2015. Local and regional-scale factors drive xerophytic shrub community dynamics on Mediterranean stabilized dunes, *Plant and Soil*. doi: 10.1007/s11104-015-2439-z.

Cornelissen, J. H. C. *et al.*, 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide, *Australian Journal of Botany*. doi: 10.1071/BT02124.

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.

Correia, M. E. F. and Andrade, A. G., 1999. Formação de serapilheira e ciclagem de nutrientes, in Santos, G. A. and Camargo, F. A. O. (eds) *Fundamentos da Matéria Orgânica do Solo: ecossistemas tropicais e subtropicais.*, pp. 197–226.

Díaz, S. and Cabido, M., 2001. Vive la différence: Plant functional diversity matters to ecosystem processes, *Trends in Ecology and Evolution*. doi: 10.1016/S0169-5347(01)02283-2.

Drezner, T. D., 2006. Plant facilitation in extreme environments: The non-random distribution of saguaro cacti (Carnegiea gigantea) under their nurse associates and the relationship to nurse architecture, *Journal of Arid Environments*. doi: 10.1016/j.jaridenv.2005.06.027.

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.

Dussourd, D. E. and Denno, R. F., 1991. Deactivation of plant defense: correspondence between insect behavior and secretory canal architecture, *Ecology*. doi: 10.2307/1941110.

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

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., 2005. 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.

Gosz, J. R., 1992. Gradient Analysis of Ecological Change in Time and Space: Implications for Forest Management, *Ecological Applications*, 2(3), pp. 248–261. doi:

10.2307/1941859.

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.

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

IPCC, *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*, *Intergovernmental Panel on Climate Change*. doi: 10.1017/CBO9781107415324.

IPCC, 2019. *IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse gas fluxes in Terrestrial Ecosystems, Summary for Policymakers Approved Draft*. doi: 10.4337/9781784710644.

Koricheva, J., 2002. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses, *Ecology*. doi: 10.1890/0012-9658(2002)083[0176:MAOSOV]2.0.CO;2.

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. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. http://doi.org/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.

Lima, E. De, 2008. Fenologia e dinâmica de duas populações herbáceas da caatinga, *Revista de Geografia*

Liu, Y. and He, F., 2019. Incorporating the disease triangle framework for testing the effect of soil-borne pathogens on tree species diversity, *Functional Ecology*. doi: 10.1111/1365-2435.13345.

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. and Lopes, A. V., 2004. Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry forest, *Annals of Botany*. doi: 10.1093/aob/mch152.

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.

Marengo Orsini, J. A. *et al.*, 2018. Climatic characteristics of the 2010-2016 drought in the semiarid northeast Brazil region, *Anais da Academia Brasileira de Ciencias*. doi: 10.1590/0001-3765201720170206.

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.

Meiado, M.V. et al., 2012. Diásporos da Caatinga: uma revisão. In: Siqueira Filho, J.A. & Leme, E.M.C. (Org.). *Flora das Caatingas do Rio São Francisco*. Rio do Janeiro: Andrea Jakobsson Estúdio Editorial Ltda.

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.

Mokany, K., Ash, J. and Roxburgh, S., 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland, *Journal of Ecology*. doi: 10.1111/j.1365-2745.2008.01395.x.

Moles, A. T. and Westoby, M., 2004. What do seedlings die from and what are the implications for evolution of seed size?, *Oikos*. doi: 10.1111/j.0030-1299.2004.13101.x.

Moro, M. F. *et al.*, 2014. A catalogue of the vascular plants of the Caatinga Phytogeographical Domain: A synthesis of floristic and phytosociological surveys, *Phytotaxa*. doi: 10.11646/phytotaxa.160.1.1.

Moro, M. F. *et al.*, 2016. A Phytogeographical Metaanalysis of the Semiarid Caatinga Domain in Brazil, *Botanical Review*. doi: 10.1007/s12229-016-9164-z.

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.

Mouillot, D. *et al.*, 2011. Functional structure of biological communities predicts ecosystem multifunctionality, *PLoS ONE*. doi: 10.1371/journal.pone.0017476.

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.

Munguía-Rosas, M. A. and Sosa, V. J., 2008. Nurse plants vs. nurse objects: Effects of woody plants and rocky cavities on the recruitment of the Pilosocereus leucocephalus columnar cactus, *Annals of Botany*. doi: 10.1093/aob/mcm302.

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.

Nunes, A. *et al.*, 2019. Local topographic and edaphic factors largely predict shrub encroachment in Mediterranean drylands, *Science of the Total Environment*. doi: 10.1016/j.scitotenv.2018.11.475.

Oksanen, J. *et al.*, 2019. *Package 'vegan' Title Community Ecology Package, Community ecology package*.

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.

Olofsson, J., Moen, J. and Oksanen, L., 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity, *Oikos*. doi: 10.1034/j.1600-0706.2002.960208.x.

Pennington, R. T., Lavin, M. and Oliveira-Filho, A., 2009. Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests, *Annual Review of Ecology, Evolution, and Systematics*. doi: 10.1146/annurev.ecolsys.110308.120327.

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

Pérez-Harguindeguy, N. *et al.*, 2016. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide, *Australian Journal of Botany*. doi: 10.1071/bt12225_co.

Petchey, O. L. and Gaston, K. J., 2006. Functional diversity: Back to basics and looking forward, *Ecology Letters*. doi: 10.1111/j.1461-0248.2006.00924.x.

Pinho, B. X. *et al.*, 2019. Plant functional assembly is mediated by rainfall and soil conditions in a seasonally dry tropical forest, *Basic and Applied Ecology*. doi: 10.1016/j.baae.2019.08.002.

Portillo-Quintero, C. A. and Sánchez-Azofeifa, G. A., 2010. Extent and conservation of tropical dry forests in the Americas, *Biological Conservation*. doi: 10.1016/j.biocon.2009.09.020.

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.

Prance, G. T., 2006. Tropical savannas and seasonally dry forests: An introduction, in *Journal of Biogeography*. doi: 10.1111/j.1365-2699.2005.01471.x.

Queiroz, L. P. de, 2009. *Legumes of the Caatinga.*, *Leguminosas da Caatinga*.

Quirino, Z. G. M. and Machado, I. C., 2014. Síndromes de polinização e sazonalidade dos recursos florais em uma comunidade vegetal na Caatinga Paraibana, nordeste do Brasil, *Brazilian Journal of Biology*. doi: 10.1590/1519-6984.17212.

Ribeiro, E. M. S. *et al.*, 2019. Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance, *Journal of Ecology*. doi: 10.1111/1365-2745.13177.

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.

Ritchik, M. E., Tilman, D. and Knops, J. M. H., 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna, *Ecology*. doi: 10.2307/176872.

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.

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.

Silva, J.L.S. et al., 2019. Divergent responses of plant reproductive strategies to chronic anthropogenic disturbance and aridity in the Caatinga dry forest. *Science of the Total Environment*. doi: 10.1016/j.scitotenv.2019.135240.

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.

Strauss, S. Y., Conner, J. K. and Rush, S. L., 1996. Foliar herbivory affects floral characters and plant attractiveness to pollinators: Implications for male and female plant fitness, *American Naturalist*. doi: 10.1086/285896.

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.

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.

Villéger, S., Mason, N. W. H. and Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology, *Ecology*. doi: 10.1890/07-1206.1.

Wilson, S. L. and Kerley, G. I. H., 2003. Bite diameter selection by thicket browsers: The effect of body size and plant morphology on forage intake and quality', *Forest Ecology and Management*. doi: 10.1016/S0378-1127(03)00114-2.

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.