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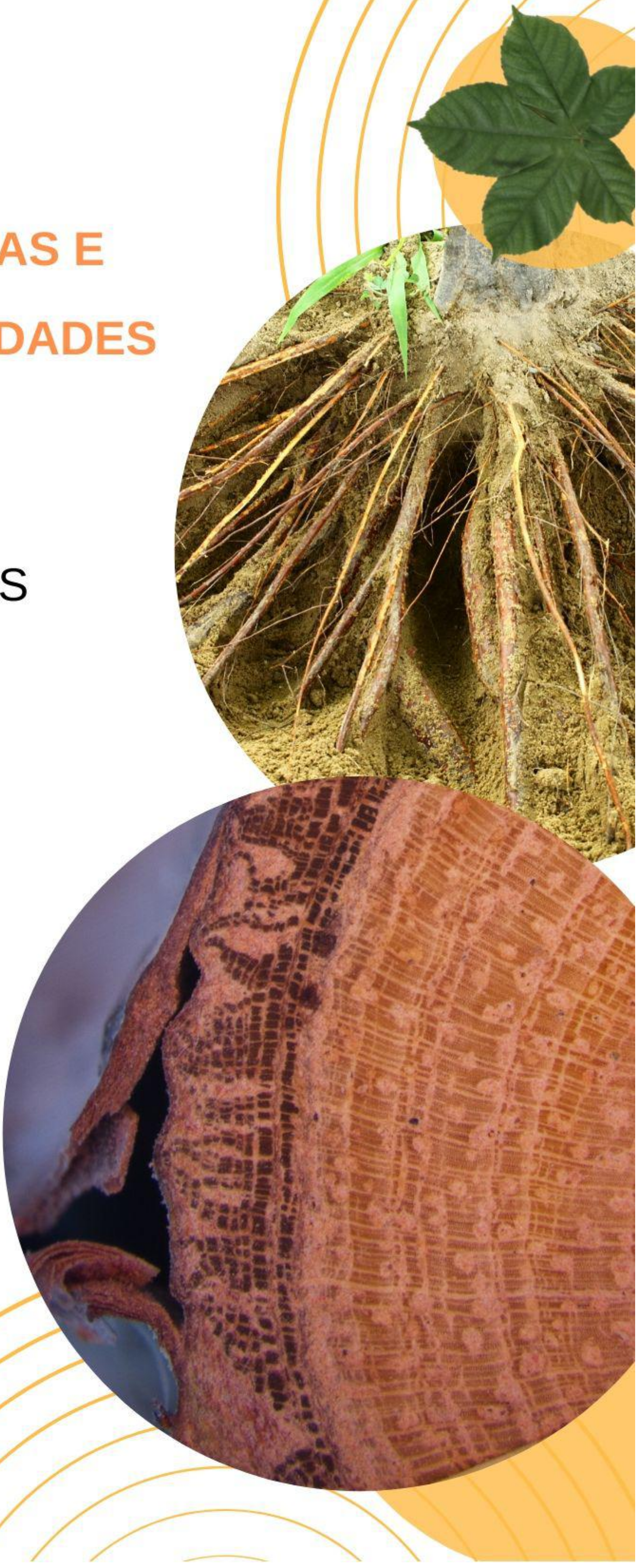

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Universidade Federal do Rio Grande do Norte
Pós-graduação em Ecologia

Natal, Fevereiro 2020

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Presidente da Banca

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Sumário

Resumo

Atributos funcionais são características fisiológicas, morfológicas, anatômicas e bioquímicas, responsáveis pelo sucesso da interação dos organismos com o meio em que habitam. Tais características adaptativas que compõem os organismos de uma região, aqui limitado à plantas arbóreas, são primeiramente selecionadas através de filtros ambientais. Neste sentido, compreender como as estratégias da vegetação são limitadas e moduladas pelos diferentes tipos de ambiente ao redor do mundo, é uma questão chave em ecologia. Os atributos funcionais das plantas, uma vez selecionados, também exercem efeitos sobre o ambiente em que vivem, alterando características abióticas como disponibilidade hídrica, radiação solar e disponibilidade de nutrientes. Além disto, estas alterações causam efeitos diretos e indiretos nos organismos vizinhos, podendo também agir como força moduladora da estrutura das comunidades. Compreender estes processos é fundamental para, além de entendermos padrões ecológicos gerais, podermos efetivar ações de restauração e montagem de comunidades com uma abordagem ecológica robusta. Neste sentido, este trabalho possui três capítulos, todos focados no ambiente sazonalmente seco Caatinga. O primeiro capítulo tem o objetivo de analisar os principais *trade-off* entre atributos funcionais de 20 espécies lenhosas, determinar seus grupos funcionais, testar se estes grupos estão associados espacialmente e se sua distribuição é limitada pela aridez. Foram coletados diversos atributos fisiológicos, anatômicos, bioquímicos e estruturais de espécies adultas *in situ.* Realizamos análises de componentes principais, para analisar os *trade-off,* análise de k-means para determinar os grupos funcionais, teste de Ripley para testar a distribuição espacial dos grupos e um gls para testar se os grupos ocorrem em locais com diferentes níveis de aridez. Encontramos que as espécies da Caatinga possuem diversos trade-offs com diferentes atributos representando um *continuum* entre estratégias aquisitivas e conservativas. Todos os *trade-off* deste continuo, colapsam em dois grupos funcionais de estratégias conservativas e aquisitivas, porém grande parte das espécies está contida no grupo de estratégias conservativas. Os dois grupos ocorrem de modo independente através do bioma e o grupo de espécies aquisitivas tende a ocorrer em locais mais áridos do bioma. O segundo capítulo busca testar como e quais os atributos funcionais das plantas afetam seus vizinhos positivamente e se atributos funcionais podem explicar as relações espécies-específicas comumente encontradas. Para isto, fizemos um

experimento *in situ* com interações entre 60 combinaçoẽs de pares de espécies, cada um replicados cinco vezes. Utilizando os atributos funcionais das espécies adultas já coletados como variáveis preditoras e a performance de plantas vizinhas como variáveis resposta, calculamos um modelo linear misto generalizado, seguido de simplificação de variáveis. Vimos que, tanto espécies com características conservativas quanto aquisitivas têm o potencial de afetar positivamente os indivíduos vizinhos e que o resultado é altamente dependente do par de espécies em interação. No entanto, os resultados positivos, surgem quando a espécie que está exercendo o efeito possui atributos funcionais, cujo efeito no ambiente, majoritariamente relacionados à água, suprem as necessidades ecológicas das plantas vizinhas. Por fim, o terceiro capítulo desatrela os efeitos de facilitação e complementariedade funcional e testa quais são as principais características funcionais das comunidades que levam a maior produção de biomassa e funcionamento das comunidades. Produzimos 4704 mudas de 16 espécies nativas. Com elas, foram montadas 147 comunidades, com 5 níveis de diversidade, monocultura, duas, quatro, oito e 16 espécies e 45 composições diferentes, cada comunidade foi montada com 32 indivíduos. Monitoramos a produtividade das comunidades em biomassa foliar produzida e também seu 'Net biodiveristy Effect' (NBE) como variáveis resposta. Como variáveis preditoras, calculamos o nível de potencial de facilitação por parcela, o valor médio de atributos ponderado pela abundância para 9 atributos separadamente, e a complementariedade funcional de cada comunidade. Calculamos quais destas variáveis melhor explicariam a produção de biomassa e o NBE através de modelos lineares mistos generalizados. A produção de biomassa foi influenciada positivamente por atributos relacionados à rapida captura de recursos e fixação de carbono como área específica foliar e comprimento específico de raiz e pelo potencial facilitativo das comunidades. O NBE foi influenciado principalmente pela diversidade funcional e pelo potencial facilitativo das espécies. Por fim, demonstramos como ecologicamente a facilitação se diferencia de complementariedade funcional e quais suas consequências para restauração e montagem de comunidades. Ademais, propomos tomadas de decisões utilizando os componentes ecológicos testados para guiar práticas de restauração e maximizar tanto a produtividade das comunidades, quanto seus serviços.

PALAVRAS CHAVE: Estratégias funcionais, Distribuição espacial, Montagem de comunidades, Restauração, Facilitação, Diversidade funcional, Florestas tropicais sazonalmente secas, Estratégias para lidar com seca.

Abstract

Functional traits are all physiological, morphological anatomical and biochemical features of an organism that allow it to survive and reproduce in its environment. The functional traits of organisms, here limited to tree species, in a given region, are primary selected by environmental filters. The understanding of how the environment modulates vegetation community is a worldwide question in Ecology. Once limited by environmental conditions, the functional traits will also exert effects on its environment, by changing abiotic resources and condition, affecting the surrounding organisms. Such effect can also modulate community structures. Understand both processes its fundamental to the understanding not only general ecological patterns, but to generate information in order to apply ecological theories to rebuild communities as in restoration programs. Mentioned that, this work is made by 3 independent chapters all focused in Seasonal dry Forest Caatinga. The first chapter aim to analyzed tree species coordinated trade-offs of one of the most biodiverse Seasonal tropical dry forest, determined its functional groups gathering above-below ground and biochemical traits, test if these groups are spatially associated over the biome and if the distribution is limited to a aridity gradient. We sampled several anatomical, physiological, structural and biochemical functional traits of 20 adult tree species in situ, and young plants of 2 and 6 months old cultivated in a greenhouse. We performed PCA test, K-means. Ripleys K analysys and gls to respond the aforesaid questions, respectively. We found distinct coordinated trade-offs representing the slow-fast growth strategies continuum. This continuum were collapsed in two main groups of acquisitive and conservative strategies, and the majority of species were selected to conservative group. Species of both groups are independently distributed over the biome, and fast-strategy species occurrence is more related to arid regions than slow-strategies. The second chapter aim to test which functional traits are important to explain facilitation capabilities of nurse plants, and if specific combinations of nurse-target functional traits explain the outcome of species-specific interaction. We performed a in-situ experiment with 60 adult plant-target tree species combination replicated 5 times. Using the already sampled functional traits as predictive variable and plant neighbour performance as response variable, we performed a GLMM followed by variable simplification. We found that both conservative and acquisitive species can exert positive effects and the outcome is highly dependent on the pair of species match. The positive outcome however, happened when the species exerting the effect, had functional traits which effect on environment, fulfill the ecological above- or below-ground requirements of its plants neighbour. At least, the third chapter, aim to disentangle the facilitation from functional complementarity effects, and test the importance of this components on biomass production and community function. We produced 4704 seedlings of 16 semiarid tree species using a new growing method. All individuals were planted in 147 experimental build communities of 13 m X 18 m, with 32 individuals each. The experimental communities were build at five levels of diversity and with distinct composition at each level replicated three times. The biomass production and the Net biodiversity Effect (NBE) were calculated and used as response variables. As a predictive variables we used facilitation community potential, community weighted mean and functional diversity based on above and below-ground traits. For both response variables, we performed a generalized linear mixed models to understand how they drive the productivity and function of communities. We showed that facilitation is a key process for restoration acting since the community biomass productivity until its net biodiversity effects. Both parts of complementarity effect, functional diversity and facilitation, are fundamental for a higher community function at the initial years of rebuilt communities.Additionally, we showed how to manipulate the three components of the Net biodiversity Effect, facilitation, functional diversity and community functional identity, in order to guide future restoration programs.

KEY WORDS: Functional Strategies, Facilitation, Community assembling, Restoration, Functional diversity, Spatial distribution, Seasonally dry Tropical Forests, Strategies to face drought.

Introdução geral

Esta tese abarca questões teóricas e aplicadas à ecologia vegetal que dizem respeito às características funcionais de espécies arbóreas e sua influência sobre a formação de grupos funcionais de árvores e sua distribuição espacial em todo a Caatinga, efeitos na interação entre espécies, e efeitos no funcionamento de comunidades vegetais restauradas. Nesta introdução, apresento conceitos, o histórico e os efeitos ecológicos dos atributos funcionais vegetais nas comunidades. Posteriormente, contextualizo a abordagem funcional em Florestas Tropicais Sazonalmente Secas; como o estudo de atributos funcionais pode contribuir com o preenchimento de lacunas teóricas fundamentais para aplicações práticas neste ambiente; e como esta tese contribui com esses avanços.

Todas espécies de organismos existentes na terra possuem características adaptativas selecionadas ao longo de seu tempo evolutivo que as permitem interagir com o mundo, de modo que possam nascer/germinar, estabelecer-se, crescer e efetivamente adquirir recursos. Essas características, sejam anatômicas, fisiológicas ou bioquímicas, são chamadas de atributos funcionais (Violle, 2007), e têm sido foco de estudo em diferentes grupos de organismos para responder questões ecológicas, desde o nível de indivíduo até o funcionamento ecossistêmico (Ding et al., 2017; Lavorel & Garnier, 2002; Pakeman & Stockan, 2016).

As diversas características funcionais das plantas foram primeiramente agrupadas em um gradiente de estratégias funcionais por Grime (1977). O estudo, baseado em atributos morfológicos, propôs que espécies submetidas a uma mesma pressão ambiental apresentariam características funcionais mais semelhantes entre si do que espécies de outras regiões, com pressões ambientais diferentes. Deste modo, pela primeira vez, houve uma sistematização de como estratégias funcionais de plantas seriam distribuídas espacialmente em larga escala, baseado em suas respostas funcionais ao estresse e sumarizadas em três grupos: *ruderais*, *estresse-tolerante* e *competitivas*. Espécies *ruderais* apresentam estruturas funcionais como folhas com curta duração e alta produção de sementes, conferindo às espécies um rápido ciclo de vida e assegurando a germinação após eventos de distúrbios. Espécies *estresse-tolerantes*, apresentam lenta aquisição de recursos e lenta taxa de crescimento em resposta a ambientes estressantes. Por fim, espécies *competitivas* possuem altas taxas de aquisição de recursos e altas taxas de crescimento em resposta a um ambiente pouco estressante e com alta disponibilidade de recursos.

A partir de então, diferentes estudos verificaram que tais gradientes de estratégias funcionais são consistentes não só entre distintos grupos de plantas, como herbáceas e lenhosas, mas também em diferentes locais do mundo (Pierce et al., 2013; Cerabolini et al., 2010). Adicionalmente, as estratégias primárias baseadas em economia foliar (relação dos custos e dos benefícios de cada estratégia relacionada à aquisição de carbono e alocação de nutrientes) foram expandidas a outras estruturas relacionadas também à aquisição hídrica, como madeira e casca (Chave et al., 2009; Rosell et al., 2014; Reich, 2014). Atualmente, a disponibilidade de dados e estudos permite que tenhamos uma compreensão mais integrada de como alguns dos atributos funcionais coordenam-se de acordo com diferentes estratégias em nível global (Diaz et al., 2016).

Estratégias funcionais de espécies não só são selecionadas e respondem aos diferentes tipos de ambientes, como também exercem efeitos e podem causar mudanças ambientais. A taxa com que as espécies adquirem nutrientes, água e produzem e perdem folhas com diferentes níveis de nutrientes, afeta diretamente as condições e recursos do ambiente. Tais efeitos podem ser fortes o bastante para estruturar comunidades (Soliveres et al., 2014), afetar sua produtividade (Tobner et al., 2016) e mediar interações entre plantas (Schöb et al., 2013; Rolhauser & Pucheta, 2016). Neste sentido, o estudo dos atributos funcionais permite não só a compreensão de como comunidades naturais são formadas e mantidas ao longo do tempo, mas também quais características devem ser manipuladas para reconstruir e restaurar ativamente e efetivamente comunidades com alta produtividade e funcionamento.

A nível global, hoje sabemos como poucos atributos funcionais facilmente mensuráveis, normalmente foliares ou estruturais, são coordenados e distribuídos no gradiente aquisitivo-conservativo. Trabalhos que incluam estruturas funcionais fundamentais, como raízes, ainda são raros e limitados a estudos locais com poucas espécies (Morales et al., 2015). Da mesma forma, faltam estudos que incluam outras medidas funcionais de maior complexidade mensurável, como potencial hídrico, isótopos estáveis ou carboidratos não estruturais. Além disto, existem biomas inteiros cujas características funcionais são pouco conhecidas, como as Florestas Tropicais Sazonalmente Secas. Para que possamos compreender de forma mais completa como as estratégias a nível global, hoje dentro de uma escala aquisitiva-conservativa, funcionam, é de fundamental importância que concatenemos dados de diversos atributos, incluindo todos os biomas.

Esta tese apresenta o estudo de atributos funcionais de espécies de árvores da maior e mais diversa Floresta Tropical Sazonalmente Seca das Américas. No primeiro capítulo, testo como diversos atributos morfológicos, bioquímicos e fisiológicos de estruturas vegetais que se encontram acima e abaixo do solo se coordenam formando grupos funcionais. Além disto, analiso como estes grupos estão espacialmente distribuídos e se eles possuem limitações às principais características abióticas do bioma, como pluviosidade e temperatura. No segundo capítulo, avalio como estes mesmos atributos funcionais mediam interações entre plantas, focando em como definir uma boa planta facilitadora, considerando a interação entre os seus atributos e os atributos das plantas por ela afetadas. No terceiro capítulo, testo quais características funcionais são mais importantes para o agrupamento de comunidades em programas de restauração, juntamente com efeitos de facilitação, e ainda como diferenciar estes dois efeitos. Desta forma, contribuo com levantamentos de novos dados funcionais, até então inexistentes para este bioma, e com o avanço do conhecimento teórico sobre grupos funcionais de Florestas Tropicais Sazonalmente Secas, interações entre plantas e funcionamento de comunidades. Por fim, proponho o desenvolvimento de métodos práticos e eficazes para a restauração de ambientes secos.

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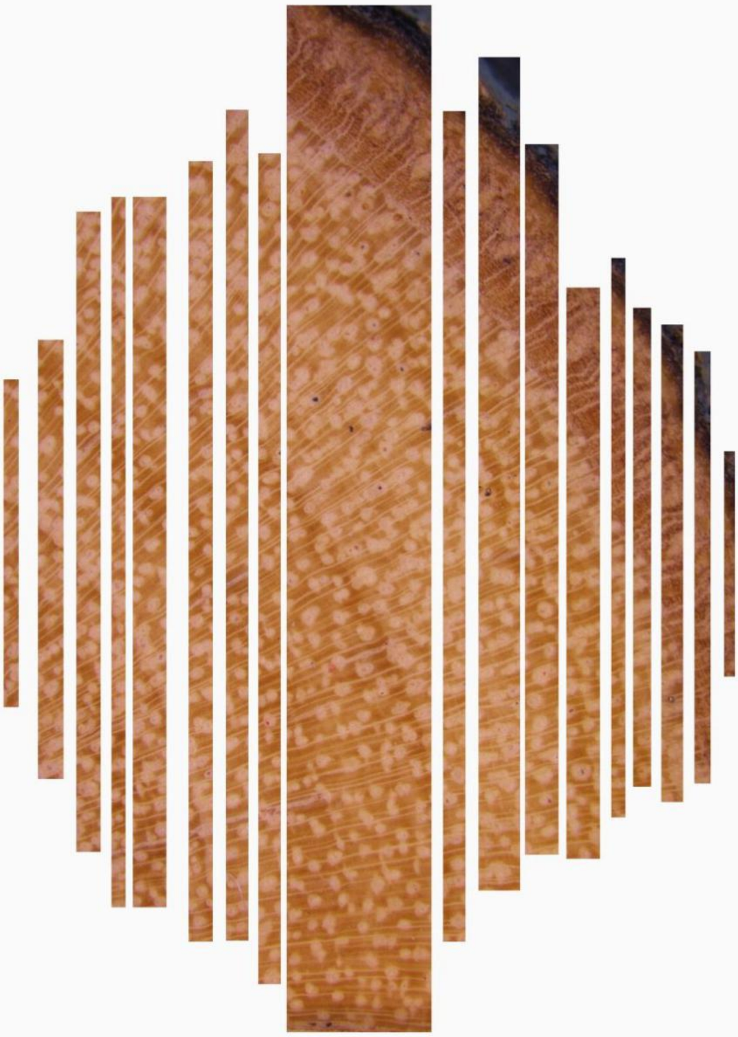

FUNCTIONAL STRATEGIES AND THE DISTRIBUTION OF TREE SPECIES IN THE CAATINGA SEASONALLY DRY TROPICAL FOREST

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Functional strategies and the distribution of tree species in the Caatinga Seasonally Dry Tropical Forest

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Abstract

1. Plant ecological strategies can be defined according to a gradient of environmental stress severity and disturbance which generates a continuum of plant adaptation strategies from conservative to acquisitive species. Stressful environments select species with conservative strategies and high resistance, whereas mild regions select species with acquisitive strategies and high vulnerability. Plants from seasonally dry environments, however, have to resist long drought periods and also be able to maximize their resource acquisition during short rainy periods. Plant functional strategies and the factors limiting functional groups distribution at such environments are still poorly understood. This work aimed to: 1. Analyze possible coordinated trade-offs of tree species traits on the largest Seasonally Dry Tropical Forests of the Americas, 2. Determine its possible functional groups and 3. Test if these functional groups are spatially associated over the biome and if their distribution is defined by an aridity gradient.

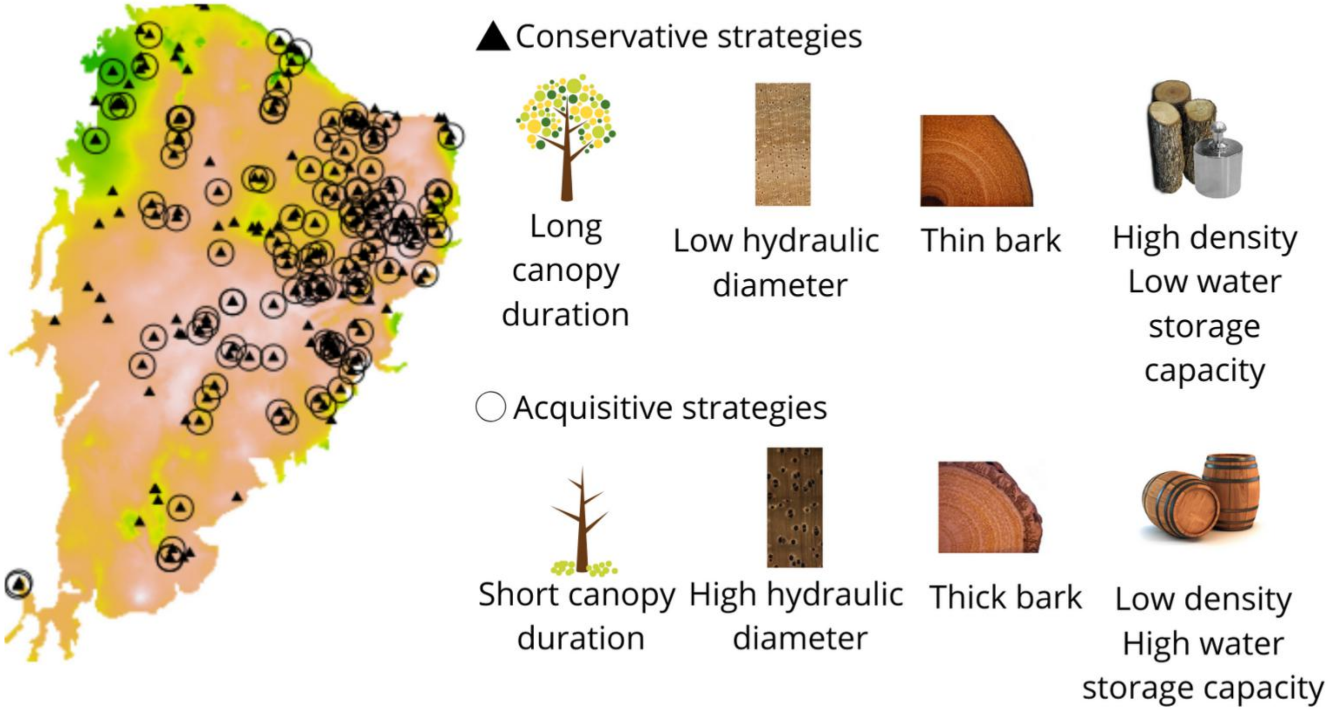
2. We sampled a range of 16 morphological, anatomical and biochemical functional traits from 20 tree species native from the Caatinga Seasonally Dry Tropical Forest. We used a PCA to understand species main trade-offs, k-mean analysis to test for functional groups and Ripley's K analysis to test for the spatial distribution of functional groups on an aridity gradient. We also used a gls model in order to test if distinct groups occurs at different aridity levels.

3. We found distinct coordinated trade-offs representing different aspects of the conservative-acquisitive strategy continuum. Water storage was positively correlated with acquisitive strategies. Additionally, bark tissues presented higher water storage capacities than wood tissues. Drought-avoidance and tolerance mechanisms also seem to be linked with conservative-acquisitive gradient. Species with conservative traits, were able to maintain their leaves for longer periods than species with acquisitive traits that avoid drought. Species of both groups are independently distributed over the biome and, contrary to our predictions, acquisitive species occurrence is more related to arid regions than conservative species occurrence.

4. Our results indicate that tree species from Caatinga Seasonally Dry Tropical Forest have a high functional diversity encompassing species from a continuum of conservative to acquisitive strategies. Furthermore, differently from other seasonally dry biomes, the acquisitive strategies are not limited by aridity. This pattern might be related to two main mechanisms: 1) Plant species have evolved to maximize the exploitation of water during short rainy periods; 2) The presence of short-term water storage-traits tamponing eventual rain fluctuations. These mechanisms might allow drought vulnerable species to coexist successfully with drought tolerant species throughout the whole biome.

Graphical abstract

Functional strategies and the distribution of tree species in the Caatinga seasonally dry tropical forest



Caatinga forest have a high functional diversity encompassing species from a continuum of Acquisitive to Conservative strategies. Both strategies occur independently and are not limited by aridity.

Introduction

The manner in which plant functional strategies evolved to colonize and persist at distinct environmental conditions is a topic of worldwide interest in plant ecology. At global scale, it is possible to define plant species strategies within conservative and acquisitive functional groups (Grime, 1977;Westoby, 1998; Diaz et al., 2016). Conservative species present high capability to deal with limited resources due to functional traits that minimize resource loss and acquisition rates, leading to slow but safe growth patterns (Chave et al., 2009; Reich, 2014). Conversely, acquisitive plant species present coordinated functional traits that maximize plant resource acquisition rates, leading to fast but vulnerable growth pattern. At large scale, these two opposite strategies are distributed through a slow-fast growth continuum in response to stress severity (Reich, 2014). Essentially, environments with high-stress conditions are favorable to conservative plants, whereas environments with low-stress levels are favorable to acquisitive plant species (Grime, 1977; Pierce et al., 2013).

However, in some biomes the stress severity is seasonally variable. The Seasonally Dry Tropical Forest (SDTF), presents seasonal cycles that alternate between high stress and low stress conditions for plant growth, mostly related to changes in rainfall and temperature (Pennington et al., 2009). High stress periods (dry season) are characterized by several months of drought and high temperatures, while favorable periods (wet season) are represented by shorter intervals of concentrated rain and lower temperatures. Even though dry climates commonly favors the establishment of conservative species (Cornwell & Ackerly, 2009; Costa-Saura et al., 2016), the wet season can promote favorable conditions for acquisitive species to establish and endure. Thus, in order to persist in such ecosystem, trees should present a range of functional traits that encompass conservative and acquisitive strategies for minimizing drought vulnerability while maximizing growth during favorable periods.

Stress avoidance is a common plant strategy to deal with such environmental pressure. By losing leaves at the beginning of the dry season, plant species limit their activity to the rainy period preventing embolism and hydraulic damage during drought (Poorter & Markesteijn, 2008). Studies performed at SDTF indicate that deciduousness is a fundamental trait to define plant species strategies (Oliveira et al., 2015; Lima et al., 2012). The authors also found that the diversity of plant functional strategies for dealing with drought might be higher than previously thought. Thus, a refined understanding of how deciduousness is coordinated with traits underlying conservative and acquisitive patterns, is fundamental to uncover plant functional strategies in the SDTF ecosystem.

The maintenance of distinct functional groups within the same biome is also modulated by spatial heterogeneity (Oliveira et al., 2018). At water-limited biomes, the combination of rainfall and temperature modulate aridity patterns (Quan et al., 2013). For several arid environments, it is known that aridity limits the occurrence of functional groups, where acquisitive species are more related to regions of lower stress (Engelbretch et al., 2007; Frenette-Dussault et al., 2012; Esquivel-Muelbert et al., 2016). For SDTF, it is known that aridity heterogeneity is the main factor modulating plant community structure (Silva & Souza 2018), but until now, no relationship between spatial gradients of resources and functional groups distribution was found (Queiroz et al., 2017).

The Seasonally Dry Tropical Forest is a complex, highly diverse, and still poorly understood environment. To comprehend such diversity one should understand how plant functional groups would be structured and spatially distributed. In this work, we studied key morphological and biochemical functional traits of 20 ecologically-important and representative tree species from the Caatinga, the largest Seasonally Dry Tropical Forest of the Americas to: (i) uncover coordinated trade-offs among species functional traits, (ii) determine species trait-based functional groups, and (iii) test if functional groups have different spatial distributions over the biome and if these distributions are related to aridity. We expect a coordination between short canopy duration and acquisitive plant traits representing the acquisitive side of the plant functional spectrum. We also expected that conservative species will be evenly distributed over the biome, whereas acquisitive strategies will be limited to areas with lower aridity.

Methods

Study Area

The study was conducted at the Caatinga Forest, the largest and richest Seasonally Dry Tropical Forest of the world, which covers 826,411 km^2, occupying 11% of the Brazilian territory (Queiroz et al., 2017). This dry forest has been threatened by fragmentation and half of its original area have been degraded

(Antongiovanni et al., 2018), while the other half remains in a state of chronic disturbance (Santos et al., 2015; Ribeiro et al., 2016). Trait surveys was performed at the Açu National Forest (Rio Grande do Norte, Brazil), a nature reserve dominated by the Seasonal Dry Tropical Forest known as Caatinga. The National Forest encompasses 528 ha, where vegetation is characterized by trees varying from 2m to 15m in height. The Caatinga vegetation varies in structure within the biome. The Caatinga vegetation structure of the National Forest region is known as "São Francisco and Sertaneja depressions" (Silva e Souza, 2018), the aridest region of the biome with a mean annual temperature of 24ºC and mean annual precipitation of 607mm.

Species and individual selection

We selected native, representative, and widely distributed tree species from Caatinga which were abundant at the National Forest of Açu. Trees individuals selected were preferably isolated to ensure below-ground samples were collected from the specific selected individual. We analyzed 20 adult species, each replicated three times with a total of 60 trees (See all species and traits in Table 1 and in Supplementary Material Table S1). All species has as trait value the average of five individuals measurements.

Trait selection and measurements

In order to encompass above and below ground structures as leaves, stem, and roots, including anatomical and biochemical features, we sampled the following plant traits: 1. Plant height (cm), as indicator of light competitive ability 2. Leaf Area (LA, mm^3), indicating potential photosynthetic surface and transpiration area 3. Specific Leaf Area (SLA, Kg/m^3) indicating the photosynthetic area per unit of mass, 4.Wood Density (WD, g/cm^3) and 5. Root density (RD, g/cm^3) indicating growth rate, mechanical and hydraulic resistance above and bellow ground respectively, and 6. Specific root area (SRA, Kg/m^3) indicating the resource uptake area per unit of biomass, 7. Canopy diameter (m) indicating overall photosynthetic area, 8. Leaf carbon isotope (∂13C) indicating water use efficiency, 9. Leaf C:N ratio (C:N) indicating leaf resource allocation on tissue resistance or photosynthesis, 10. Number of months without leaves (MWL) indicating species stress-tolerance,11. Bark density (BD, g/cm^3) and 12. Bark thickness (mm) indicating tree protection and potential water content, 13. Bark storage capacity (%) and 14. Wood storage capacity (WSC %) indicating water storage capability, 15. Hydraulic diameter (DH) indicating plant water conductivity capacity and 16. Root volume occupied per ground area (RV) indicating capacity for soil resource foraging. See complete trait ecological information in Table S2.

Structural traits

The two structural traits representing plant size, Plant height and Canopy diameter, were obtained in the field using a measuring tape. Plant height was recorded by a perpendicular measure of the tree from soil to the end of canopy. Canopy diameter was established by measuring two perpendicular canopy widths directed north and south respectively. Both canopy measurements were subsequently averaged to calculate Canopy diameter

Leaf traits

For LA and SLA three fully developed sun-exposed leaves were sampled of each individual and stored in plastic bags to maintain leaf moisture for image scan. Fresh leaf area was scanned with a Hp Officejet 4500 desktop, excluding the petiole, once it can influence leaf weight but does not represent photosynthetic area (Pérez-Harguindeguy et al., 2013). Subsequently, leaves were dried for 48h at 60ºC and weighted. The LA was calculated using ImageJ program, and SLA was calculated using the fresh leaf area divided by its dry weight. For C:N ratio and ΔC^{13} isotope, three leaves were sampled and dried for 48h at 60ºC, macerated, encapsulated, and sent to UC Davy's laboratory for chemical and isotopical analysis, respectively. Months without leaves were obtained from the literature (Lima e Rodal, 2010).

Wood traits

For each tree, we collected two samples from the larger branch after the first tree bifurcation, in order to minimize plant injuries. The first sample was stored in plastic bags to maintain humidity for measurements of Bark Density, Wood Density, Bark and Wood water storage capacity, and Bark thickness. Bark was detached from its wood and the fresh volume of both structures were obtained by water displacement. Bark and wood were submerged for 48 hours, re-weighted to obtain saturated weight and subsequently dried at 70ºC for one week and re-weighted to obtain dry weight.

Bark and wood density were calculated dividing dry weight by fresh volume. Bark and Wood water storage capacity were calculated by the difference between saturated and dry weight divided by dry weight. Bark thickness was calculated by averaging two perpendicular lengths measured from vascular cambium to the external part of the fresh bark.

The second sample was stored in paper bags to measure Hydraulic diameter. To calculate Hydraulic diameter, samples were naturally dried, polished with different sandpaper grains until the anatomic structures were evident. Images of all samples were obtained using stereo microscope Nikon SMZ1500. For each sample, the diameter of 100 vessels were measured using ImagePro Plus software, guided by Scholz (2013) method.

Root traits

For each individual tree, we dug 1/4 of a cylinder (40cm radius, 20cm of depth) around the stem and carefully removed all the soil until the roots were exposed. To obtain the Specific root area (SRA), calculated as the fresh root area divided by Root dry mass (g/cm^3), we sampled roots with a diameter smaller than 1mm. The samples were stored in zip-locks inside a cooler bag in order to avoid moisture loss. Fresh root area was scanned with a Hp Officejet 4500 desktop, and measured with the free software ImageJ. Subsequently, root samples were dried at 70ºC for one week and weighted in order to obtain their dry mass. To obtain the Root volume all roots larger than 1 mm had their largest diameter (D) and length (L) measured and their volume (V) was calculate per root using the cylinder formula ($V = \pi.r^2.L$). The Total root volume per tree was calculated as the sum of all root volume measurements. The average of all root volumes collected from the three trees of each species represented the species Root volume trait. The Root density trait was calculated dividing root dry mass per root fresh volume (g/cm^3). We sampled and stored in a cooler bag one root larger than 10mm of diameter to obtain its volume which was calculated by the water displacement method. Subsequently, the samples were dried at 70ºC for one week and weighted to obtain the Root dry mass.

Traits and aridity geographical distribution

In order to understand how plant functional strategies are distributed along the biome, we used the species occurrence data gathered by Silva & Souza (2018). We grouped species based on its functional group as determined by k-mean analysis. In order to test if the distribution of functional groups was related to aridity, we accessed the data of Caatinga mean annual pluviosity from Worldclim (Fick & Hijmans, 2017), considering 30 years of data between 1970 to 2000s, and average temperature. We then calculated the aridity index according to Quan et al. (2013), by dividing the mean precipitation by the mean temperatures, adding a constant number of 33 (AI= precipitation / mean temperature + 33). We built the map of functional groups distribution over the annual aridity index availability by using QGis software.

Statistical analysis

In order to establish strategy trade-offs, we performed a Principal Coordination Analysis, after data normalization procedures, using the “principal” function of “psych” package (Revelle, 2018). To determine axis loading significance, we used ‘keiser’ criteria and to determine variable scores significance within axes, we selected just the variables with scores higher than 0.5 following Hair et al. (2014).

To test if there were functional groups related to these traits, we performed a K-means analysis, after data normalization procedures, using the “cascadeKM” function of “vegan” package (Oksanem et al., 2018), with five groups set as the maximum group numbers, according to PCA analysis result. The model was run with 1000 iterations using the default ‘Kalinski’ criteria.

To test if the functional groups were independently distributed over the Caatinga, we performed a Ripley’s K test, using the “k12fun” function from “ads” R package. We tested our model against the null hypothesis of independence once we are interested in understanding if there is spatial aggregation/repulsion between functional groups (Pelissier & Goreaud, 2015). The confidence limits were established by 1000 Monte Carlo simulations.

To test if aridity levels were different in areas where the distinct functional groups occurred, we used the aridity index as the dependent variable, and the categories of functional groups found as independent variables. We first extracted the aridity index relative to the geographical points of occurrence for conservative and acquisitive functional groups and also extracted aridity data from 120 random geographical points. All geospatial procedures were made using the “rdgal” (Bivand et al., 2019) and “raster” (Hijmans, 2019) packages. We tested the data for spatial autocorrelation using the “Moran.I” function from “ape” package (Paradis & Schliep, 2018). Because our data presented spatial autocorrelation, we performed a generalized least squared analysis using “gls” function from “nlme” package (Pinheiro et al., 2019). This incorporates the latitude and longitude coordinates in order to remove spatial bias (see analysis in Supplementary material, Figures S2 and S3).

Results

Caatinga traits

Trade-offs and strategies

The coordinated traits of 20 semiarid tree species (Table 1) were explained by five significant axis, explaining respectively 39%, 17%, 17%, 14%, and 13% of the data variation (Table 2, see species list on Table S1). The first axis (Figure 1) was positively correlated with conservative traits such as high wood and root density tissues, thin bark and low leaf area while negatively correlated with acquisitive traits such as low density tissues, high leaf area, high water storage capacity of stem, roots and bark and high bark thickness. The second axis was positively correlated with conservative strategy traits such as high C:N ratio and low canopy diameter while negatively related to acquisitive strategy traits such as high canopy diameter and low C:N leaf ratio. The third axis was negatively related to species with high SLA and longer periods without leaves. The fourth axis was represented by species with high bark storage capacity and was negatively correlated with high root volume occupied per ground area. The fifth axis was positively correlated with Leaf Area and a high water use efficiency represented by Leaf ∂^{13}C .

Table 1. Mean, maximum, minimum, and standard deviation of 16 functional traits from 20 adult Caatinga tree species.

Caatinga species					
Trait	**Unit**	**Mean**	**Max**	**Min**	**SD**
Tree Height	cm	532.83	1100	200	192.46
Canopy diameter	m	5.35	18.5	0.74	3.38
Leaf Area	mm^2	7039	32929	215	6865.19
Specific Leaf Area	m^2/Kg	15.34	27.3	5.383	4.271
Months without leaves	months	5.15	9	0	2.21
∂13C leaf isotope	ratio	-27.77	-25.69	-29.54	0.841
C:N Leaf Ratio	ratio	22.91	43.21	13.73	5.769
Wood density	g/cm^3	0.68	0.91	0.262	0.175
Wood water storage capacity	%	0.72	2.412	0.365	0.504
Hydraulic diameter	mm	0.06	0.118	0.02	0.025
Bark density	g/cm^3	0.58	0.846	0.276	0.162
Bark water storage capacity	%	1.82	5.0	0.80	0.795
Bark thickness	mm	1.39	5.0	0.25	0.963
Root volume occupied	vol/cm^3	0.04	0.20	0.0009	0.046
Root density	g/cm^3	0.58	0.881	0.192	0.181
Specific Root Area	g/cm^3	9.95	38.77	3.37	6.23

Table 2. Table of the five significant axis of a Principal component analysis considering 20 tree species of Seasonally tropical dry forest (see the species list on Table S1). The significance of scores was established as values higher than 0.5.

Trait	PC1	PC2	PC3	PC4	PC5
Height	0.46	0.7	0.24	-0.01	0.18
Canopy diameter	0.29	**0.62**	-0.04	0.02	0.42
SLA	0.06	0.12	**0.96**	-0.01	-0.03
LA	**0.59**	-0.03	0.04	0.1	**0.72**
Wood density	**-0.84**	0.1	-0.16	0.38	0.08
Root volume occupied per ground unit	0.25	0.33	-0.44	**0.59**	0.1
Bark density	**-0.68**	-0.22	0.20	0.64	-0.03
Wood water storage capacity	**0.85**	-0.05	0.07	-0.39	-0.03
Bark thickness	**0.86**	0.19	-0.02	0.07	0.11
Bark water storage capacity	0.32	0.24	0.05	**-0.85**	0.01
Hydraulic diameter	**0.81**	0.06	0.09	0.05	0.14
d13C	-0.17	0.22	-0.24	0.01	**0.80**
C:N ratio	0.08	**-0.87**	0.15	0.1	0.02
Months without leaves	0.25	-0.23	**0.68**	-0.04	-0.44
Root density	**-0.87**	-0.15	-0.06	0.26	0.15
SRA	0.32	-0.5	-0.18	**-0.55**	-0.17
Eigenvalues	5.05	2.27	1.83	2.17	1.65
Variation explained	0.39	0.17	0.14	0.17	0.13

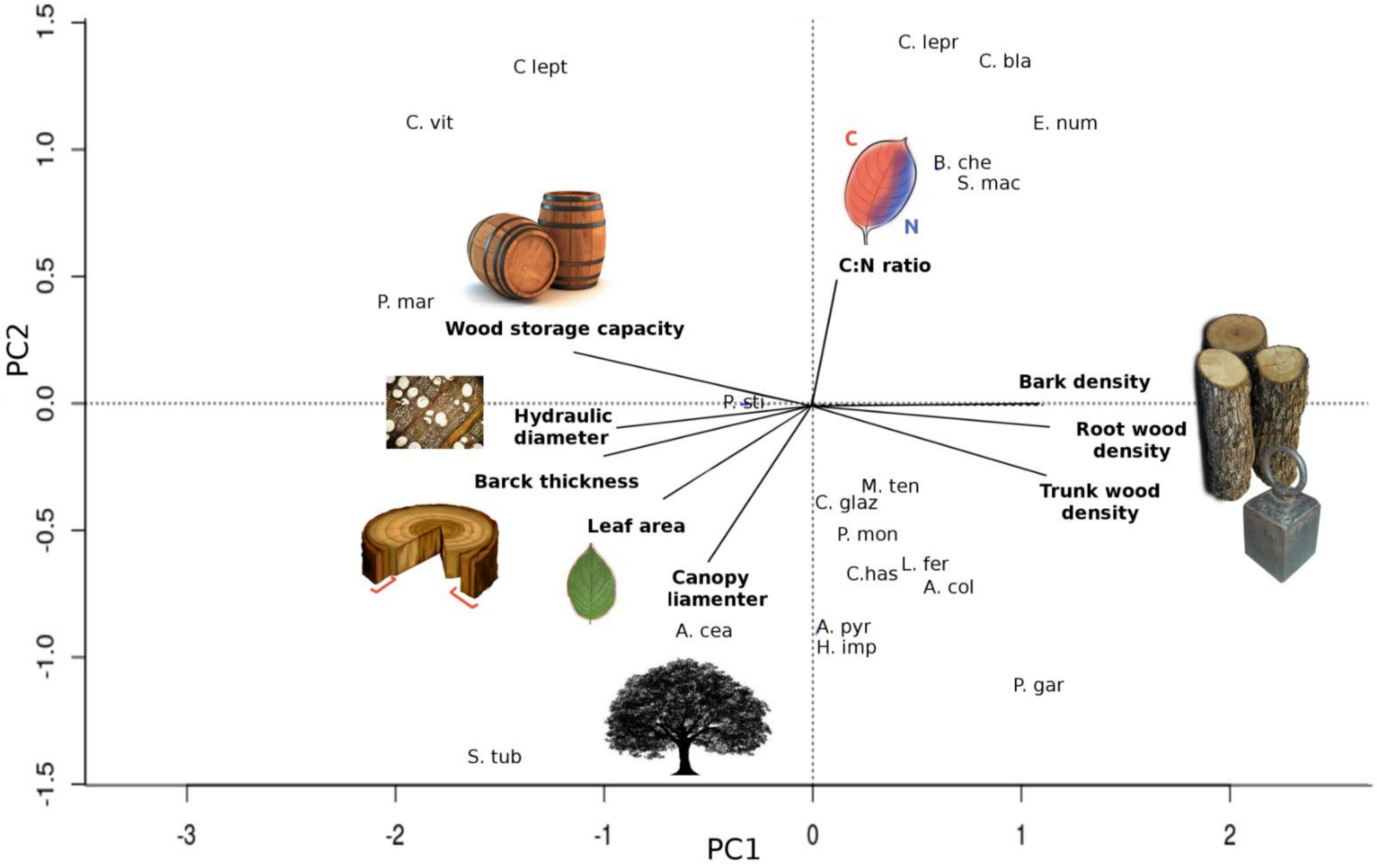


Figure 1. Results of the two first axis of a PCA analysis with selected traits scores higher than 0.5. On PC1 Leaf area, Wood density, Wood storage capacity, Bark density, Bark thickness, Hydraulic diameter, and Root density. PC2 represented by Canopy diameter and Leaf C:N ratio. The analysis was performed with 20 tree species of Seasonally tropical dry forest, names, and abbreviations can be found in Table S1.

Functional groups

Caatinga tree species were divided into two main functional groups according to K-means analysis (Calinski = 8.287). The first group included 16 species that were characterized by higher tissue density, low storage capacity, low bark thickness, low hydraulic diameter, and low SRA (i.e. conservative group, Figure 2). The second group, represented by the other four species: *Spondias tuberosa, Pseudobombax marginatum, Cochlospermum vitifolium*, and *Comiphora leptophloeos*, was characterized by low tissue density, high storage capacity, high bark thickness, high hydraulic diameter, and high SRA (i.e. acquisitive group, Figure 2).

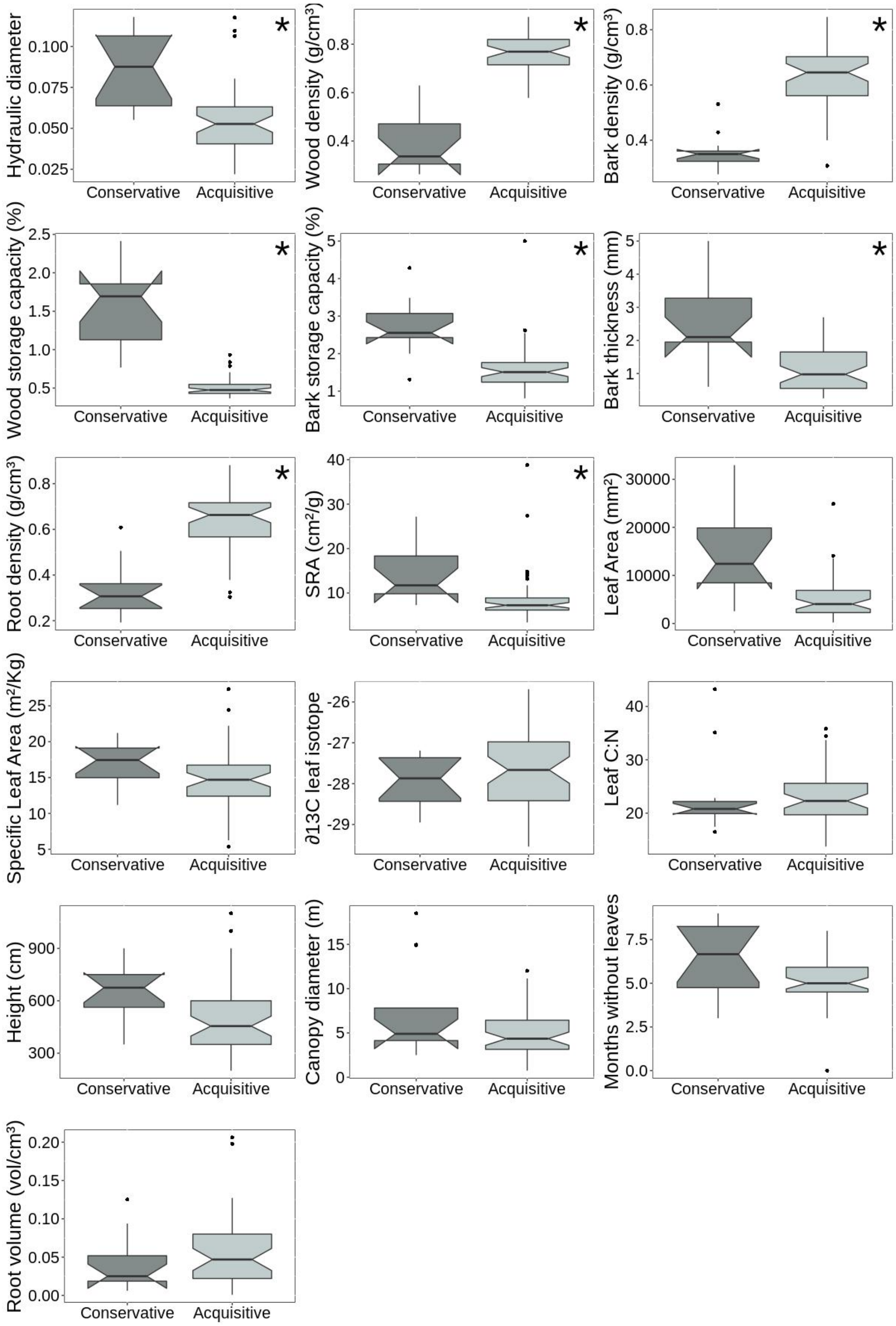


Figure 2. Boxplots with traits median and standard error values for the two functional groups (1- conservative and 2-acquisitive) with trait values separated by groups partition based on Calinski criteria. Traits that differed between groups by ANOVA test are represented by '*', see all values on Table S3.

Functional groups spatial distribution

The aridity index varied from 0 to 30, representing the higher and the lowest aridity values, respectively. The lower aridity values were found at the border with the north part of Cerrado biome, and the highest aridity values occurred at the center of the biome. The acquisitive and conservative functional groups are distributed independently from each other along the Caatinga biome (Figure 3, and graphical analysis on Figure S1). However, contrary to our predictions, the acquisitive group were more related to regions with higher aridity (Table 3 and Figure 4).

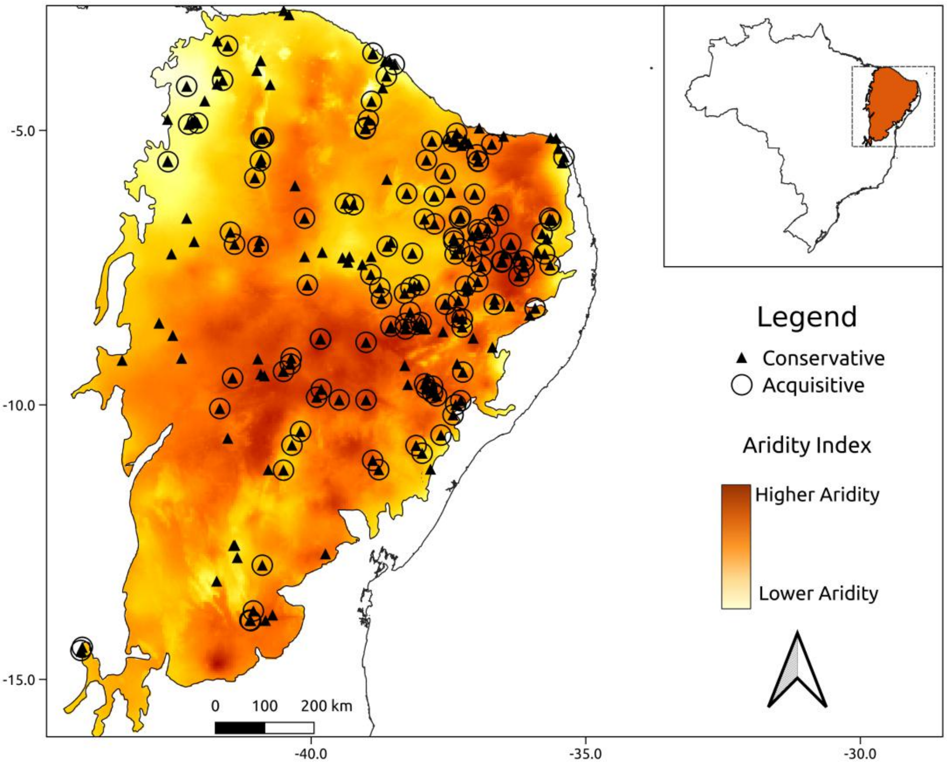


Figure 3. Distribution of functional groups acquisitive (transparent circles) and conservative (black triangles) along the Caatinga biome. Colors indicate the aridity index calculated over 30 years, from 1970 to 2000, lighter colors and low values indicate higher aridity, whereas greener colors and higher values represent lower aridity.

Table 3. Results from model considering the spatial autocorrelation. Aridity data extracted from conservative and acquisitive functional groups coordinates and from

120 random points. Averages where compared using “gls” function in order to control for spatial autocorrelation.The“acquisitive” group was used as intercept.

	Coefficient Value	Std.Error	t-value	p-value
Intercept	2.951	0.272	10.814	<0.001
Random	-0.042	0.011	-3.566	0.004
Conservative	0.000	0.000	0.014	0.988

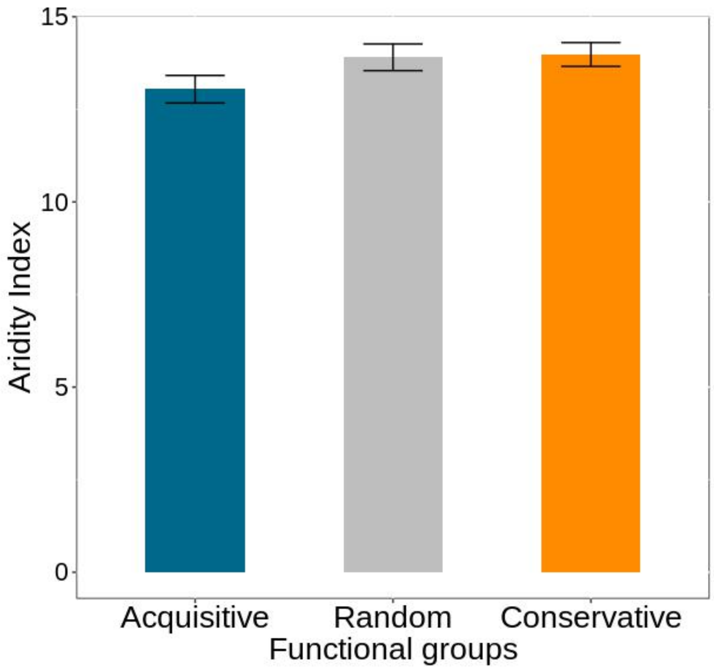


Figure 4. Bars represent the mean aridity index extracted from geographical points of occurrence of acquisitive groups (blue), random (gray) and conservative groups (orange) The error bars represent standard deviation.

Discussion

Coordinated Trade-offs and Plant Strategies

The functional traits of 20 Caatinga Dry Tropical Forest tree species were organized into distinct trade-offs of the conservative-acquisitive gradient. The first embraces the well-known trade-off between safe but slow growing tissues on the conservative side versus vulnerable but fast-growing tissues on the acquisitive side (Grime, 1977, Diaz et al, 2016). This is an expected relationship for organs such as stem (Borchet, 1994; Stratton et al, 2000), but here we show that this pattern also extends to root and bark tissues. Furthermore, this trade-off is not limited to tissue density, but includes water-related traits, which have been fundamental in explaining the coordination of species strategies (Reich, 2004). A greater water conductance capacity of the species, measured as the hydraulic diameter (Scholz et al, 2013), was coordinated with the acquisitive side of the spectrum. Similar results were found in a study conducted in a dry forest with rainfall and temperature equivalent to Caatinga (Straton et al, 2000). When considered, water-related traits tend to coordinate with conservative-acquisitive nuances, indicating that including them is essential to better understand dry tropical forests.

The conservative-acquisitive gradient encompasses other fundamental mechanisms of survival in the Caatinga Dry Tropical Forest, the plant ability to avoid or tolerate periods of drought (Piñeda-García et al., 2013, Pinho et al., 2019). Species with conservative characteristics, such as low SLA, generally have lower photosynthetic and growth rates (Poorter and Bongers, 2006). A slow growth rate allows the species to have low water loss through the leaves, higher embolism xylem resistance and lower probability of dehydration (Pérez-Ramos et al., 2013; Eamus, 1999). As a consequence, these species are able to safely hold their canopy leaves for longer periods of time, resisting drought (Brodribb et al., 2002), as seen in species found on the conservative side of the spectrum. On the other hand, in the acquisitive side of the spectrum, we find species with high SLA and a short canopy duration. By losing leaves and avoiding dry periods, these species are able to decrease their risk of mortality during drought, and flush their leaves in the next rainy season (Lima et al., 2012) .

The importance of short-term storage

The Caatinga Seasonally Dry Tropical Forest is a complex unique environment and it is one of the semiarid systems with higher rainfall unpredictability (Garreaud et al., 2008). Despite the ability of species to lose their leaves, avoiding drought periods, they have to deal with rainfall gaps, even within the rainy period. In environments where the rainy period is not constant, short-term water storage traits such as bark and wood structures can be of great importance (Borchet, 1994; Rosell et al., 2014). Bark tissues presented 40% higher storage capacity than wood tissue (Table 1). Even though bark storage may represent a short-term water availability compared to other specific storage organs, it might have a powerful role for plant species with acquisitive strategies (Rosell et al., 2014). Short-term storage structures are easily accessed and might act as a water buffer, preventing embolism in plants with acquisitive strategies during the rainfall gaps (Stratton et al., 2000). Short-term storage structures can maintain the physiological processes (Poorter et al., 2014; Pérez-Ramos et al., 2013), such as water flux, that decreases the risk of plant damage or embolism due to dehydration (Stratton et al., 2000). Thus, short-term storage might be an essential mechanism by which plants with acquisitive strategies can be successful in semiarid lands.

Functional groups

All of the coordinated trade-offs described were collapsed into two main groups, one representing conservative and the other acquisitive strategies. Such result, indicates that Caatinga trees are represented by either stress-tolerant strategies, with capabilities to tolerate several months of drought, or species with high competitive strategies, limited to a few months of rain. The most important traits to define conservative-acquisitive groups were tissue density. The same traits were decisive to define functional groups of arid environments (Méndez-Alonzo et al., 2012) and for Seasonally Dry Tropical Forests (Oliveira et al., 2015; Lima & Rodal, 2010; Lima et al., 2012). It is important to highlight, however, that the analysis presented at this work was performed with a limited number of species, 20 out of 886 tree species that occur in the Caatinga forest (BGF, 2005). Although these 20 species are widespread and quite abundant in the Caatinga forest, future works must embrace a more extensive number of species to generalize our understanding of the functional strategies of tropical semiarid trees.

Spatial distribution of species strategies

In this work, acquisitive and conservative strategy groups were distributed independently over Caatinga, indicating that both strategies are not spatially segregated. However, acquisitive strategies are able to occur at a slightly higher aridity regions. These results are contrary to what has been commonly found in the literature, where species have substantial spatial segregation and acquisitive species are commonly limited by water availability (Engelbretch et al., 2007; Baltzer, 2008; Lebrija-Trejos et al., 2010; Frenette-Dussault et al., 2012; Esquivel-Muelbert et al., 2016).

Similar results were found for Caatinga by Pinho et al (2019), showing that areas with low pluviosity and high soil fertility are occupied by species with acquisitive traits as low wood density. Another study conducted for Ribeiro et al (2019) also showed that areas with higher stress due antrhopogenic disturbances select species with acquisitive traits. Until now, this pattern was thought to be found only in small-scale, but the results found here indicate that this may be a general pattern of Caatinga SDTF, distinct from other semiarid forests.

At SDTF, the several nuances of species strategies described in this work might allow them to widely occupied the biome through the most of its aridity gradient. At higher aridity regions, however, acquisitive strategies might have perform better during the absence of rainfall due three characteristics: the ability to rapidly acquire water during the limited growing season, greater water storage capacity and rapid leaf loss. The rainy season in the SDTF is short and irregular (da Silva et al, 2017; Garreud et al 2009), a greater capacity to acquire available water for short periods may be advantageous in relation to conservative species, which need longer periods for water acquisition (Reich, 2014). The acquired water can be stored, ensuring photosynthetic mechanisms (Poorter et al., 2014) and preventing embolism (Stratton et al., 2000) during the absence of rain. Finally, the rapid response of leaf loss at the end of rainy season can give the acquisitive species a rapid dormancy, avoiding the stress of drought (Eamus, 1999).

Conclusion

Our results indicate that species of Caatinga Seasonally dry forest have a high functional diversity that can support a continuum of acquisitive to conservative strategies, modulated by seasonality of resource availability. The mechanism of resistance or avoidance is an important part of species strategy to survive during contrasting seasons. The short-term storage structures as bark and wood, might be the mechanism responsible for the successfully maintenance of the risky acquisitive strategy in this environment of intermittent pluviosity. The understanding of how distinct environments modulate plant strategies is fundamental to fulfill the gaps between acquisitive-conservative extreme strategies, as showed for Seasonally Dry Tropical Forests. Thus, future works should focus on increasing not just the number of species analyzed but the traits related to its limiting resources in order to increase the robustness of plant strategies predictions for such diverse and complex biome.

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Supplementary Material

Uncovering functional strategies and distribution of tree species from the most diverse Seasonally dry tropical forest

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Table S1. Information of scientific name of species, abbreviations and popular name

.Family	Abbreviation	Focal specices	Popular name
Anacardiaceae	S. tub	*Spondias tuberosa*	Umbuzeiro
Apocynaceae	A. pyr	*Aspidosperma pyrifolium*	Pereiro
Bignoniaceae	H. imp	*Handroanthus impetiginosus*	Ipê roxo
Bixaceae	C. vit	*Cochlospermum vitifolium*	Algodão do mato
Boraginaceae	C. glaz	*Cordia glazioviana*	Pau-branco
Burseraceae	C. lept	*Commiphora leptophloeos*	Imburana de cheiro
Capparaceae	C. has	*Cynophalla hastata*	Feijão-Bravo
Combretaceae	C. lep	*Combretum leprosum*	Mofumbo
Erythroxylaceae	E. num	*Erythroxylum nummularia*	Favelinha
Euphorbiaceae	C. bla	*Croton blanchetianus*	Marmeleiro
Euphorbiaceae	S. mac	*Sebastiania macrocarpa*	Burra-leiteira
Fabaceae - Caesalpinoideae	B. che	*Bauhinia cheilantha*	Mororó
Fabaceae - Caesalpinoideae	P.gar	*Poincianella gardneriana*	Catingueira
Fabaceae - Mimosoideae	M. ten	*Mimosa tenuiflora*	Jurema-Preta
Fabaceae - Mimosoideae	P. sti	*Piptadenia stipulacea*	Jurema-Branca
Fabaceae - Mimosoideae	A. col	*Anadenanthera colubrina*	Angico
Fabaceae - Papilionoideae	A. cea	*Amburana cearensis*	Cumaru
Fabaceae- Caesalpinoideae	L. fer	*Libidibia ferrea*	Pau-Ferro
Fabaceae- Mimosoideae	P. mon	*Pityrocarpa moniliformis*	Catanduva
Malvaceae	P. mar	*Pseudobombax marginatum*	Imbiratanha

Table S2 Caatinga traits specification, measurements methods, ecological function, consequences of high and low values and related references

Trait	Initials	Measurement	Function	Consequence of high values	Consequence of low values	References
Tree Height	H	Height of above-ground structure measured in meters	Light competition	Higher light competitor	Low light competitor	1 ; 2
Canopy diameter	CD	Average of two canopy perpendicular axis measured in meters	Maximize photosynthetic production	Higher area of light acquisition	Lower area of light acquisition	2
Leaf Area	LA	Fresh leaf area measured in mm^2	Potential area of photosynthesis and water loss	Higher photosynthetic area and higher water loss	Low photosynthetic area and low water loss	3
Specific Leaf Area	SLA	Fresh leaf area divided by dry leaf mass Kg/m^2	Light capturing area per unit of mass	Higher investment in photosynthesis per unit of mass	Lower investment in photosynthesis per unit of mass	2 ; 4
Months without leaves	MWL	Number of months a individual remains without leaves	Avoid stressful periods	Tolerate stressful periods.	Higher stress tolerance	5
∂13C leaf isotope	∂13C	The proportion of stable isotope ∂13C related to C^{12} present in tree leaves.	Leaf water use efficiency	Higher water use efficiency	Lower water use efficiency	2; 6

C:N Leaf Ratio	C:N	Ratio of Carbon and Nitrogen present in a leaf.	Trade-off between resistance and photosynthesis	Leaves with tough tissue and lower photosynthetic rates	Leaves with soft tissue and higher photosynthetic rates	2; 7
Wood density	WD	Dry wood mass divided by fresh volume g/cm³	Related to relative growth rate, mechanical resistance, water stress-resistance and water storage	High-density wood with high mechanical resistance, low growth-rates and low water storage capacity	Low-density wood with higher mechanical vulnerability, high growth rates and high water storage capacity	8; 9
Wood storage capacity	WSC	Saturated wood weight minus dry weight (g)	The capacity to store water within and between wood fibers and parenchima tissues	Higher capacity to store water	Lower capacity to store water	8;10
Hydraulic diameter	HD	Vessels diameter and hydraulic conductivity capacity	Conduct water through plant vessels	Higher water conductivity capacity	Lower water conductivity capcity	11
Bark density	BD	Dry bark mass divided by fresh volume g/cm³	Protection, water storage	Low tissue protection, low water storage capacity	High tissue protection, Higher water storage capacity	12
Bark storage capacity	BSC	Saturated wood weight minus dry weight (g)	The capacity of store water within bark tissues	Higher capacity to store water	Low capacity to store water	12

Bark thickness	BT	Average of two perpendicular width measurements from vascular cambium to the external part of the bark.	Related to protection and water storage	Higher storage capacity.	Low storage capacity	12
Root volume	RVO	Volume of fresh roots occupying the first 20cm of soil.	Investment in roots on shallow soil, which is, not rarely, the area were semiarid short rains percolates.	Higher access to superficial water	Lower access to superficial water	Unpublished data - Empirical information
Root density	RD	Dry mass divided by fresh volume g/cm³	Response to growth rate, mechanical resistance, water stress-resistance and opened-space between fibers	Dense woods with high mechanical resistance, low growth-rates and low water storage capacity	Low-density wood with higher mechanical vulnerability, high growth rates and high water storage capacity	13
Specific Root Area	SRA	Soil resource exploitation.	Intensity of soil exploration or the capacity to acquire resources	Higher resource acquisition rates	Lower resource acquisition rates	2

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Table S3. MANOVA e ANOVA results of 16 functional traits compared between the two functional groups defined by the k-means analysis.

MANOVA					
	df	pillai	aprox F	num df	P-value
Functional group	1	0.91134	21.843	16	<0.001
Residuals	49				
ANOVAs					
Hydraulic diameter					
	df	SS	F-value	p-value	
Functional group	1	0.01061	22.58	<0.001	
Residuals	58	0.02726			
Height					
	df	SS	F-value	p-value	
group	1	151504	4.32	0.0421	
Residuals	58	2033915			
Canopy diameter					
	df	SS	F-value	p-value	
Functional group	1	50.9	4.726	0.0338	
Residuals	58	624.7			
SLA					
	df	SS	F-value	p-value	
Functional group	1	36.8	2.053	0.157	
Residuals	58	1039.6			
Leaf Area					
	df	SS	F-value	p-value	
Functional group	1	7.68E+08	22.12	<0.001	

Residuals	58	2.01E+09		

Wood density

	df	SS	F-value	p-value
Functional group	1	1.341	164.4	<0.001
Residuals	58	0.473		

Root volume

	df	SS	F-value	p-value
Functional group	1	0.00195	0.914	0.344
Residuals	49	0.1045		

Bark density

	df	SS	F-value	p-value
Functional group	1	0.7728	57.54	<0.001
Residuals	58	0.779		

Wood storage capacity

	df	SS	F-value	p-value
Functional group	1	11.262	173.7	<0.001
Residuals	58	3.761		

Barck thickness

	df	SS	F-value	p-value
Functional group	1	17.5	27.22	<0.001
Residuals	58	37.28		

Bark storage capacity

	df	SS	F-value	p-value
Functional group	1	11.46	25.66	<0.001
Residuals	58	25.9		

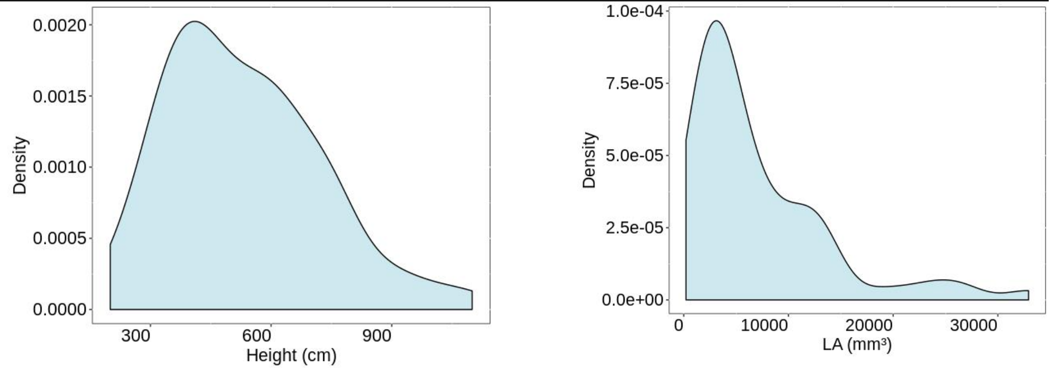
Stable Carbon isotope 13

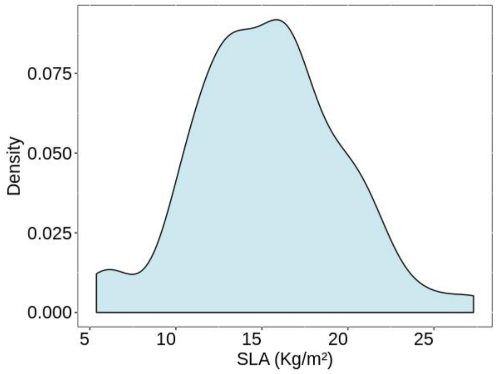
	df	SS	F-value	p-value
Functional group	1	0.24	0.341	0.561
Residuals	58	41.57		

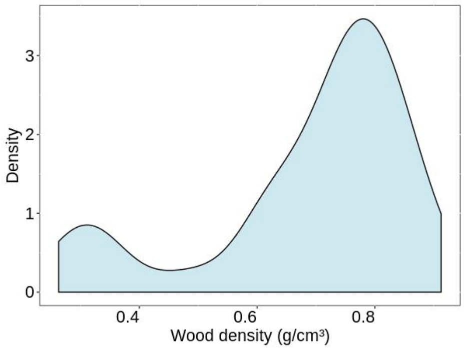
Leaf C:N

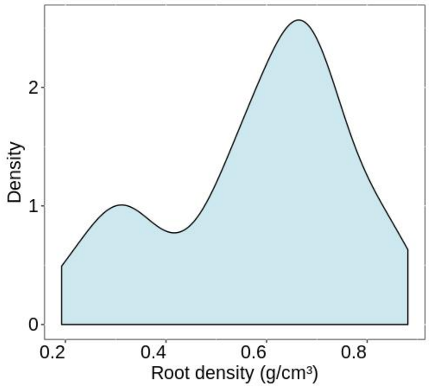
	df	SS	F-value	p-value
Functional group	1	1.6	0.046	0.83
Residuals	58	1962.4		
Months without leaves				
	df	SS	F-value	p-value
Functional group	1	18.15	3.877	0.0537
Residuals	58	271.5		
Root density				
	df	SS	F-value	p-value
Functional group	1	0.9219	52.07	<0.0001
Residuals	58	1.027		
SRA				
	df	SS	F-value	p-value
Functional group	1	254	7.234	0.00933
Residuals	58	2036		

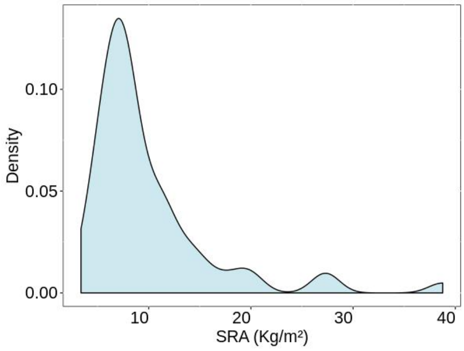
Figure S1. Density distribution of trait values for 20 tree Caatinga species calculated using the mean of 5 individuals per species.

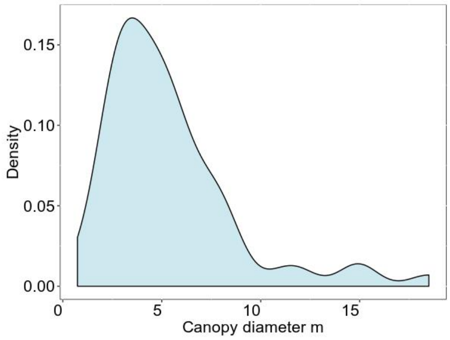


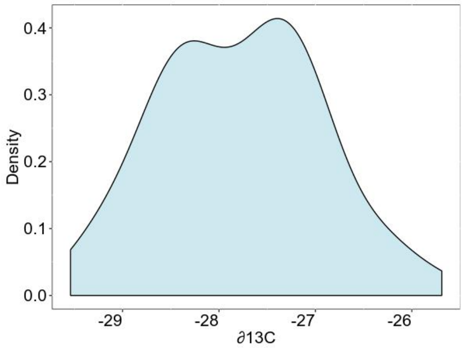

Density
0.075
0.050
0.025
0.000
5
10
15
20
25
SLA (Kg/m²)

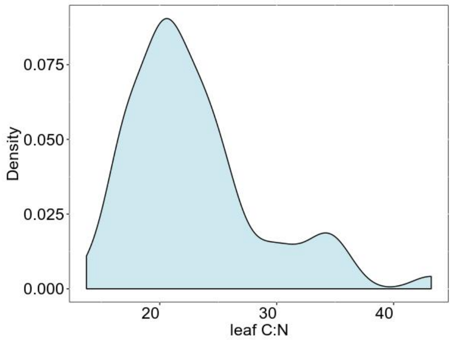

Density
3
2
1
0
0.4
0.6
0.8
Wood density (g/cm³)

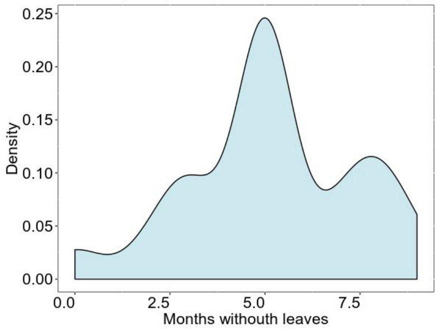

Density
2
1
0
0.2
0.4
0.6
0.8
Root density (g/cm³)


Density
0.10
0.05
0.00
10
20
30
40
SRA (Kg/m²)


Density
0.15
0.10
0.05
0.00
0
5
10
15
Canopy diameter m


Density
0.4
0.3
0.2
0.1
0.0
-29
-28
-27
-26
∂13C


Density
0.075
0.050
0.025
0.000
20
30
40
leaf C:N


Density
0.25
0.20
0.15
0.10
0.05
0.00
0.0
2.5
5.0
7.5
Months withouth leaves

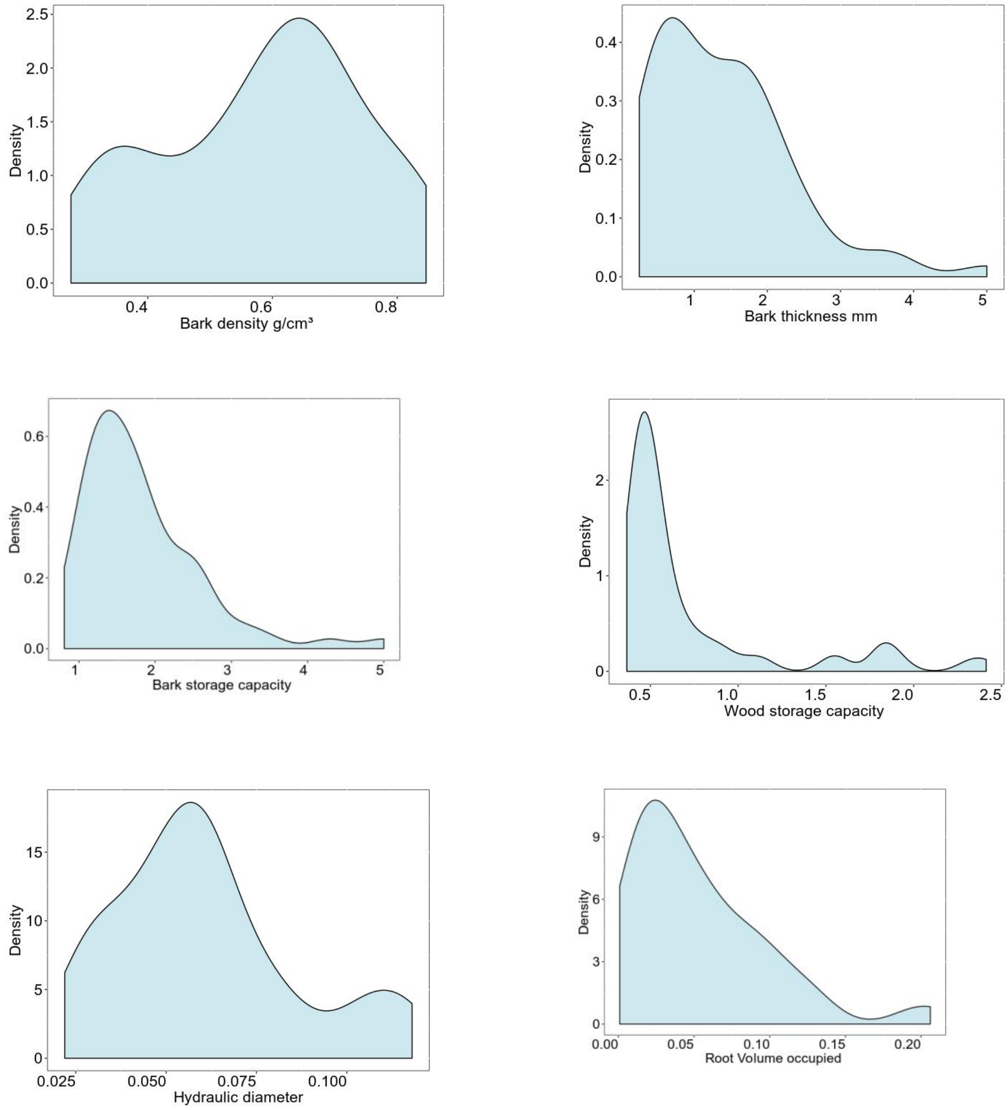


Figure S2. Ripley's k analysis testing if fast and slow functional species were more attracted or more separated from expected by null models. The dashed lines represent the confidence interval. If observed values are above the IC, the species are aggregated, if the observed values are under the IC, the species are repulsing each other. Once the observed values did not trespass the IC, the spatial distribution of two groups is independent.

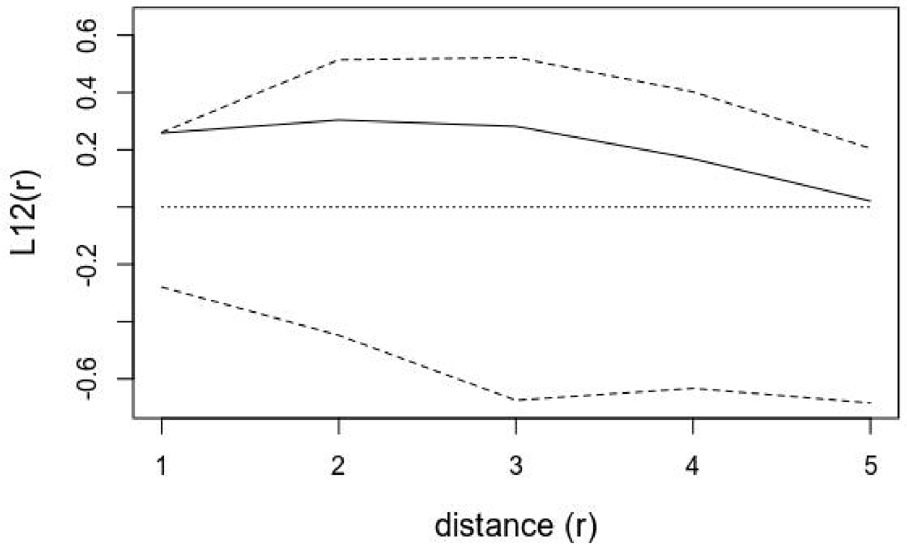
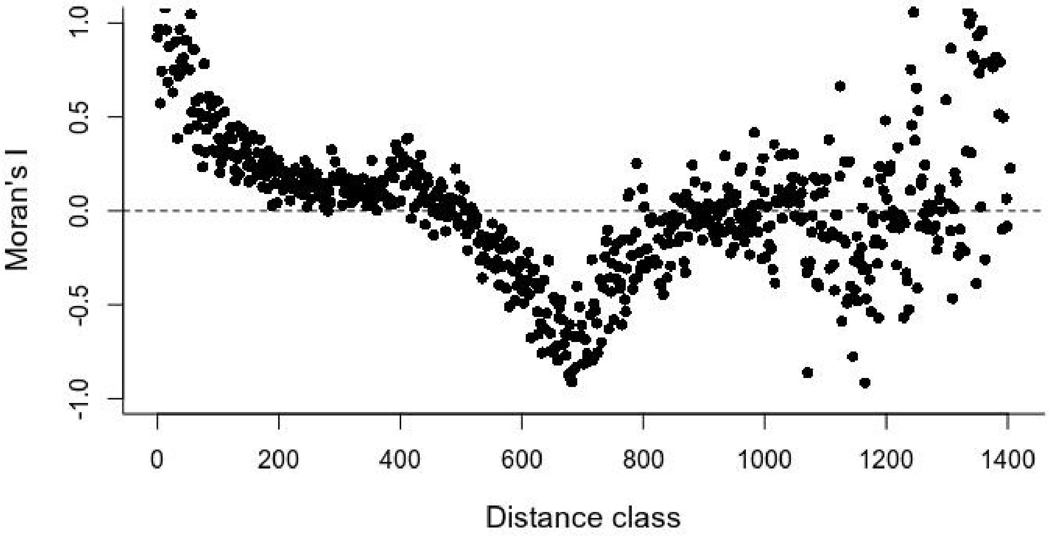


Figure S3. Spatial autocorrelation and Moran I test using "Moran.I" from "ape" package, autocorrelogram and Correlogram from "correlog" function from "cnf" package.

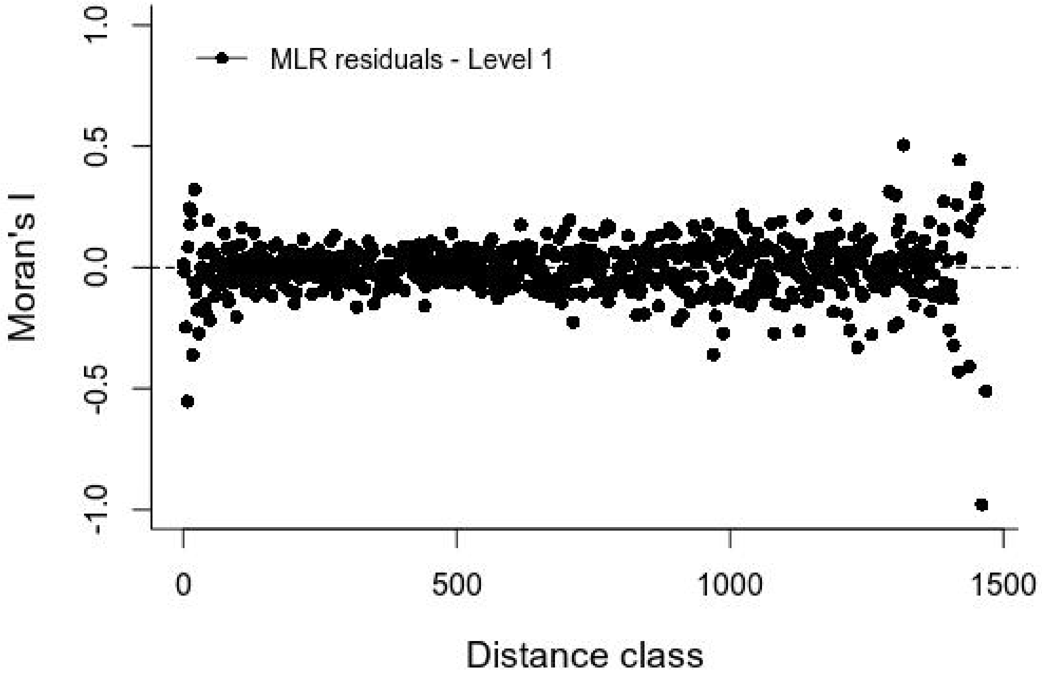
Moran's test of model without controlling for spatial autocorrelation:

Observed = 0.34852, expected= -0.00225, sd=0.00935, P-value= 0.000



Moran's test of the model controlling for spatial autocorrelation:

Observed= -0.004, expected= -0.002, sd=0.048, p-value=0.95


MLR residuals - Level 1
Moran's I
1.0
0.5
0.0
-0.5
-1.0
0
500
1000
1500
Distance class

What makes a good nurse plant?

Marina Fagundes
Rafael Oliveira
Gislene Ganade

What makes a good nurse plant?

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Abstract

1. Facilitation is an important force modulating plant communities, and its strength could be determined by the functional strategies of nurse-target interacting species. Combinations of acquisitive and conservative plant traits are commonly used as predictors of facilitative interactions. However, the results are contradictory, and there is still a lack of empirical information on how nurse plant functional traits can influence the performance of target plants.

2. We investigate: (i) if there are specific nurse plant functional traits that are important to explain their facilitation capabilities, and (ii) if specific combinations of nurse-target functional traits explain species-specific interaction outcomes. We hypothesized that nurse traits with potential to ameliorate environmental conditions related to limiting resources would be the best predictors of nurse performance, and that species-specific interaction outcomes would be related to the match between nurse effects on key resources they supply for above and below-ground target plant requirements.

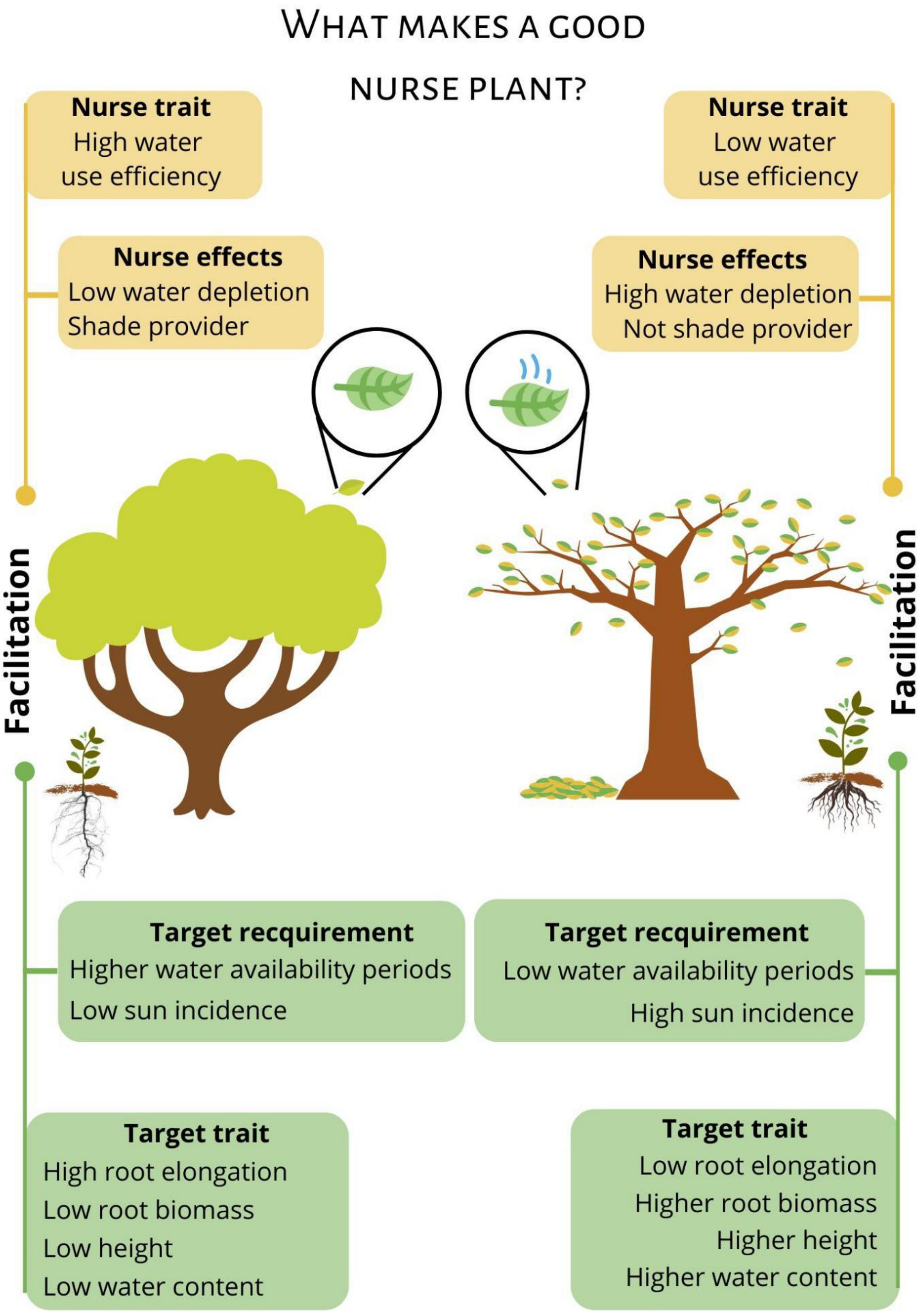
3. We performed a field interaction experiment with 60 combinations of nurse-target tree species, replicated five times. We sampled nine adult plant traits (Stem diameter, Canopy diameter, Leaf C:N ratio, Leaf $\partial^{13}C$, SLA, Number of months without leaves, Wood density, Hydraulic diameter and Root volume). To estimate target plant strategies, a greenhouse experiment was performed exposing saplings to drought and water availability.

4. Traits of adult nurse plants were not capable of explaining facilitation outcomes by themselves. Species-specific outcomes were explained by the combination of nurse water use efficiency traits and target strategies to deal with drought. Conservative nurse plants, with traits related to high water use efficiency, were more likely to facilitate target-plants with higher root elongation. Whereas acquisitive nurse plants, with traits related to low water use efficiency, were more likely to facilitate targets with lower root elongation but high tissue water storage and above-ground growth.

5. This is the first *in situ* experiment testing the effect of multiple traits on a large set of tree species interactions. Being a good nurse relies on its capability of improving water and light resources that match target plant requirements. This study brings a new light to species-specific interaction outcomes, predicting nurse facilitation skills using nurse and target functional traits.

Keywords: Functional traits, Plant interaction mechanisms, Positive outcomes, Seasonally Dry Tropical Forests.

Graphical abstract



WHAT MAKES A GOOD NURSE PLANT?

Nurse trait
High water use efficiency

Nurse effects
Low water depletion
Shade provider

Facilitation

Target recquirement
Higher water availability periods
Low sun incidence

Target trait
High root elongation
Low root biomass
Low height
Low water content

Nurse trait
Low water use efficiency

Nurse effects
High water depletion
Not shade provider

Facilitation

Target recquirement
Low water availability periods
High sun incidence

Target trait
Low root elongation
Higher root biomass
Higher height
Higher water content

Introduction

Facilitation is the process by which a nurse plant improves the establishment, growth, or survival of a target plant. Such process is commonly reported for stressful environments such as arid, semiarid and alpine ecosystems (Gomez-Aparicio, 2009; Soliveres & Maestre, 2014) and is frequently described as being species-specific (Landero & Valiente 2010; Michalet et al., 2015; Paterno et al., 2016; Fagundes et al., 2018). Additionally, the outcome of interactions varies depending on the nurse-target species match. However, the mechanisms explaining the specificity of nurse-target outcomes are still unclear (Soliveres et al., 2015; Paterno et al., 2016), and there is no general feature that designates a good facilitator.

Several studies have reported plant functional strategies as a good predictor of nurse facilitation capabilities (Gomez-Aparicio, 2009; Schöb et al., 2013; Soliveres et al., 2014; Zhang & Zhao, 2015; Lopez & Caballero, 2017; Schöb et al., 2017). Functional strategies define how adult plants use the available resources and subsequently affect their neighbor’s environmental conditions (Soliveres et al., 2011; Souza et al., 2015). Adult plants with conservative strategies for resource acquisition such as high water use efficiency (less negative ∂13C), low specific leaf area (SLA), high wood density (WD), and low hydraulic diameter (HD) will likely have a low rate of resource depletion (Diaz et al., 2016), leaving more resources available for target species that regenerate under their crown. On the other hand, it is expected that adult plants with acquisitive strategies (more negative ∂13C, high SLA, low WD, high HD) will have higher rates of resource depletion and, therefore, will reduce resources available for target plants (Grime, 1977; Reich, 2014). However, plants with both types of resource acquisition strategies have been reported as feasible facilitators (Maestre et al., 2009; Graff & Aguiar, 2017). Thus, a deeper understanding of how nurse plant characteristics might influence environmental changes is required to predict facilitation effects (Maestre et al., 2009).

Facilitation studies that address target performance, frequently look at target stress tolerance as a key mechanism to predict facilitation (Liancourt et al., 2005; Butterfield & Briggs, 2011; Graff and Aguiar 2017). Stress sensitive targets tend to have a higher potential to be facilitated while stress-tolerant targets might not rely on facilitation for survival and growth (Liancourt et al., 2005; Rolhauser & Puchet, 2016). However, there is no consensus that these broad functional groups are able to explain the multitude of species-specific nurse target interactions found in the literature (Gómez-Aparício, 2009; Bertoncello et al., 2016; Fagundes et al., 2018). Thus, to understand what makes a good nurse, one has to distinguish which nurse plant functional traits might lead to the environmental changes that improve target required resources (Paterno et al., 2016).

Stressful environments characterized by a clear limiting resource represent a good background to test how nurse and target traits have the power to explain plant interactions. In semiarid lands, rainfall occurs only over a few months of the year. Therefore, low water availability and high temperatures are critical limiting conditions. This work investigates how nurse and target plant traits influence facilitation in the Caatinga Seasonally Dry Tropical Forest in Brazil. We aim to test two main questions: (i) Are there specific nurse plant functional traits that explain facilitation capabilities? And (ii) Are there matches between nurse and target strategies that could explain the nature of their species-specific facilitation? We expect that nurse plant traits related to the use of a limiting resource (water) or affecting a limiting condition (light and temperature) will be good predictors of nurse facilitation effects. We also predict that species-specific outcomes will be related to two features: (a) The way nurse traits affect limiting resources and conditions above and below-ground, and (b) the way target traits respond to those conditions. For instance, it is expected that nurse plants with lower water depletion capability will facilitate target plants with lower investment in root growth, and therefore lower capability to face drought.

Material and Methods

Study Site

The study was carried out in the Caatinga Seasonally Dry Tropical Forest, located in northeast Brazil. The forest that originally occupied 826.411 km² has at least 50% of its territory degraded, and the remaining forest is fragmented and suffers chronic disturbances (Marinho et al., 2016; Ribeiro et al., 2016; Antongiovanni et al., 2018). Therefore, standing nurse trees are key landscape features to improve natural regeneration in this ecosystem. The experiment was conducted in the Açu National Forest, (Rio Grande do Norte, Brazil (05º35'02,1''S - 36º56'41,9''W). The protected area that encompasses 528 hectares is located at an arid portion of the biome with a mean temperature of 24ºC and nutrient-rich soils (Silva & Souza, 2018). The average annual precipitation of 607 mm is concentrated during a few months of the rainy season. The vegetation is dominated by drought-deciduous trees, varying from 2 m to 15 m in height.

Nurse-target experiment

In order to estimate nurse effects, a multifactorial field experiment was conducted between June 2014 and April 2015, using 60 nurse-target combinations in 100 blocks (see Fagundes et al., 2018 for detailed information). As nurse plants we used 100 individuals from 20 abundant tree species, five tree replications per species (find species list in Table S1). The individuals had to be adults and be as isolated as possible from other adult trees to avoid native tree removal during experimental manipulations. As target plants, 600 saplings of 3 abundant tree species were used, *Anadenanthera colubrina* (Vell.) Brenan, *Myracrodruon urundeuva* (Allemão). and *Poincianella pyramidalis* (Tul.) L.P Queiroz. Target saplings, approximately six months old, were obtained from a commercial greenhouse. The species were choose based on their abundance, local occurrence at the field site and availability at the greenhouse. The experiment consisted of monitoring the number of leaves produced under and far from nurse trees as a measure of target performance. Under each nurse individual, an area of 4 m^2 had all herbaceous vegetation removed, representing "nurse treatment". Using 2.5 m of distance from any tree canopy influence, another 4

m^2 area had their herbaceous vegetation removed, characterizing “no nurse treatment”. In each treatment, one sapling of each three species of targets was planted with 70 cm of distance from each other. Target growth performance was monitored for 275 days. Nurse effect was calculated for each nurse-target combination using the Relative Interaction Intensity index (RII).

$$\mathrm{RII} = \frac{\mathrm{Bw} - \mathrm{Bo}}{\mathrm{Bw} + \mathrm{Bo}}$$

Where, Bw represent the performance of a target plant under the nurse plant and Bo represents the performance of target plant without the effect of nurse plant. This index varies between -1 and 1, values larger than zero represent Facilitation, and smaller than zero represent Competition (Armas et al., 2004).

Adult plants trait measurements

Nine functional traits were sampled for the adult plants, following the methods described in Pérez-Harguindeguy et al. (2013): 1) Stem diameter, 2) Canopy diameter, 3) Leaf C:N ratio, 4) Leaf $\partial^{13}C$, 5) SLA, 6) Number of months without leaves, 7) Wood density, 8) Hydraulic diameter and 9) Root volume. Traits were sampled from 60 out of the 100 trees used to conduct the nurse-target interaction experiment, where 3 individuals were randomized out of the 5 individuals available per nurse species. For all species, the average calculated from the measures taken for each individual plant was used as a trait value.

Stem diameter was measured at soil level, in cases where adult species showed more than one main stem, the total area occupied by all stems was considered. Canopy diameter was obtained by measuring two perpendicular canopy widths and subsequently calculating the average canopy measurements.

Leaf samples were taken from sun-exposed leaves of each adult tree studied. For SLA measurements, three leaves of each individual tree were used. Leaf samples were stored in plastic bags, their fresh area was scanned with a Hp Officejet 4500 desktop and analyzed using the program ImageJ. Leaf petioles were removed, once they influence leaf weight but do not represent leaf photosynthetic area. Subsequently, leaves were dried for 48h at 60ºC and weighted. The SLA was calculated by the fresh leaf area divided by dry weight. For C:N and $\partial^{13}C$ ratios, three leaves were sampled, dried for 48h at 60ºC, macerated, encapsulated and sent to the UC Davis Stable Isotope Facility for analysis. The number of months without leaves, related to solar incidence amelioration and rates of resource depletion, was obtained from the literature (Lima e Silva et al., 2014).

Wood traits were obtained from two samples taken from the larger stem of each tree after the first tree bifurcation to minimize plant injuries. The first group of samples was stored in plastic bags to maintain humidity, each sample bark was detached, and wood volume obtained by water displacement. Samples were subsequently dried at 70ºC for one week and weighted. Wood density was calculated dividing dry weight by fresh volume. For Hydraulic diameter measurements, the second group of samples was naturally dried and polished with different sandpaper grains until the anatomic structures were evident. Images of all samples were obtained using a stereo microscope Nikon SMZ1500. For each sample, the diameter of 100 vessels was measured using the ImagePro Plus software, using the Scholz (2013) method.

Root volume was measured as the area occupied by roots in a known volume of soil. Root samples were collected around the stem of each individual tree, three trees in total. Samples were extracted by exposing the roots of 1/4 of a circle around the tree with 40 cm radius and 20 cm depth. All roots that were larger than 1 mm had their largest diameter (D) and length (L) measured, and their volume (V) was calculated based on the cylinder formula (V = π.r2.L). For each individual tree, root volume was calculated as the sum of all root volume measurements. The average of all root volumes collected from the three trees of each species represented the species root volume trait.

Experiment on target response to drought

In order to understand target plant functional strategies for facing drought, a greenhouse experiment was performed in a full factorial block design. Five replication blocks were used, each consisting of 10 individuals per target species in which the following two treatments were randomly assigned: ‘high water availability’ with water at maximum soil field capacity, and ‘low water availability’, with water at 15% of soil field capacity. Seeds from the three target species were germinated and, once their cotyledons flushed, they were transplanted to a 1 m long PVC tube, 70 mm in width to allow root development.

The experiment was performed for four months. During the first month, all target plants were irrigated equally to guarantee early development and survival. Treatments were only applied when plants were one month old. After four months, all individuals were harvested, measured, and plant material was subsequently dried for one week at 70ºC.

This experiment allowed the measurement of target trait strategies in their full developmental potential when looking at the “high water availability” treatment. We assumed that target responses to water treatments represent their strategy to optimize survival during the dry season. To understand changes in target trait allocation as a function of drought, we analyzed traits measured using low and high water availability treatments. We measured the following five target traits: 1. Total dry biomass (the sum of above and below-ground biomass in grams); 2. Plant water content (total fresh biomass minus total dry biomass, the result divided by total dry biomass); 3. Dry tissue root:shoot ratio (below-ground dry biomass divided by above-ground dry biomass, in grams); 4. Plant height (cm) and; 5. Root depth (cm).

Statistical analysis

To respond the two questions proposed in this work, we performed generalize linear mixed models (GLMM). The models started considering all variables from an orthogonal dataset. Less important variables were removed from the model in cases where residual deviance was not significant, following Crawley (2007). The analysis was performed using 'lmer' function from lme4 package (Bates et al., 2015). Pseudo r^2 were obtained from "r.squaredGLMM" function of package MuMIn (Bartón, 2019).

To understand if there are specific nurse functional traits able to explain nurse facilitation capabilities, we build a GLMM where the interaction index values (RII) were used as response variables, and the nine nurse traits measured were predictive variables. A block, which included one nurse species and three target species from the interaction experiment, was set as a random effect to account for the spatial structure of the experimental design (for more details see Fagundes et al., 2018).

To define the target plant strategies to face drought, we performed a Factorial ANOVA with Blocks for each of the five target traits measured. The response variable represented each target trait, and the explanatory variables represented: 1) Target species (*A. colubrina*, *M. urundeuva*, *P. pyramidalis*); Drought treatment (water, drought); and 3) The interaction between target species and drought treatment. Block was included as a fixed factor. These analyses allowed the understanding of possible differences in drought response strategies between distinct target species.

To understand whether the combination of the attributes of the nurse and the target could explain species-specific relationships, a GLMM model was built using the Relative Interaction Intensity index (RII) values, calculated for all nurse-target pairwise combinations as response variable. As explanatory variables, we used pairwise combinations between all nine nurse traits and relevant target traits. Relevant target traits were defined as the ones that differ significantly between target species and water treatments in the ANOVA model applied to the data of the greenhouse experiment described above.

Results

Adult plant effects

Most of the tree species (14 out of 20) demonstrated facilitative effects on target growth, indicating their potential to be nurse plants. However, the effects were species-specific depending on the adult and target species combination, therefore the same adult species exerted simultaneously positive and negative effects depending on the interacting target species in question (see Fagundes et al., 2018 for detailed information of pairwise outcomes). Trait values varied substantially between adult species, indicating a wide diversity of acquisitive and conservative strategies for adult plants (Table 1). Contrary to our predictions, adult traits alone were not sufficient to explain facilitation effects, given that none of the nine nurse traits analyzed had a significant influence on the RII interaction index (Table 2).

Table 1. Mean, maximum, minimum, and standard deviation values of the nine morpho-physiological traits measured for 20 potential nurse trees from the Caatinga Tropical Dry Forest of Brazil.

Trait	**Unit**	**Mean**	**Max**	**Min**	**SD**
Stem diameter	m	0.19	0.82	0.04	0.14
Canopy diameter	m	5.35	18.5	0.74	3.38
Specific leaf area	m^2/Kg	15.34	27.3	5.383	4.271
Months without leaves	months	5.15	9	0	2.21
∂^{13}C leaf isotope ratio	ratio	-27.77	-25.69	-29.54	0.841
C:N leaf ratio	ratio	22.91	43.21	13.73	5.769
Wood density	g/cm^3	0.68	0.91	0.262	0.175
Hydraulic diameter	mm	0.06	0.118	0.02	0.025
Root volume occupied	vol/cm^3	0.04	0.20	0.0009	0.046

Table 2. Model performed with the Relative Interaction Index (RII) values as response variable and nine nurse traits as explanatory variables.

Random Effects	Variance	SD		
Plot	0.009	0.098		
Residual	0.077	0.278		
Fixed Effects	Estimate	SE	t-value	P-value
Intercept	**0.0571**	**0.0244**	**2.343**	**0.023**
Nurse SLA	-0.0181	0.0301	-0.601	0.550
Nurse stem diameter	-0.0059	0.0333	-0.179	0.858
Nurse canopy diameter	0.0184	0.0366	0.504	0.616
Nurse root volume	0.0262	0.0278	0.943	0.350
Nurse wood density	0.0095	0.0352	0.271	0.787
Nurse months without leaves	0.0128	0.0361	0.356	0.723
Nurse leaf C:N	0.0365	0.0263	1.387	0.171
Nurse hydraulic diameter	0.0286	0.0332	0.860	0.393
Nurse leaf d13C	-0.020	0.0284	-0.727	0.470

Target strategies

All species presented the same total biomass production within species but vary between treatments of low and high water availability (Table 3, Fig. 1). However, target species differed in above- and below-ground responses and water storage capacity. Target *P. pyramidallis* presented a lower root:shoot ratio compared to target *A. colubrina,* lower water content when compared to *M. urundeuva,* and was the only target species to present higher root depth at high water availability.

Table 3. Table with F-values of factorial ANOVA analysis testing the difference between target traits at high water and low water treatments. Biomass and Root:shoot were measured using target dry biomass. Height and Root length was measured using target fresh mass. Water content was calculated as the difference between fresh and dry biomass divided by dry biomass. The * represent p-values ≤ 0.05, **≤ 0.01 and ***≤ 0.001.

	df	Biomass	Water content	Root:shoot	Height	Root length
Treatment	1	31.256***	3.128*	0.039	5.195**	7.133**
Species	2	0.198	8.086***	3.988**	15.315***	5.908***
Block	4	1.939	1.097	1.844	2.591	2.210
Treatment x Species	2	0.395	1.248	0.104	1.152	3.933**
Residuals	19					

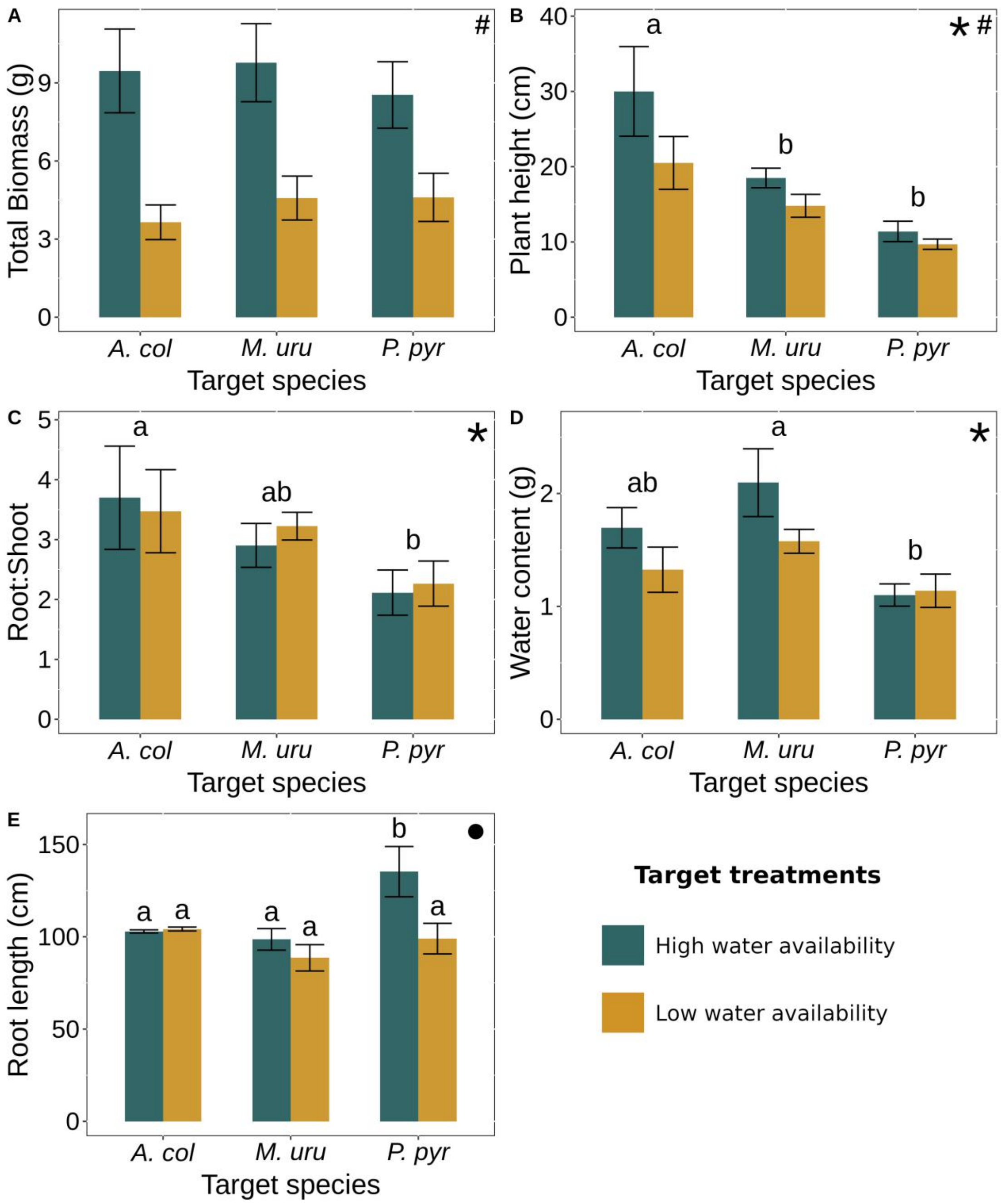


Figure 1. Target traits measured at high water availability treatment (blue bars) and low water availability treatment (orange bars). A. col = *Anadenanthera colubrina* ; M. uru = *Myracrodruon urundeuva*; P. pyr = *Poincianela Pyramidalis*. Total biomass (a) and Root:shoot (c) were measured using plant dry mass. Height (b) and Root depth (e) were measured using fresh plant tissue. Water content (d) was calculated as the difference between fresh and dry biomass divided by dry biomass. The "#" represent statistical differences between water availability treatments, "*" represent statistical differences between target species and black circle represent the interaction between species and treatment (see details in Table 3).

Nurse traits x Target requirement

Species-specific facilitation effects were significantly explained by interactions between adult and target plant strategies to face drought. Pairwise interactions between nurse leaf ∂13C, a measure of water use efficiency, with target root elongation, were the best predictors for the RII interaction values representing the intensity of interaction response. Adult nurse plants with high water use efficiency were capable of facilitating target plants with high root elongation and presented negative or neutral effects on targets with no root elongation. On the other hand, adult plants with low water use efficiency showed a positive effect on target plants that did not vary root length as a response to drought (Table 3, Fig. 2).

Table 3. Model simplification performed with RII interaction values as the response variable, and interactions between nurse and target traits as explanatory variables. Nine nurse traits were included as interacting variables in the full model: stem diameter, canopy diameter, leaf C:N ratio, leaf ∂^{13}C, SLA, number of months without leaves, wood density, hydraulic diameter, and root volume. The target trait related to their strategy for facing drought used in this model was root length in cm. ∂^{13}C, the leaf stable isotope carbon ratio that represents water use efficiency was the only interacting nurse variable remaining in the final model.

Nurse traits x Target root length				
Random effects	Variance	SE		
Plot	0.12	0.346		
Residual	0.8319	0.912		
Fixed Effects	Estimate	SE	t-value	P-value
Intercept	0.0000	0.081	0	1
Nurse ∂^{13}C X Target root length	0.2329	0.068	3.407	**0.0008**
pseudo r^2= 0.17				

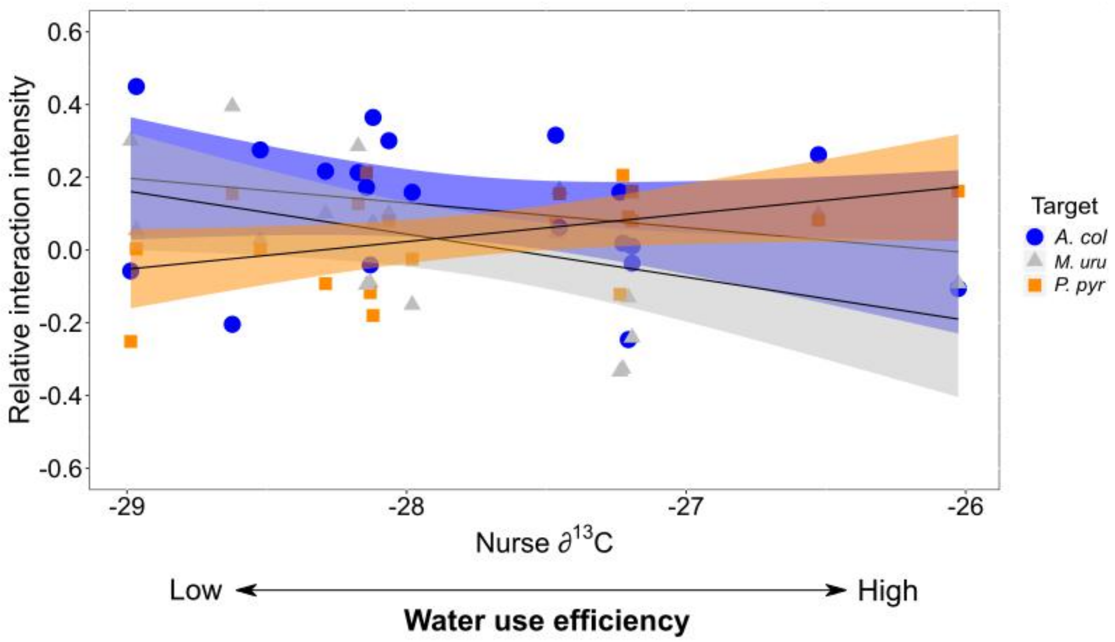


Figure 2. Nurse tree facilitation explained by the interaction between leaf ∂C^{13} (the key nurse trait remained after model simplification) with root length, a target strategy to face drought. The Y-axis represents the RII facilitation index (Armas et al., 2004), where positive values are facilitative, and negative values are competitive effects. The x-axis represents the nurse leaf ∂C^{13}, where more negative values represent lower water use efficiency, and less negative values represent higher water use efficiency. The orange line represents target *Poincianella pyramidalis*, with higher root elongation in water treatments. Blue line represents target *Myracrodruon urundeuva* and the grey line *Anadenanthera colubrina*, both showing no differences in roots depth in high water availability.

Discussion

No nurse trait could alone explain their facilitation skills in Caatinga Seasonally Dry Tropical Forest. We found instead that nurse traits could only predict facilitation potential when associated with target strategies. Therefore, by looking at sapling requirements, we were able to explain why adult trees with strategies ranging from acquisitive to conservative could both perform as good nurse plants. More specifically, we found that facilitation could be predicted based on nurse traits related to water use efficiency and target traits related to their strategy to face drought. This work reveals a feasible procedure to predict species-specific interactions during plant community regeneration by studying the ecological strategies of adult trees and saplings using functional traits.

Nurse traits

We found nurse species with distinct values of water use efficiency, a trait related to species ability to minimize water loss during photosynthesis (Farquhar et al., 1989). The more efficient at water use a species is, the higher its ability to maintain its physiological activity for longer periods without dehydration (Poorter & Bongers, 2006). In the present study, higher water use efficiency was positively correlated with species with longer canopy duration (Pearson= 0.48, p-value <0.001). Indeed, at water-limited environments, longer canopy duration during drought are only possible when coordinated with other conservative traits such as high wood density (Lima & Rodal, 2010; Oliveira et al., 2015; Souza et al., 2015). This conservative strategy, often results in low resource acquisition rates (Grime, 1977; Reich et al., 2014, Diaz et al., 2016), and as a consequence provides a higher resource availability for neighboring plants. Therefore, we expected that trees with such strategy would have a greater potential to facilitate a wide range of target species in dry environments because they preserve soil moisture. However, our results showed that adult species of both sides of the conservative-acquisitive spectrum might be good nurse plants, depending on target traits.

Target traits

Target species possess distinct strategies to face drought. The target *P. pyramidalys* presented low values of water content, height and root:shoot ratio, but was the only species to change its root elongation when water was abundant. Such characteristic implies strong foraging behavior to optimize water uptake (Olmo et al., 2014; Bucci et al., 2009), increasing the species chance to achieve deeper soils with higher humidity to resist future drought. The target *A. colubrina,* showed a higher root:shoot and height investment when compared with *P. pyramidalis.* A higher below-ground biomass allocation, confers *A. colubrina* a higher water uptake power (Poorter et al., 2011), this extra water would allow this species to invest in above-ground growth during rainy periods and compete for light (Pérez-Ramos et al., 2013). The target *M. urundeuva*, on other hand, did not differ from *P. pyramidalys* on root:shoot or height, but in water content. Higher water storage implies higher water supply for plant activity, even at dry periods, which would confer protection against embolism (Borchet 1994; Rosell et al., 2014), and higher independence of long-term soil water availability.

Facilitation Mechanisms

The target species with low investment in below-ground structures and water storage, but that responded to water availability by elongating its roots, was facilitated by nurse plants with higher water use efficiency. These nurse plants with higher water use efficiency might increase soil humidity due to low water depletion. That would allow *P. pyramidalis* to invest in root elongation to face future dry periods, improving its performance. On the other hand, target species with higher root:shoot and higher storage capacity were benefited by nurses with low water use efficiency. Because these targets have structures that allow them to acquire and store water more efficiently (Borchet & Pockman, 2005), they might be more independent of nurse below-ground effects, and therefore, nurse above-ground effects became more important. The rapid leaf loss of acquisitive nurse plants, decrease the shade provided by the nurse tree canopy, benefiting targets that tend to be taller, and therefore have higher light requirements (Woods & Miriti, 2016). In biomes were plants are adapted to high solar incidence, a subtle amelioration such as the shade provided by leafless tree trunks might be enough to improve target performance (Peters et al., 2008).

In semiarid environments where light is abundant, it is expected that the primary driver for plant performance is water availability. However, we found that targets that are benefited by acquisitive nurse plants, suffered negative effects of conservative nurse plants that blocked light for longer periods. Plants from Seasonally Dry Tropical Forests are adapted to a short period of water availability and high light intensity (Pennington et al., 2009). Species that do not present structures to acquire water and prevent dehydration are more benefited by nurse plants that minimize water loss through shading. On the other hand, species that are able to acquire water rapidly can stand higher luminosity, making light an essential component to optimize its growth. Thus, at SDTF, nurse effects that impact both water and light can explain facilitation mechanisms (Table 4).

Table 4. Mechanisms of facilitation in SDTF considering target plant traits and their requirements combined with nurse strategy and their effects. Target plants with low water tissue content and low root:shoot investment are more dependent of prolonged soil moisture and more vulnerable to desiccation due to high solar incidence. Therefore, they are facilitated by nurse plants with conservative strategies which implies higher soil water availability and longer periods of canopy duration. On the other hand, taller target species that are able to rapidly acquire and store water are less dependent on longer periods of water availability and more dependent on light. Therefore, they are facilitated by acquisitive nurse plants that deplete soil water in higher rates, but have a short period of shade due to fast leaf deciduousness.

Target	Root elongation in response to water	Tissue water content	Height	Root:shoot ratio	Dependency of prolonged moist periods	Response to prolonged shade periods	Conservative nurse plant effect	Acquisitive nurse plant effect
P. pyramidalis	Yes	Low	Low	Low	High	Positive	Facilitation	Inhibition
A. colubrina	No	Low	High	High	Low	Negative	Inhibition	Facilitation
M. urundeuva	No	High	Low	Low	Low	Negative	Inhibition	Facilitation

The nature of species-specific facilitation

The idea that facilitation outcomes in drylands rely on the combination of how much nurse plants can deplete soil moisture combined with target drought sensitivity has been tested in different ecosystems (Liancourt et al., 2005; Butterfield & Briggs, 2011). However, a general and measurable mechanism its still lacking. Our results showed that nurse water use efficiency, which is highly correlated with canopy duration, is a good proxy to estimate nurse effects on plant neighbors, however, this facilitation effect is dependent on target strategies to face drought. The understanding of target strategies might rely on above- and below-ground biomass allocation, with a crucial role of below-ground structures to predict target strategies in responses to nurse effects (Engelbrecht & Kursar, 2003; Olmo et al., 2014; Graff & Aguiar 2017). Additionally, our results showed that what makes a nurse species facilitate a target species can go further than just the depletion of limiting soil resources. Even in drylands, nurse facilitation skills can be related to changes in light conditions, where both conservative and acquisitive nurse plant strategies can influence target performance.

Conclusion

This study brings a new light to the species-specific outcomes found in various facilitation studies, given that species-specific relationships are hard to generalize and predict. Understanding how the combination of nurse and target functional traits can lead to facilitation is a novel step towards a better understanding of plant interactions during regeneration and restoration of plant communities. In the present work, we provide a general and feasible measurement of facilitation skills for Seasonally Dry Tropical trees and their related targets. Future tests on the role of nurse water use efficiency and related traits combined with target strategies to face drought could be performed on different ecosystems to predict species-specific interactions at large scale.

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Data Availability Statement

The data will be available on Dryad repository once the paper is published.

Authors' contributions

MF, GG and RO conceived the ideas

MF and GG designed methodology;

MF and GG collected the data;

MF and RO performed lab analysis

MF and GG and RO analyzed the data;

MF led and GG and RO contributed to the writing of the manuscript.

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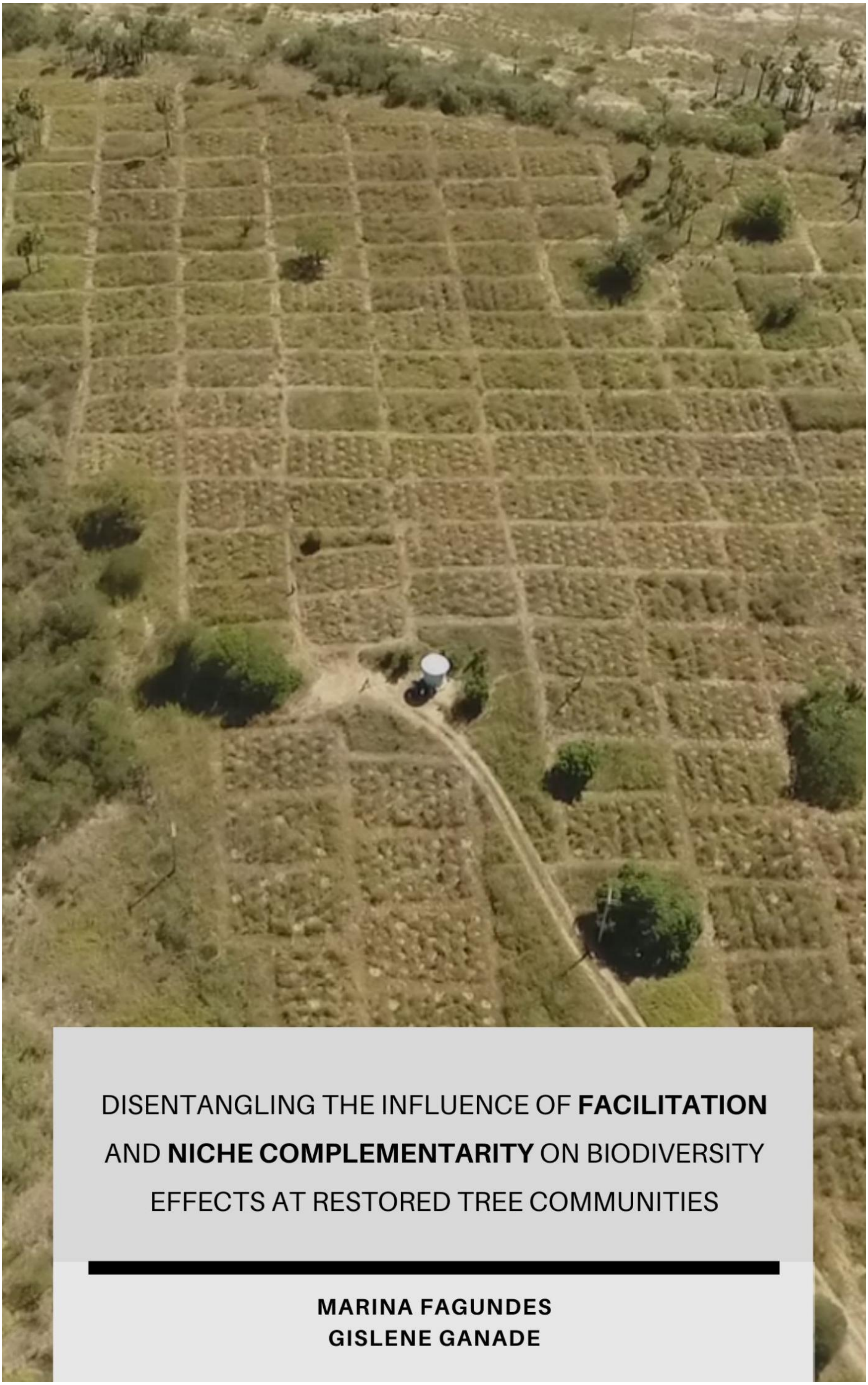
Supplementary Material

What makes a good nurse plant?

Marina Vergara Fagundes , Rafael Oliveira & Gislene Ganade.

Table S1. Family, and species names for all adult plants used as potential nurse plants.

Family	**Nurse specices**	**Popular name**
Anacardiaceae	*Spondias tuberosa*	Umbuzeiro
Apocynaceae	*Aspidosperma pyrifolium*	Pereiro
Bignoniaceae	*Handroanthus impetiginosus*	Ipê roxo
Bixaceae	*Cochlospermum vitifolium*	Algodão do mato
Boraginaceae	*Cordia glazioviana*	Pau-branco
Burseraceae	*Commiphora leptophloeos*	Imburana de cheiro
Capparaceae	*Cynophalla hastata*	Feijão-Bravo
Combretaceae	*Combretum leprosum*	Mofumbo
Erythroxylaceae	*Erythroxylum nummularia*	Favelinha
Euphorbiaceae	*Croton blanchetianus*	Marmeleiro
Euphorbiaceae	*Sebastiania macrocarpa*	Burra-leiteira
Fabaceae - Caesalpinoideae	*Bauhinia cheilantha*	Mororó
Fabaceae - Caesalpinoideae	*Poincianella gardneriana*	Catingueira
Fabaceae - Mimosoideae	*Mimosa tenuiflora*	Jurema-Preta
Fabaceae - Mimosoideae	*Piptadenia stipulacea*	Jurema-Branca
Fabaceae - Mimosoideae	*Anadenanthera colubrina*	Angico
Fabaceae - Papilionoideae	*Amburana cearensis*	Cumaru
Fabaceae- Caesalpinoideae	*Libidibia ferrea*	Pau-Ferro
Fabaceae- Mimosoideae	*Pityrocarpa moniliformis*	Catanduva
Malvaceae	*Pseudobombax marginatum*	Imbiratanha



DISENTANGLING THE INFLUENCE OF **FACILITATION** AND **NICHE COMPLEMENTARITY** ON BIODIVERSITY EFFECTS AT RESTORED TREE COMMUNITIES

MARINA FAGUNDES
GISLENE GANADE

Disentangling the influence of facilitation and niche complementarity on biodiversity effects at restored tree communities

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Abstract

1. Active restoration programs of Seasonally dry lands are an urgent demand on current days. The increasing of deforestation pressure combined with erratic rainy periods make semiarid forests a low resilient biome, where natural regeneration is not enough to ensure species long-term survival. For an effective restoration, the understanding of the drivers of productivity are a key factor to achieve the maintenance of local plant communities. Disentangling the factors that influence effects of net biodiversity effect, such as species diversity, functional diversity, functional identity and facilitation, is essential and has been rarely tested experimentally at large scale.

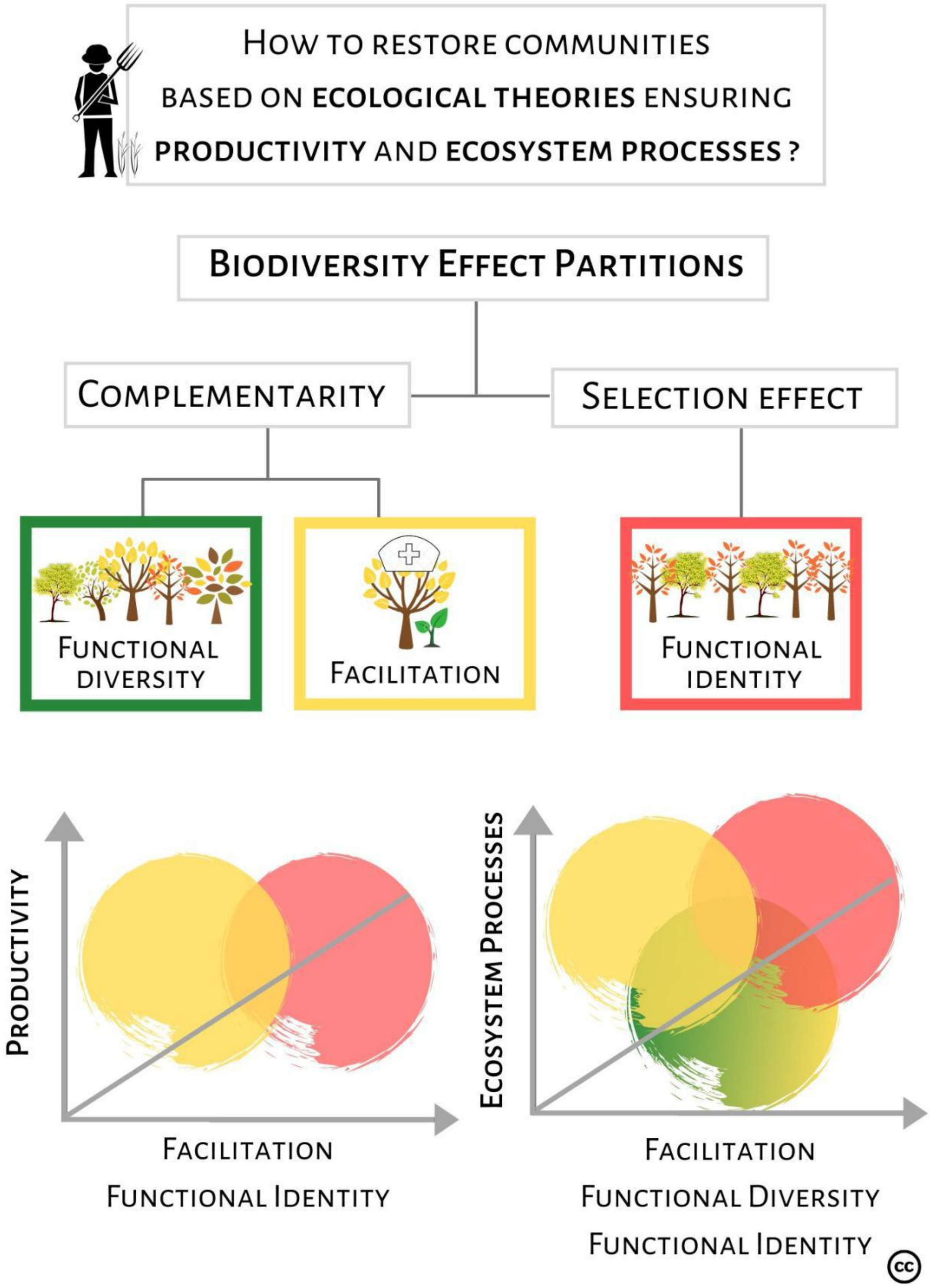
2. We built 147 restoration experimental tree communities of 13 m X 18 m, with five levels of diversity and 45 species composition with three replicas each. We produced 4704 seedlings of 16 semiarid tree species using a new growing method. The biomass production of all individuals were monitored for three years. We measured above and below-ground traits to calculate community weighted mean (CWM) and functional diversity. The facilitation index was calculated based on a second in situ experiment. We performed a generalized linear mixed models to understand how Facilitation, Functional diversity, and CWM drive the productivity of communities.

3. The majority of plant species were more productive in polycultures than monocultures. Of the three effects tested, the facilitation and community identity related to high capacity of water uptake were important on both biomass production and community functions.

4. This is the first experiment showing that the pattern of Tropical semiarid communities agreed with general worldwide tendencies of diversity effects, and its

mechanisms. Additionally, we showed how to manipulate the three components of the Net biodiversity Effect, facilitation, functional diversity and community functional identity, in order to guide future restoration programs.

Graphical abstract



Introduction

The use of ecological theories to understand long-term ecosystem functioning is fundamental for restoration planning. Preserving ecological interactions and ecosystem services, as productivity are the main achievements for restoring degraded communities (Ruiz-Jaen & Aide, 2005; Bullock et al., 2011). Facilitation has been shown as an important mechanism for increasing restoration success (Gómez-Aparicio, 2009; Teixeira et al., 2016; Fedriani et al., 2019). Facilitative species ameliorate abiotic conditions and improve resource availability on their surrounding, maximizing plants survival and increasing community production (Brooker et al., 2008; Soliveres et al., 2011). However, the proportional influence of facilitation effects on ecological functions are poorly understood. One of the reasons is that facilitation effects are hardly disentangled from functional complementarity effects.

Functional complementarity occurs when species with distinct functional traits use resources in a complementary way, maximizing plant survival and community productivity (Loreau, 2000; Loreau & Hector, 2001; Vanelslander, 2009; Brassard et al., 2011). Because the effect of both mechanisms, facilitation and functional complementarity, can together improve community functioning, they are commonly not separated in plant community studies. In fact, a well established biodiversity measurement, the Net Biodiversity Effect (NBE) proposed by Loreau & Hector (2001), assumes that a higher than expected productivity of a diverse community arises from facilitation and/or functional diversity. However, most of studies that measure community productivity or NBE, use just the Functional complementarity (or functional diversity) measurement as a predictive variable (Hector et al., 1999;

Finegan et al., 2015; Van de Peer, et al., 2018), leading to a lack of understanding of the role of facilitation on such processes.

Additionally, facilitation and complementarity might operate through distinct mechanisms, causing different consequences to community function. The functional complementarity optimizes the use of available resources due to species functional diversity (e.g. distinct root depths that can explore the whole dimensions of the water and nutrients available (Postman & Lynch, 2012), while facilitation increases the overall amount of available resource (Scholz et al., 2002; Carlsson & Callaghan, 1991; Cavieres et al., 2008). See Fig. 1 for schematic description.

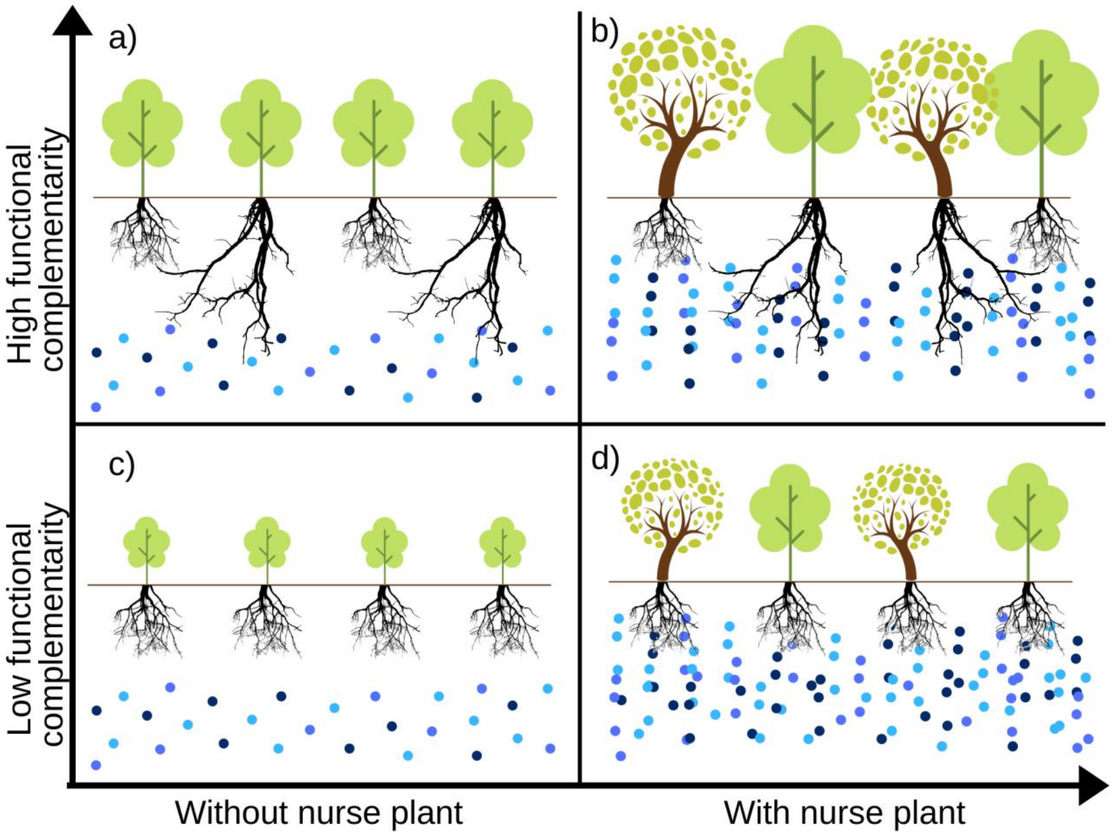


Figure. 1. Effects of functional complementarity and facilitation in plant communities. The functional complementarity is represented by roots architecture, facilitative plants are represented by the doted canopy, the amount of resources is represented by below

ground blue dots, and the community response is represented by canopy size. Scenario a) High functional complementarity and no facilitative plants, the community presents a better performance due to complementary of resource use. Scenario b) represents the best scenario for restoration, where facilitative plants increase the amount of resources, and functional complementarity performs a better use of those resources, allowing the community to increase performance compared with just the complementarity scenario (a), or just the facilitation scenario (d). Scenario c) represents a community with low functional complementarity and no facilitative plants resulting in low performance. Scenario d) Low functional complementarity but with facilitative plants that increase the amount of resources.

Facilitation can act by increasing water in the system through hydraulic lift (Dawson, 1993; Liste & White, 2008; Scholz et al., 2002), by enhancing the amount of nutrients through fixation or increasing the nutrient cycling rates (Armas et al., 2012; Navarro-Cano et al., 2014). Facilitation can also improve microclimate, increasing the air humidity by evapotranspiration and controlling high temperatures (Graff & Aguiar, 2017). Moreover, it is known that facilitation has important roles in structuring communities (McIntire & Fajardo, 2014). Facilitation can increase the species diversity of a given community, allowing species occurrence at sites where establishment would not be possible (Le Bagousse-Pinguet, 2014). Furthermore, facilitation can expand the functional niche of beneficiary species (Bulleri et al., 2016). Facilitative effects are often recorded at stressful environments (Gomez-Aparício, 2009; Soliveres & Maestre, 2014; Paterno et al., 2016; Fagundes et al., 2018), having a great potential to improve restoration of such systems. Thus, in order to advance restoration practices, one should be able to measure and manipulate the facilitation effects.

The dominant functional traits on a given community is an important factor that influence community productivity and restoration practices (Loreau & Hector, 2001; Tobner et al., 2016). Plant communities will perform better (e.g a higher productivity), depending on their functional identity (Laughlin, 2014; Finegan et al., 2015; Laughlin et al., 2018). For restoration programs, is possible to manipulate the community functional composition in order to achieve better results. In environments where water is a limiting resource, available only during particular months of the year, its possible to build communities in which species traits that are based on high root area (SRA, calculated as the fresh root area divided by its dry weight) or root depths in order to increase water and nutrients absorption during periods of high resource availability.

Understand how to manipulate plant community functional structure is a primordial step to restoration success (Laughlin et al., 2014), not just for biomass production, but also for long-term community maintenance. There is an urgent need to guide future restoration programs supported by ecological theory tests (Ruiz-Jaen & Aide, 2005). Thus, it is urgent that one disentangles the ecological processes that make up the Net Biodiversity Effect, measuring their relative importance. In this work, we aim to disentangle the effects of functional complementarity, facilitation, and functional identity on tree community productivity in order to improve our capability to rebuilt plant communities.

Methods

The present work was developed at the Caatinga forest, the largest and most diverse Seasonally Dry Tropical Forest of Americas (Queiroz, 2017), The Caatinga forest total area encompasses 826,411 km^2, occupying 11% of Brazilian territory, although nowadays occupies half of its original area, being distributed in 47100 fragments (Antongiovanni et al., 2018). This study was conducted in the Açu National Forest (Rio Grande do Norte, Brazil). The National Forest encompasses 528 ha, where vegetation is characterized by trees varying from 2m to 15m tall, with mean temperature of 24ºC and annual rainfall of 607mm (Silva e Souza, 2018).

Greenhouse Seedling production

In a greenhouse 4704 seedlings of 16 Caatinga tree species were produced. All the seeds were sampled from at least five distinct adult trees present in Caatinga forest nearby the experiment region. After germination, the seeds were planted in 1m PVC tubes in order to improve root growth, nutrients and water storage, maximizing plant hydrological stress resistance. The seedlings received water daily in the first month, and weekly until they achieve six months. After the fourth month, all species had reach 1m of root depth and more than 50cm of shoot height. In the fifth month, the greenhouse poly shade cloth (50%) was removed for acclimation during a month period until field planting in the sixth month.

Experiment design and implementation

The experiment was implemented in July 2016 during the dry season in a degraded area of 3.3ha. The design consists in 147 experimental build communities of 13 m x 18 m, with 32 individuals planted 1m from each other. The communities vary in richness from monoculture, two species, four species, eight species and 16 species mixture with distinct species composition within each richness level mixture.

The species composition was sorted following the random partition design (Bell et al., 2009) where different compositions are randomly sorted in a way to guarantee that a given species will be present in each richness level. Beyond the species composition, communities were built within a gradient from low to high facilitation, in a manner that each level of diversity was built with species with high facilitative potential and low facilitative potential. Each of the follow compositions was replicated three times: 16 monocultures, 16 different compositions of two species mixture, eight different compositions of four species mixture, four different compositions of eight species mixtures and the total pool of species mixture with 16 species was replicated 15 times (see detailed specifications in Supplementary material Table 1).

Facilitation index

The values of facilitation were obtained from an in situ experiment with 60 combinations of pair-wise tree species (For detailed information, see Fagundes et al., 2018). We measured the pair-wise interaction values calculating the Relative Interaction Index based on target plants survival (Armas et al., 2004), which vary from -1 to 1. Negative values indicate competition, whereas positive values indicate facilitation. We calculated a facilitative potential for each species, by averaging its effects on all target species. To obtain the value of facilitation for each assembled community, we summed the facilitative potential values of all individuals present in the community. Our design was structured in a way that community facilitation was not correlated with species diversity (details in Supplementary material Fig. S1).

Experiment monitoring

In 2017, the plant mortality was recorded, and all dead plants were replaced. After the replacement of dead plants, all 4704 individuals had the number of leaves counted and registered to measure initial size.

Biomass production

Leaf biomass production was calculated for each individual that survived until 2018, considering differences in growth between 2017 and 2018. In the Caatinga ecosystem, most trees flush and maintain their leaves during the rainy season, for approximately four months. Thus, the number of leaves counted represents the leaf annual biomass production. For each individual, we counted the number of leaves produced and multiply it by the species leaf dry weight. The dry weight was calculated previously as the average of three sun exposed leaves from five individuals of each plant species. The biomass production was calculated for each individual, considering differences in growth between 2018 and 2017.

Functional traits

Plant functional traits were sampled from six months old greenhouse individuals. The individuals were exposed to two months of direct solar radiation for acclimatization before measurements. For each species, five individuals were randomly sampled and the following above and below-ground traits measured: Leaf area (cm^2) , Specific leaf area - SLA (fresh area divided by dry weight), Shoot height (cm), Root depth(cm), Trunk wood density (g/cm^3), Root wood density(g/cm^3). All traits were measured following the Pérez-Harguindeguy (2013) protocol.

Functional diversity

The functional diversity was calculated for each assembled community, using all functional traits measured, based on Patchey and Gaston (2002),which allows for the inclusion of communities with low diversity. The method uses a pairwise distance matrix with trait values and a abundance matrix to calculate the diversity of each community, considering the total branch length of a functional dendrogram. The functional diversity increased with species diversity with the lowest values of 0.11 on monocultures to 1 on communities with 16 species (Supplementary material Fig. S1).

Community functional identity

The community functional identity was calculated for the traits LA, SLA,, Height, Wood density, Root density, and SRA. We obtained the community weighted mean (CWM) of each trait by calculating the average trait value of all species, weighted by the abundance of individuals per plot. Despite all communities were built with the same number of individuals per species, the abundance changed due to mortality, and here we considered just the alive individuals.

Net biodiversity, Complementarity and Selection effects

The Net biodiversity, complementarity and selection effects proposed by Loreau & Hector (2001) were calculated for each built community as follow:

$$\mathrm{NBE} = N\,\overline{\Delta\mathrm{RY}}\,\overline{M} + N\,\mathrm{cov}(\Delta\mathrm{RY}, M)$$

The Net biodiversity effect (NBE) = Complementarity + Selection effect, where Complementarity = $N\,\overline{\Delta\mathrm{RY}}\,\overline{M}$ and Selection effect = $N\,\mathrm{cov}(\Delta\mathrm{RY}, M)$. In this equation, N is the number of species in a mixture, M is the yield of species in monoculture, $\Delta\mathrm{RY}$ is the deviation from expected relative yield of a given species in a mixture. Such approach allows to understand if mixtures are overyielding when compared with species production in monocultures due to two effects: selection and complementarity.

The selection effect (SE) measures the covariance of the relative yield of species in mixture compared with their monocultures, which helps to understand which species are overyielding. SE will be positive if the more productive species in monocultures have a better production in mixtures than in monoculture, and SE will be negative if the less productive species in monocultures have a better production in mixtures than in monoculture. The Complementarity Effect (CE), will measure if the yield of a mixture is higher or lower than expected, based on the average biomass production of monocultures taken into consideration the proportion of a given species in the mixture. When CE is positive, a better use of resources (complementarity) or facilitation effects are occurring, when CE is negative, negative interactions are limiting biomass production of mixtures.

We performed the calculations of NBE, CE and SE for each community using the "apm" function developed by Delory (2019). To test if NBE values and its components are different from zero, we performed a T-test using the grand mean of NBE, CE and SE separately.

Statistical analysis

To test for spatial autocorrelation, first all plots were rasterized and georeferenced. The autocorrelation test was made using the function *Moran.I* from "ape" package (Paradis & Schliep 2018), accusing absence of spatial autocorrelation for productivity and NBE values (observed= -0.0038, expected= 0.0119, sd= 0.0119, p-value=0.5922).

To understand what drives the productivity of different plant communities, we performed two generalized linear mixed models. In the first model, leaf biomass production was the response variable (Y), while in the second model the Net Biodiversity Effect was the response variable (Y). The predictive variables for both models were functional diversity, species diversity, facilitation, and the community weighted mean of the following traits LA, SLA, Height, Wood density, Root density, and SRA. Species composition was set as a random effect due to the nature of the experimental design (Hector et al., 2011). The predictive variables were standardized and the residuals of the models were checked for homoscedasticity. For both models we extracted the percentage of variables relative importance, using the function “calc.relip.mm” (Berenz, 2015). See code and math details in Supplementary material.

Results

Leaf biomass production (g) varies between diversity levels and within compositions (Fig. 2 and detailed information on Supplementary material Fig. S2). In average, the values of monocultures were 2.61g ± 0.4, for species diversity two, four, eight and 16 the values were 3.78 ± 1.10, 1.53g ± 0.26, 3.63g ± 1.11 and 1.31g ± 0.24 respectively. The species with higher leaf biomass production varied between diversity levels, but in general, *M. tenuiflora*, presented the highest biomass investment within diversity levels and *A. cearensis* one of the lowest (Fig. S2 of Supplementary material). The leaf biomass production was explained by facilitation effects, explaining 37.6% of model variance, and community functional identity (CWM) of Specific root area, explaining 39.8% of model variance, Specific leaf area, explaining 14.4% of model variance and Wood density, explaining 8.3% of model variance (See analysis results at Table 1 and Fig. 2).

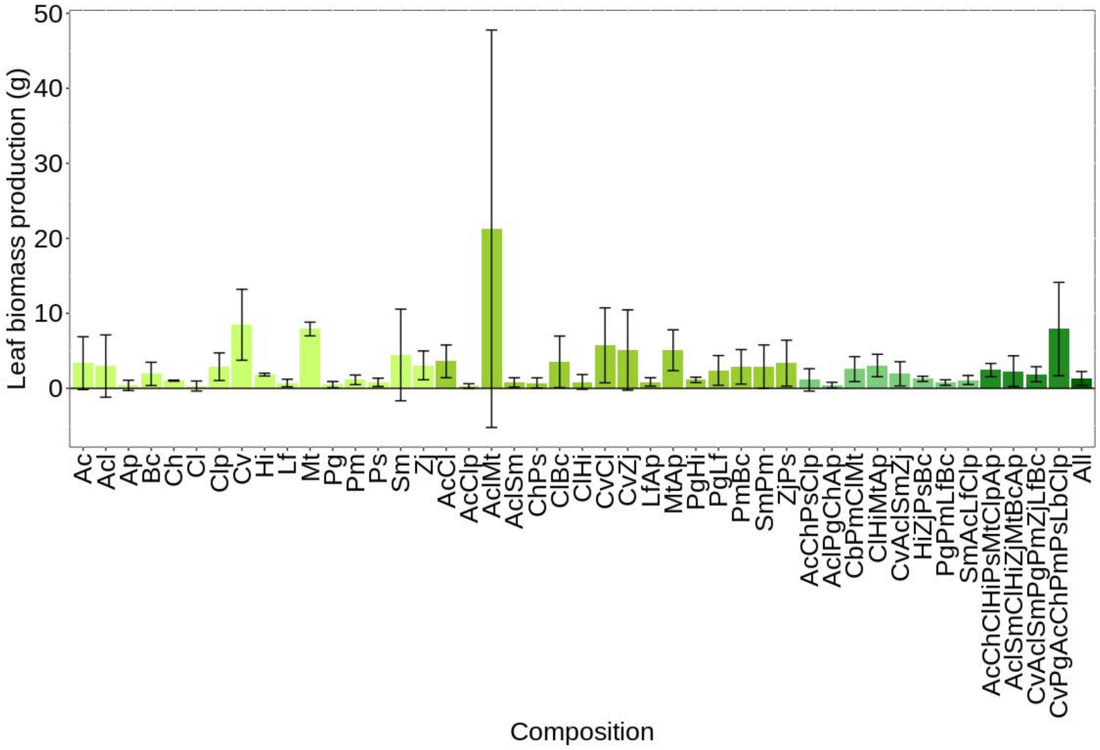


Figure. 2. Mean leaf biomass production for monocultures and species mixtures of experimental species assemblages built for each diversity level (1sp, 2sp, 4sp, 8sp and 16 sp). Error bars represent standard errors. Plant species identifications for each legend can be found in Supplementary material Table S1.

Table 1. Mixed Model testing the effect of facilitation, functional diversity, and community identity on leaf biomass production. Community identity is represented by the Community Weighted Mean (CWM) of selected traits Specific Root Area (SRA), Specific Leaf Area (SLA) and Wood density. Species composition was set as a random variable.

Random Effects				
	Variance	SE		
Composition	0.1143	0.3381		
Residuals	0.6998	0.8365		
Fixed effects				
	Estimate	SE	T-value	P-value

Intercept	0.0203	0.086	0.234	0.816
Facilitation	0.312	0.085	3.648	**<0.001**
SRA (CWM)	0.375	0.100	3.72	**0.000**
SLA (CWM)	0.260	0.121	2.135	**0.038**
Wood density (CWM)	0.273	0.131	2.077	**0.043**
Total pseudo $R^2 = 0.33$				

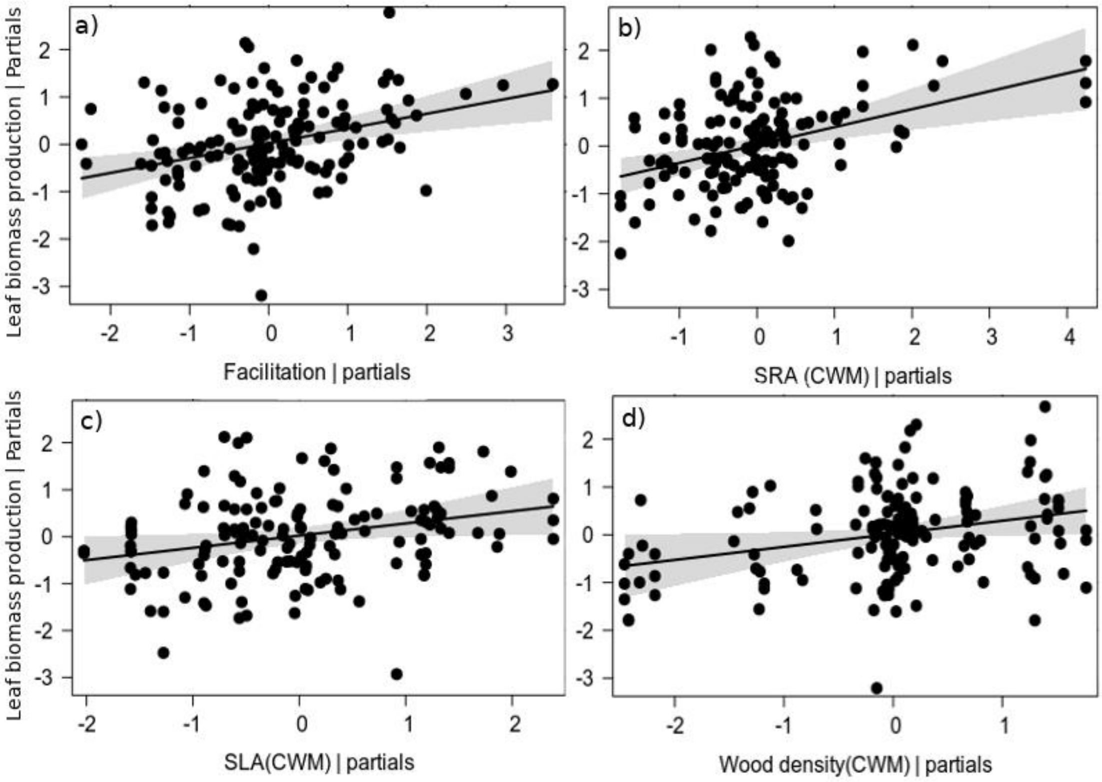


Figure. 3. Effects of each significant predictive variable presented in the mixed model of Table 1 on the Y variable Leaf biomass production. a) Partial effect of facilitation controlled by SRA (Specific Root Area), SLA (Specific Leaf Area) and Wood density, b) Partial effect of SRA controlled by facilitation, SLA and Wood density, c) Partial effect of SLA controlled by Facilitation, SRA and Wood density and d) Partial effect of Wood density controlled by facilitation, SRA and SLA.

Net biodiversity effect

The Net biodiversity effect values varied from -4.15 to 82.46. The general mean of all diversity levels differed from zero (t = 4.9982, df = 98, p-value <0.001), where 22 communities out of 29 showed on average, larger productivity than its respective monocultures (Fig. 4). The Selection Effect values were different from zero (t = -3.3285, df = 98, p-value = 0.001), and negative for 75.75% of all communities, where the overyield was stronger for the species with the lowest productivity in monoculture. The Complementarity effect also differed from zero (t = 4.4164, df = 98, p-value = <0.001) and was positive in 79.8% of all communities (Fig. 4) .

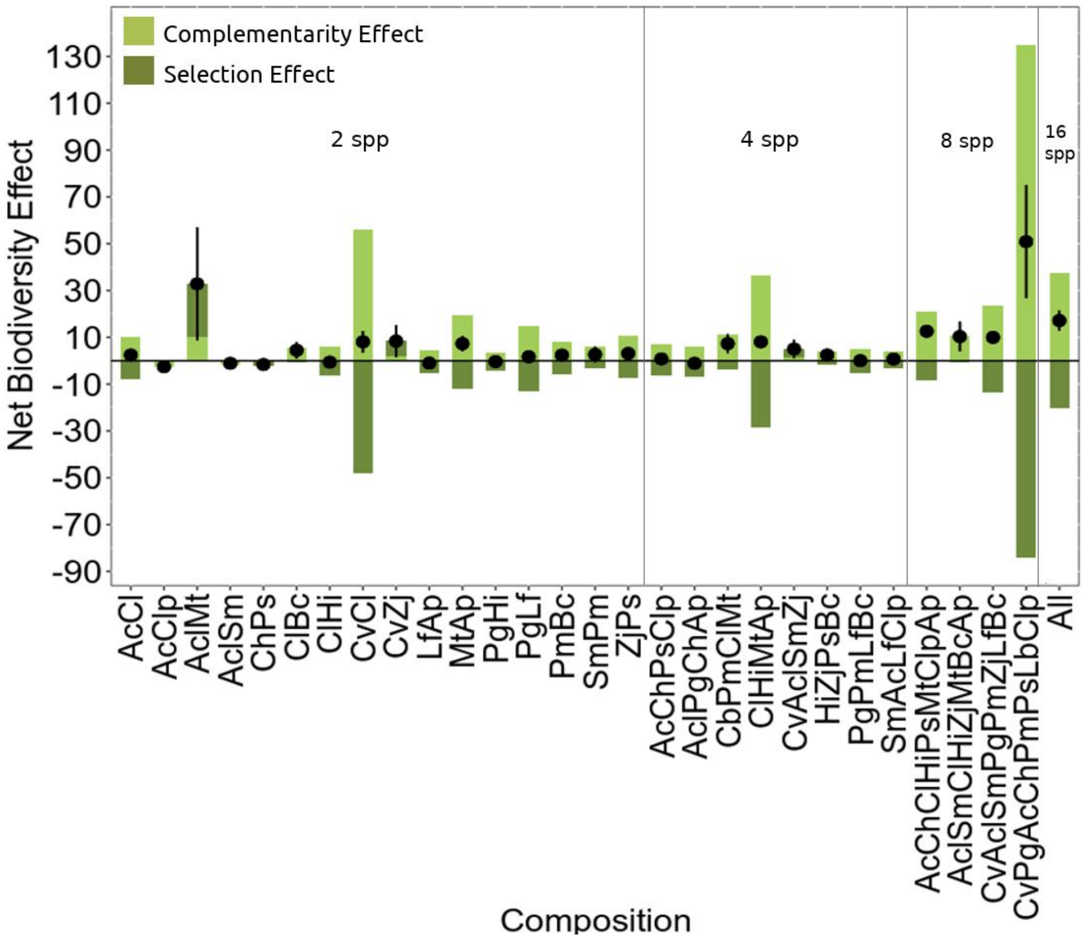


Figure. 4. Net biodiversity effect - NBE (black dots) and its standard error (black lines) plotted for communities with distinct compositions for different diversity levels (2sp, 4sp, 8sp and 16 sp). Light green bars represent the Selection effect (SE) for each composition, where positive values represent a better plant performance in mixtures in comparison to monocultures. Dark green bars represent the Selection Effect (SE), where negative values represent that species with the lowest production at

monocultures, performed better when placed in mixtures. Plant species identifications for each legend can be found in Supplementary material Table S1.

The main factors positively influencing the Net biodiversity effect were facilitation explaining 36.4% of variance, functional diversity explaining 49.5% of variance and Community identity related to SRA explaining 13.9% of total variance (Table 2, Fig. 5). See Supplementary material to further information about the calculation of variables importance.

Table 2. Mixed Model testing the effect of facilitation, functional diversity and community weighted mean of Specific root area (SRA) on Net Biodiversity Effect. Species composition was set as a random variable.

Random effects				
	Variance	SD		
Composition	0.151	0.388		
Residuals	0.608	0.779		
Fixed effects				
	Estimate	SE	T-value	P-value
Intercept	0.040	0.113	0.359	0.723
Facilitation	0.369	0.102	3.598	**<0.001**
Functional Diversity	0.463	0.143	3.217	**0.007**
SRA CWM	0.234	0.104	2.239	**0.033**
Total pseudo R^2= 0.47				

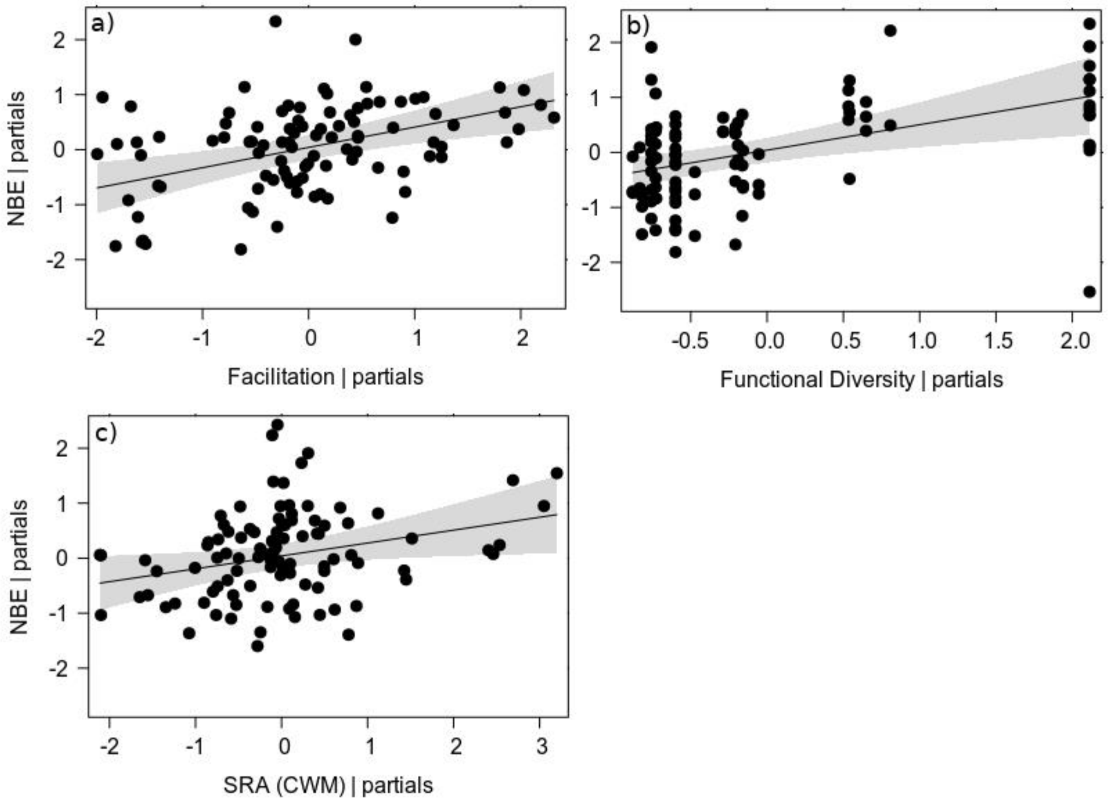


Figure. 5. Effects of significant predictive variables selected in the mixed model of table 2 on the Y variable Net Biodiversity Effect (NBE). a) Partial effect of Facilitation controlled by Functional diversity (FD) and the Community Weighted Mean (CWM) of Specific Root Area (SRA) b) Effect of FD controlled by Facilitation and SRA CWM, c) Effect of SRA CWM controlled by Facilitation and FD.

Discussion

For the first time, the relative importance of facilitation and functional complementarity of Complementarity Effect were disentangled to provide a better understanding of the role of the Complementarity Effect on plant community functioning. Facilitation effects had a fundamental role in increasing biomass production and presented a similar importance compared to Functional diversity, increasing overall ecosystem processes (Net Biodiversity Effect). Additionally, our study provided a new approach to disentangle the three components of the Net biodiversity Effect, facilitation, functional diversity, and community functional identity, in order to guide future restoration programs.

Disentangling facilitation from Functional diversity

The process of functional diversity increasing biomass production and ecosystem functions has been extensively demonstrated (Hector et al., 1999; Lasky et al., 2014; Liang et al., 2016; Van de Peer, et al., 2018). In the present study, functional diversity was important to improve ecosystem functions, however, facilitation had also a high proportional influence on ecosystem functions (49.5% and 36.4% for Functional diversity and Facilitation, respectively). Although both functional diversity and facilitation are part of the same general effect called and calculated as Complementarity Effect, facilitation is usually considered as an intrinsic portion of functional diversity. Thus, the impact of Complementarity Effect of NBE calculated just as Functional diversity on current studies is probably overestimated. Not just facilitation has a distinct effect on plant communities, but this effect might potentialize the amount of limiting resources available to be used by different plant functional groups in a complementary way.

A better understanding of how facilitation modulates plant communities is fundamental for restoration programs (Gómez-Aparicio, 2009). Here we showed that facilitation was important through several steps from biomass production until community functioning. Furthermore, studies show that facilitative species also have the capacity to improve species recruitment diversity (Cruz-Alonso et al., 2019; Tíscar & Linares, 2014), naturally increasing long-term the community functional diversity (Noumi, et al., 2016). Thus, facilitative species can be used not only to increase biomass production, but also to accelerate the community establishment and subsequently increase community function.

Community Identity

The functional identity of plant communities also influenced community performance measurements, biomass production, and community functioning. Functional identity was shown to improve community performance in other studies, with the selected traits of each study varying due to distinct environmental limitations (Finegan et al., 2015; Van de Peer et al., 2018). In this study, the prevalent community trait explaining biomass production and plant interactions was related to a high capacity of below-ground resources acquirement (high SRA). Degraded semiarid forests present low natural establishment and high seedling mortality due to environmental stressful conditions (Maestre et al., 2006; Paterno et al., 2016; Fagundes et al., 2018). Species with higher SRA are able to acquire a higher amount of water by maximizing soil foraging (Olmo et al., 2014), this would not just increase plant species survival but would allow them to growth for longer periods.

Applying the three NBE factors to restoration purposes

Once we understand the importance of facilitation, functional diversity, and community identity mechanisms, we can propose practical scenarios for restoration. In the best scenario, communities should be built with facilitative species, high functional diversity, and species with high specific root length. However, at several restoration programs, there are practical and financial limitation to the number of plant species to be used. However, contrary to functional diversity, the effect of facilitation in our work was not related to species diversity. Such characteristic of facilitation allows managers to rebuild more productive communities with a lower number of species. Because facilitation increases the recruitment and establishment of new species, a low diversity community with highly facilitative species included since the beginning, should present better long term performance. Future experiments implemented on different semiarid regions are certainly needed to test how long-term facilitation effects can increase performance of restored communities.

Conclusion

Here we showed that facilitation is a key process for restoration, influencing community biomass productivity and the net biodiversity effect. Indeed, both dimensions of the complementarity effect, functional diversity and facilitation, are fundamental to provide higher community functioning at the initial years of community restoration. Moreover, plant functional identity related to a high capture of below-ground resources is also important to increase community success in water-limited environments. The chances of restoration success are strictly connected with ecological theories, and we believe that the manipulation of plant communities based on this work results will help to improve semiarid restoration practices.

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Supplementary Material

Disentangling the influence of facilitation and niche complementarity on biodiversity effects at restored tree communities

Marina Fagundes & Gislene Ganade

Table 1. Tree species combinations for each diversity treatment and their replication levels applied to the Biodiversity and Ecosystem Function field experiment implemented at a degraded Catinga Seasonally Tropical Dry Forest in Brazil. Species abreviation: Zj: *Ziziphus joazeiro*, Clp: *Combretum leprosum*, Ac: *Amburana cearensis*, Lf: *Libidibia ferrea*, Ch: *Cynophala hastata*, Acl: *Anandenanthera colubrina*, Pm: *Pseudobombax marginatum*, Ps: *Piptadenia Stipulaeae* Clp: *Combretum leprosum*, Cv: *Cochlospermum vitifolium*, Pg: *Poincianela gardneriana*, Hi: *Handroanthus impetiginosus*, Bc: *Bauhinha cheilanta*, Ap: *Aspidosperma pirifolium*, Mt: *Mimosa tenuiflora.*

Richness	Composition	Number of composition	Replicates by composition	Total plots per richness
1 sp	Cv	16	3	48
	Acl			
	Sm			
	Pg			
	Ac			
	Ch			
	Pm			
	Clp			
	Hi			
	Zj			

	Ps			
	Mt			
	Lf			
	Clp			
	Bc			
	Ap			
2 sp	Cv + Zj	16	3	48
	Acl + Mt			
	Pg + Lf			
	Zj + Ps			
	Cv + Clp			
	Acl + Sm			
	Pg + Hi			
	Lf + Ap			
	Sm + Pm			
	Clp + Hi			
	Clp +Bc			
	Mt + Ap			
	Pm + Bc			
	Ch+ Ps			
	Ac + Ch			
	Ac + Clp			
4 sp	Cv + Acl + Sm + Zj	8	3	24
	Cv + Pm + Clp + Mt			
	Acl + Pg + Ch+ Ap			
	Sm + Ac + Lf + Clp			
	Ac+ Ch+ Ps+ Clp			
	Pg + Pm + Lf +Bc			
	Clp + Hi + Mt + Ap			
	Hi + Zj + Ps+ Bc			
8 sp	Cv + Pg + Ac + Ch+ Pm+ Ps+ Lf+ Clp	4	3	12
	Cv + Acl+ Sm + Pg + Pm + Zj + Lf + Bc			
	Acl +Sm + Clp + Hi + Zj + Mt + Bc + Ap			
	Ac+ Ch+ Clp + Hi + Ps+ Mt + Clp + Ap			

16 sp	Pm + Pm + Ac + Clp + Cv + Ap + Ch+ Acl + Zj + Lf + Clp + Pg + Bc + Ps + Hi + Mt	1	15	15

Figure S1. Relation between species diversity and facilitation, followed by relation between species diversity and functional diversity for all experimental communities.

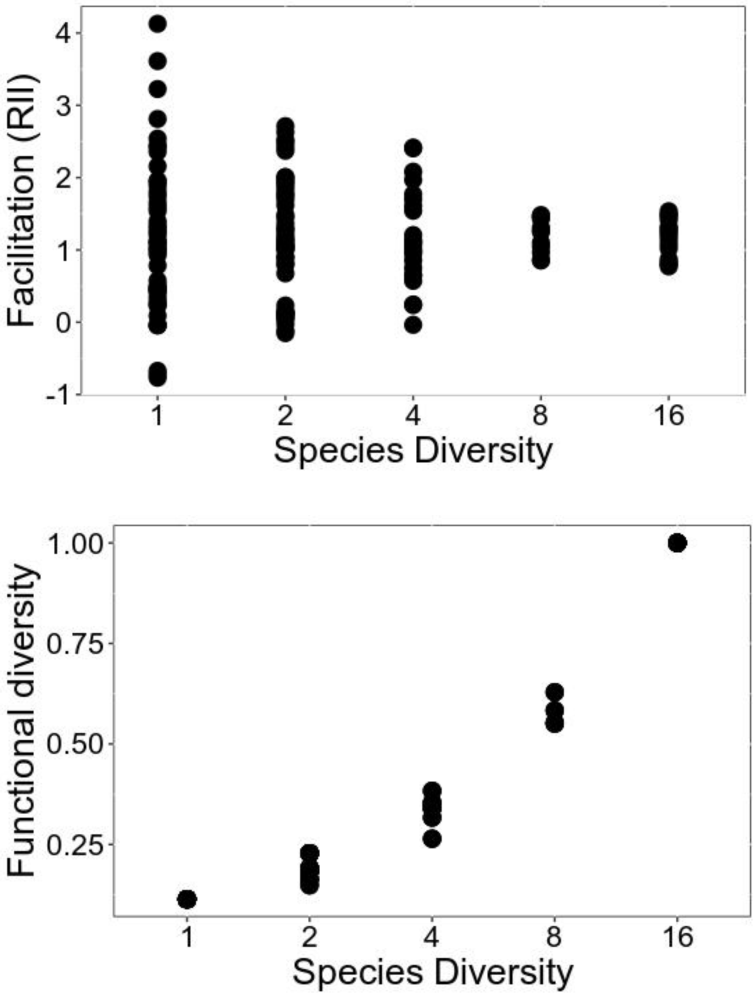
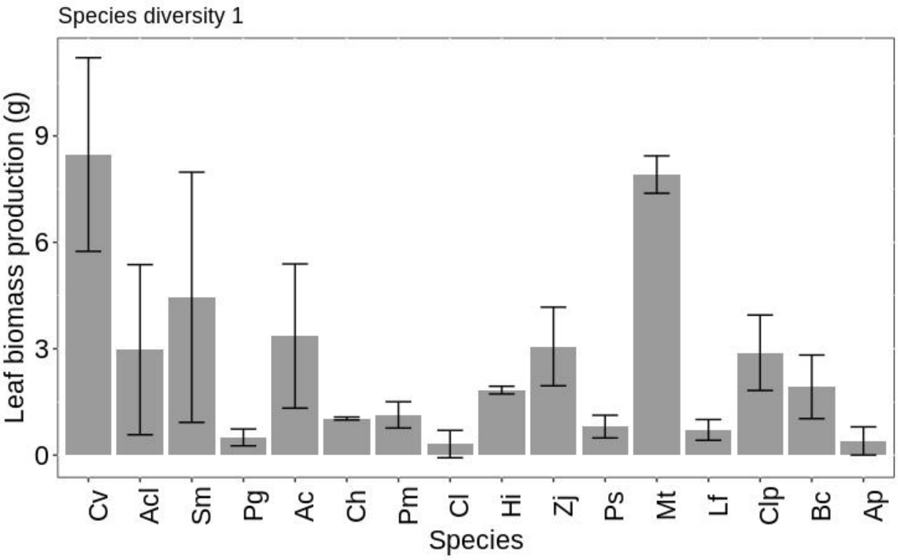
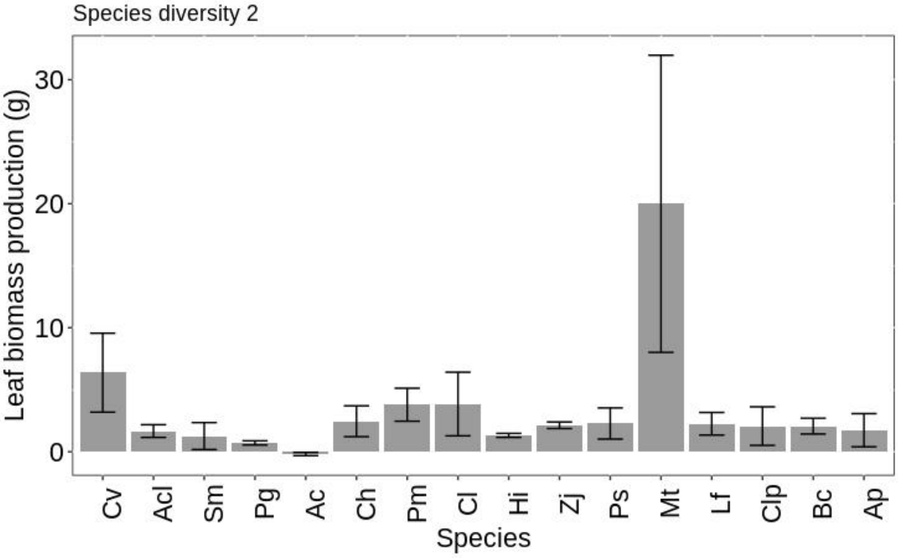
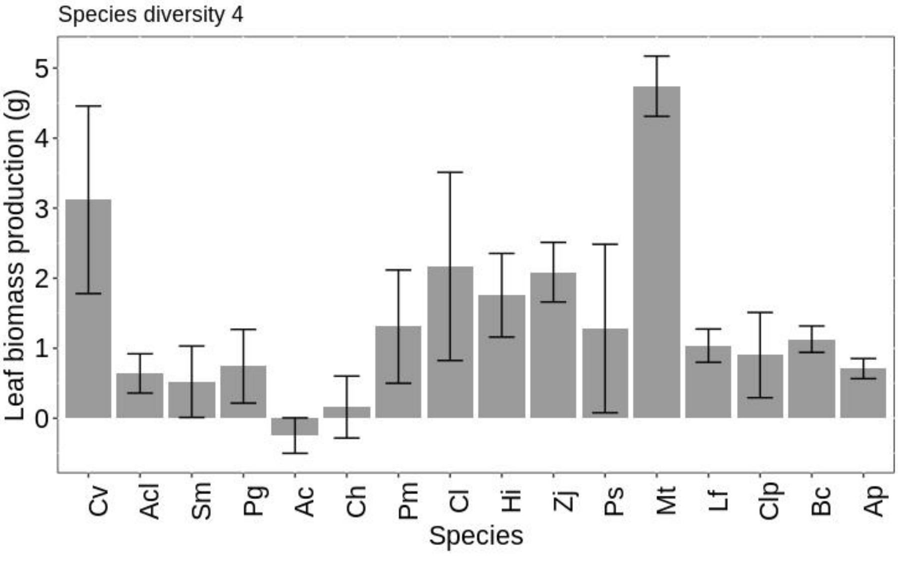
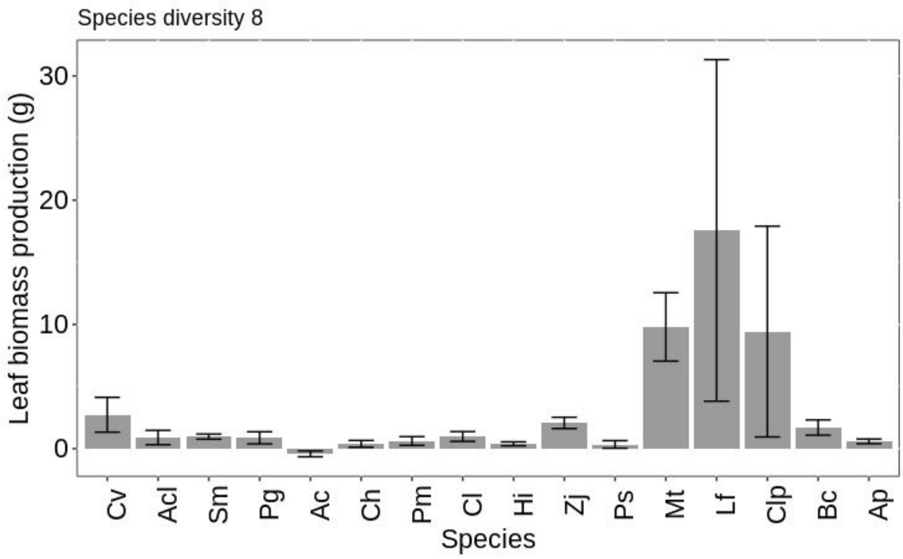


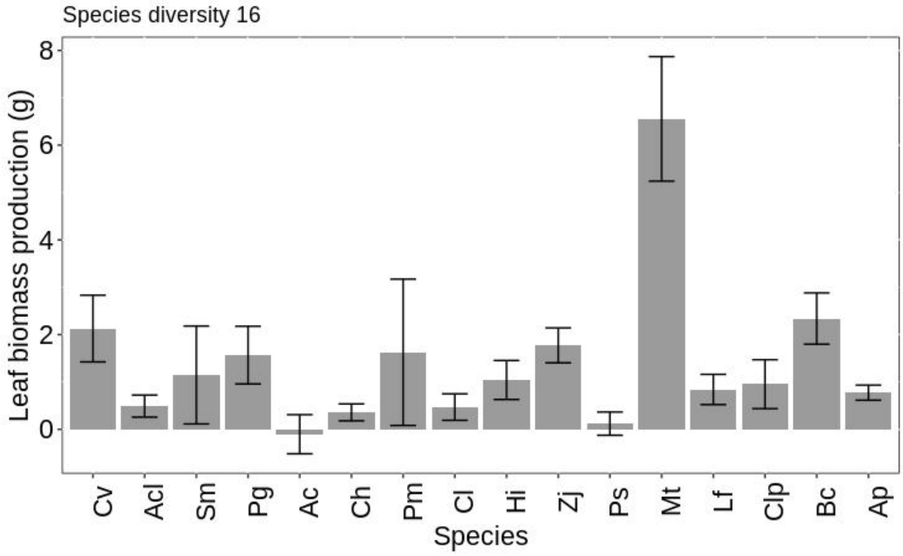
Figure S2. Mean Leaf biomass production per plant species for each level of community diversity (1sp, 2sp, 4sp, 8sp and 18sp). These calculations take into account individuals present at all species compositions. Error bars represent standard error.


Species diversity 1
Leaf biomass production (g)
0
3
6
9
Cv
Acl
Sm
Pg
Ac
Ch
Pm
Cl
Hi
Zj
Ps
Mt
Lf
Clp
Bc
Ap
Species


Species diversity 2
Leaf biomass production (g)
0
10
20
30
Cv
Acl
Sm
Pg
Ac
Ch
Pm
Cl
Hi
Zj
Ps
Mt
Lf
Clp
Bc
Ap
Species


Species diversity 4
Leaf biomass production (g)
0
1
2
3
4
5
Cv
Acl
Sm
Pg
Ac
Ch
Pm
Cl
Hi
Zj
Ps
Mt
Lf
Clp
Bc
Ap
Species





Variable importance function script

https://gist.github.com/BERENZ/e9b581a4b7160357934e#file-calc-relip-mm-r

```
calc.relip.mm <- function(model,type='lmg') {
  if (!isLMM(model) & !isGLMM(model)) {
```

```
        stop('Currently supports only lmer/glmer objects', call. = FALSE)
    }
    require(lme4)
    X <- getME(model,'X')
    X <- X[,-1]
    Y <- getME(model,'y')
    s_resid <- sigma(model)
    s_effect <- getME(model,'theta')*s_resid
    s2 <- sum(s_resid^2,s_effect^2)
    V <- Diagonal(x = s2,n=nrow(X))
    YX <- cbind(Y,X)
    cov_XY <- solve( t(YX) %*% solve(V) %*% as.matrix(YX))
    colnames(cov_XY) <- rownames(cov_XY) <- colnames(YX)
    importances <- calc.relimp(as.matrix(cov_XY),rela=T,type=type)
    return(importances)
}

```

Conclusão Geral

As espécies arbóreas da Caatinga apresentam diversas nuances de estratégias funcionais distribuídas entre o gradiente de grupos conservativos e aquisitivos. As espécies conservativas apresentam características esperadas para ambientes estressantes, como altas densidades de tecido vegetal present acima e abaixo do solo, folhas com alta razão C:N e longa duração de copa. Mesmo sendo um ambiente cuja disponibilidade hídrica seja o principal fator limitante, a Caatinga também abriga espécies do grupo aquisitivo, com características como baixa densidade de madeira, grandes diâmetros hidráulicos, cascas com grandes espessuras, folhas com baixa razão C:N e curta duração da copa. Ambas estratégias são distribuídas ao longo do bioma de forma independente, onde, surpreendentemente, as estratégias aquisitivas apresentam em média,maior ocorrência em locais levemente mais áridos.

Em ambientes estressantes espera-se que estratégias conservativas sejam dominantes e que níveis de estresse limitem a ocorrência de certos grupos funcionais. Porém, na Caatinga, a variação temporal parece afetar mais os grupos funcionais do que a variação geográfica, onde, durante períodos chuvosos, espécies com características aquisitivas são capazes de capturar e armazenar água, e em seguida entrar em rápida dormência, evitando períodos mais estressantes. Desta forma, é possível que espécies aquisitivas ocupem, inclusive, locais com maior aridez do que espécies conservativas, que possuem uma menor taxa de aquisição de recursos e menor gasto hídrico. Espécies conservativas parecem estar mais suscetíveis ao limite hídrico anual, possivelmente por manterem suas atividades por longos períodos.

Além de espécies com estratégias aquisitivas e conservativas estarem distribuídas em todo o bioma Caatinga, ambas também possuem potencial facilitador. Espécies com atributos conservativos facilitam plantas jovens de pequena estatura e menor quantidade de biomassa nas raízes, mas que são capazes de alongar seus tecidos subterrâneos em busca de água. Pelo fato de espécies conservativas apresentarem uma menor taxa de aquisição hídrica e maior duração de copa, diminuindo a transpiração do solo, o tempo de disponibilidade hídrica abaixo do solo também aumenta. Por outro lado, espécies com características aquisitivas facilitam espécies de plantas jovens mais independentes de sua influência facilitadora em termos de aquisição e armazenamento de água. Por terem a capacidade de adquirir recursos hídricos e armazená-los, estes indivíduos jovens conseguem ainda competir melhor por luz. Desta forma, árvores aquisitivas que, por apresentarem altas taxas de gasto hídrico perdem suas folhas rapidamente, provém maior disponibilidade solar para plantas que regeneram sob sua copa do que árvores conservativas.

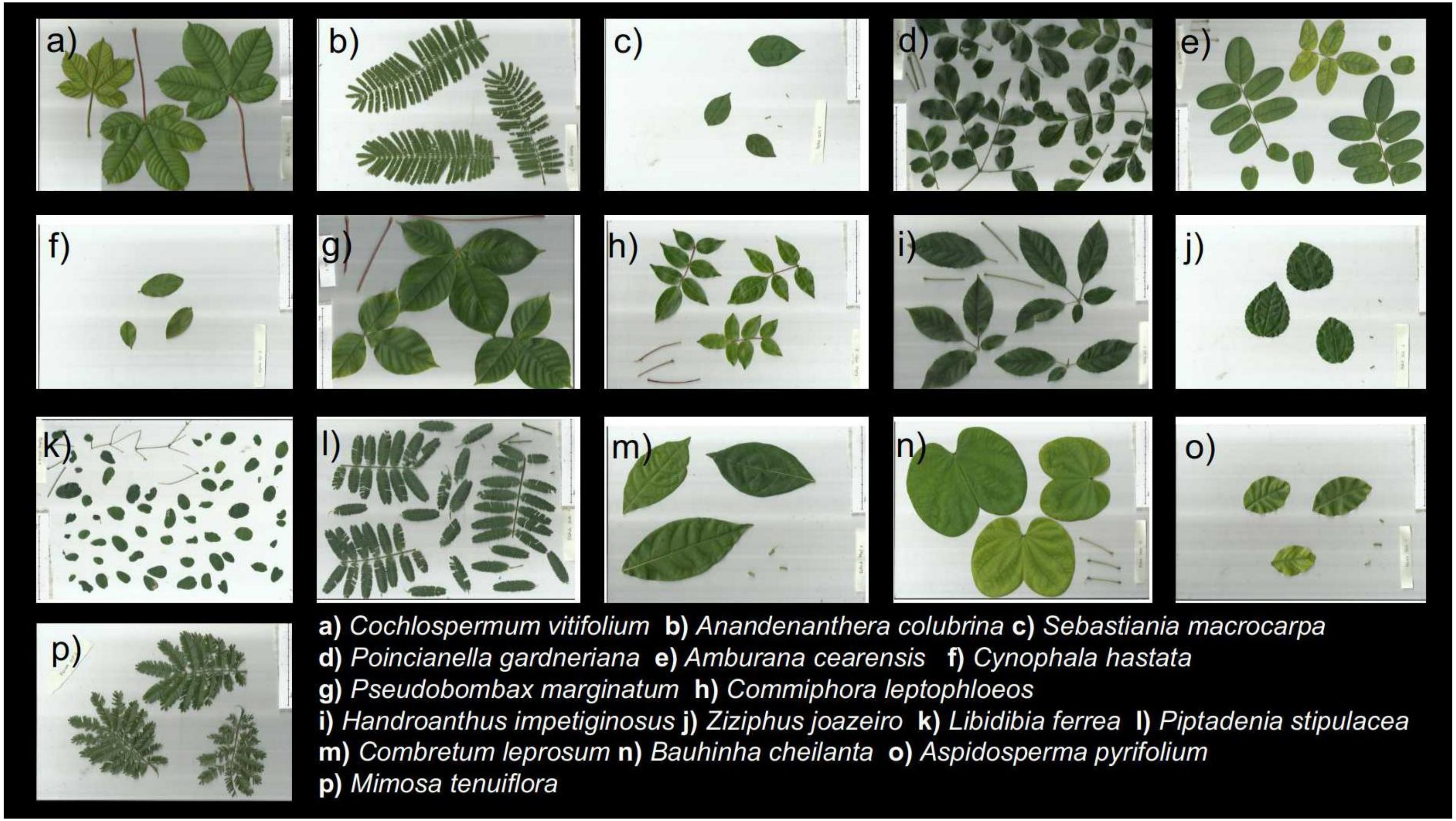
Sabemos então que a grande diversidade de estratégias funcionais encontradas na Caatinga permite um sucesso de colonização em ampla escala e que processos de facilitação são importantes nesse ecossistema. A aplicação destas abordagens teóricas são fundamentais para programas efetivos de restauração. Em comunidades restauradas, a produção de biomassa foi maior nas comunidades cujas espécies apresentavam características funcionais como alta área de raíz, alta área foliar específica, e que continham facilitadoras. Os processos ecossistêmicos foram mais dinâmicos nas comunidades cujas espécies apresentaram maior área de raiz, maior diversidade funcional, e que continham facilitadoras. Desta forma, vemos que, para maximizar o sucesso de restauração de comunidades semiáridas, a presença de espécies facilitadoras e a utilização de espécies que maximizam a aquisição do recurso limitante, neste caso, a água, são fundamentais.

Este trabalho elucida a diversidade funcional de espécies arbóreas da Caatinga, um ambiente historicamente negligenciado e que acreditava-se conter baixa diversidade. Além disto, mostramos que estas espécies possuem alto potencial facilitativo, e que devem ser utilizadas em programas de restauração. É importante, no entanto, que futuros trabalhos ampliem a quantidade de espécies lenhosas estudadas para uma compreensão mais refinada das diversas estratégias encontradas. Ademais, aqui demonstramos os efeitos funcionais e facilitativos em anos iniciais de programas de restauração. Porém, o acompanhamento prolongado também é fundamental para compreendermos como estes elementos modulam as comunidades a longo prazo.

ANEXOS

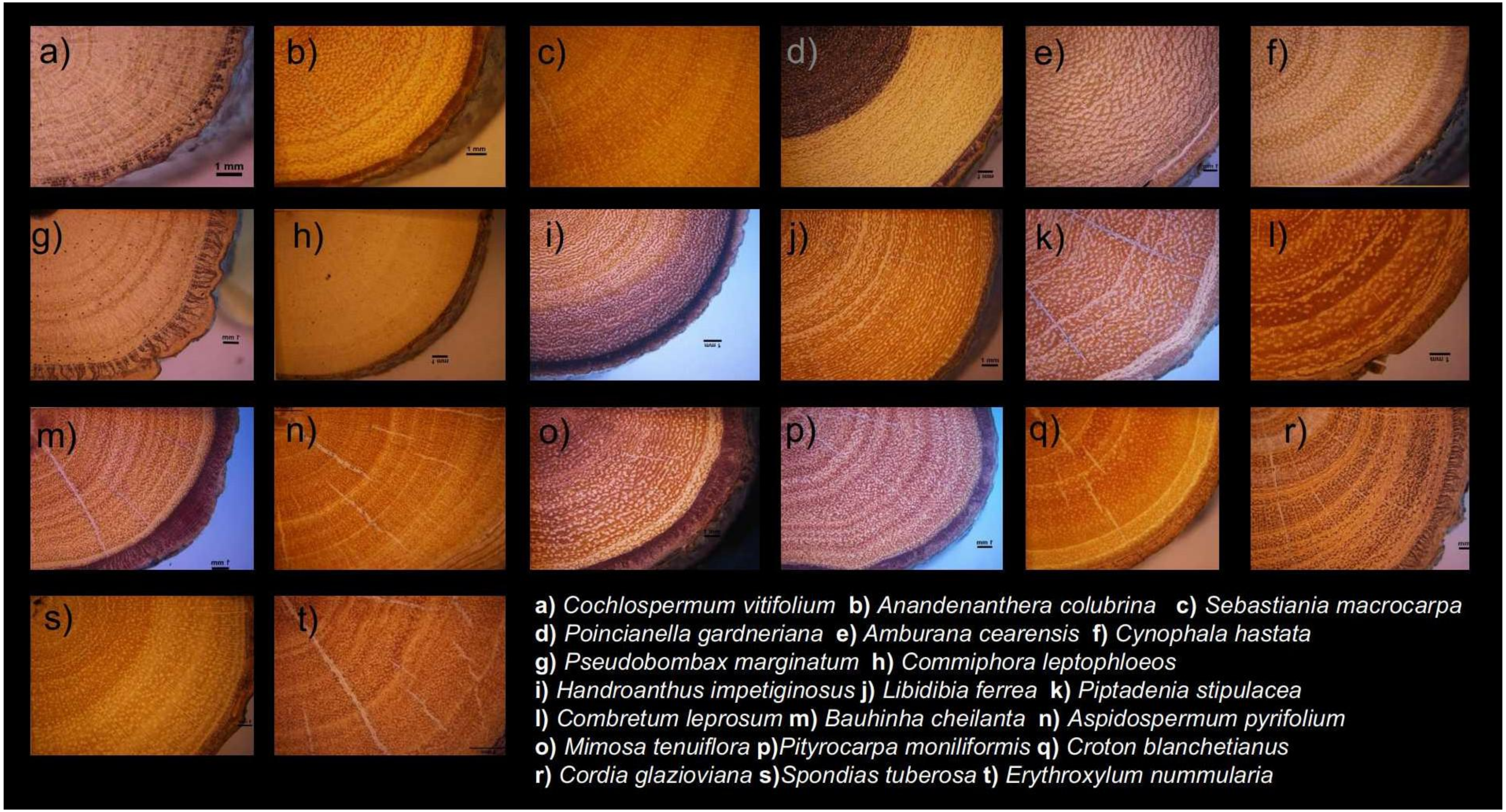
Fotos de estruturas funcionais foliares, de lenho e raízes das epécies arbóreas da Caatinga estudadas ao longo deste trabalho.

Amostras adaxiais das folhas das espécies arbóreas da Caatinga.



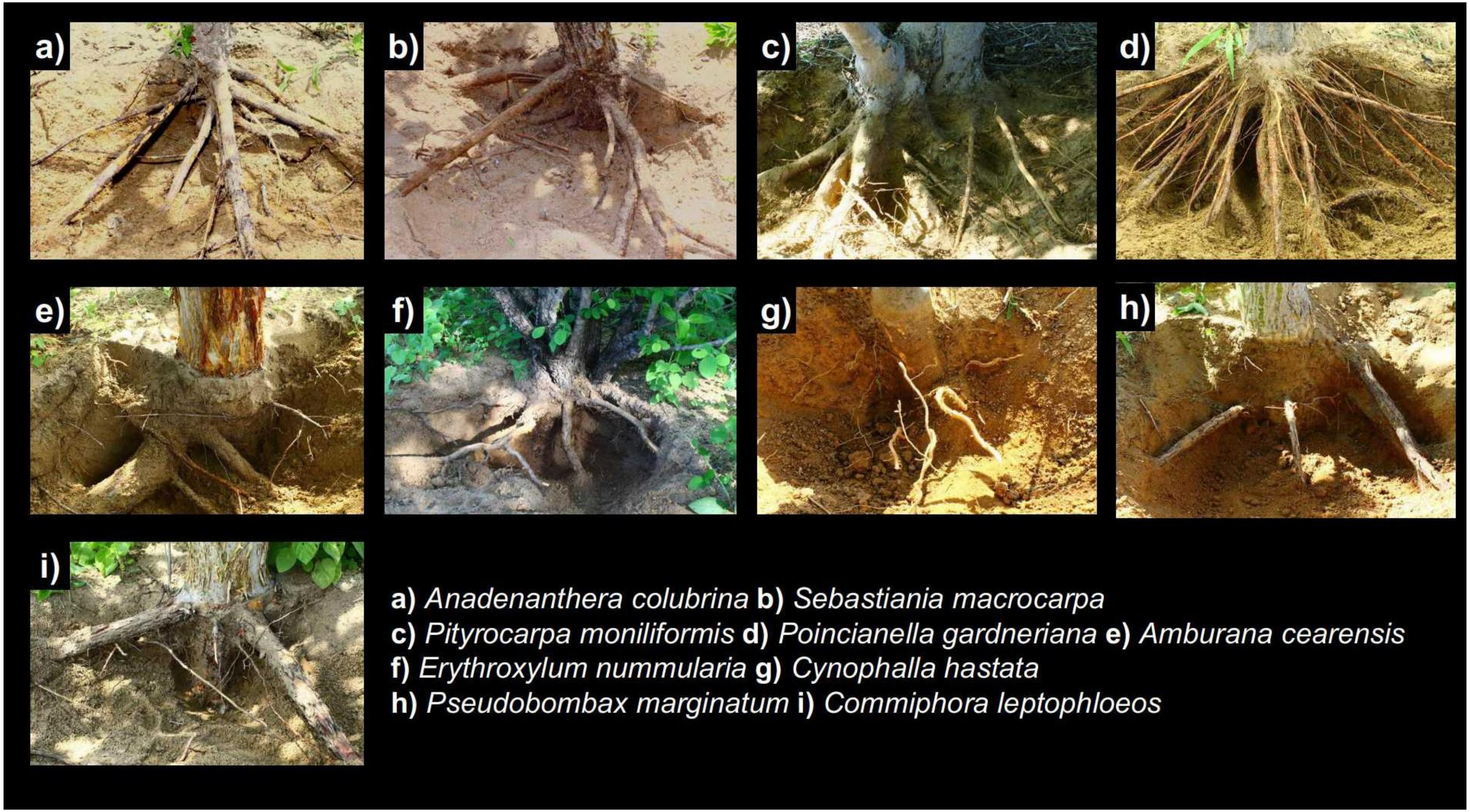
a) *Cochlospermum vitifolium* **b)** *Anandenanthera colubrina* **c)** *Sebastiania macrocarpa*
d) *Poincianella gardneriana* **e)** *Amburana cearensis* **f)** *Cynophala hastata*
g) *Pseudobombax marginatum* **h)** *Commiphora leptophloeos*
i) *Handroanthus impetiginosus* **j)** *Ziziphus joazeiro* **k)** *Libidibia ferrea* **l)** *Piptadenia stipulacea*
m) *Combretum leprosum* **n)** *Bauhinha cheilanta* **o)** *Aspidosperma pyrifolium*
p) *Mimosa tenuiflora*

Cortes transversais de lenho das espécies arbóreas da Caatinga.

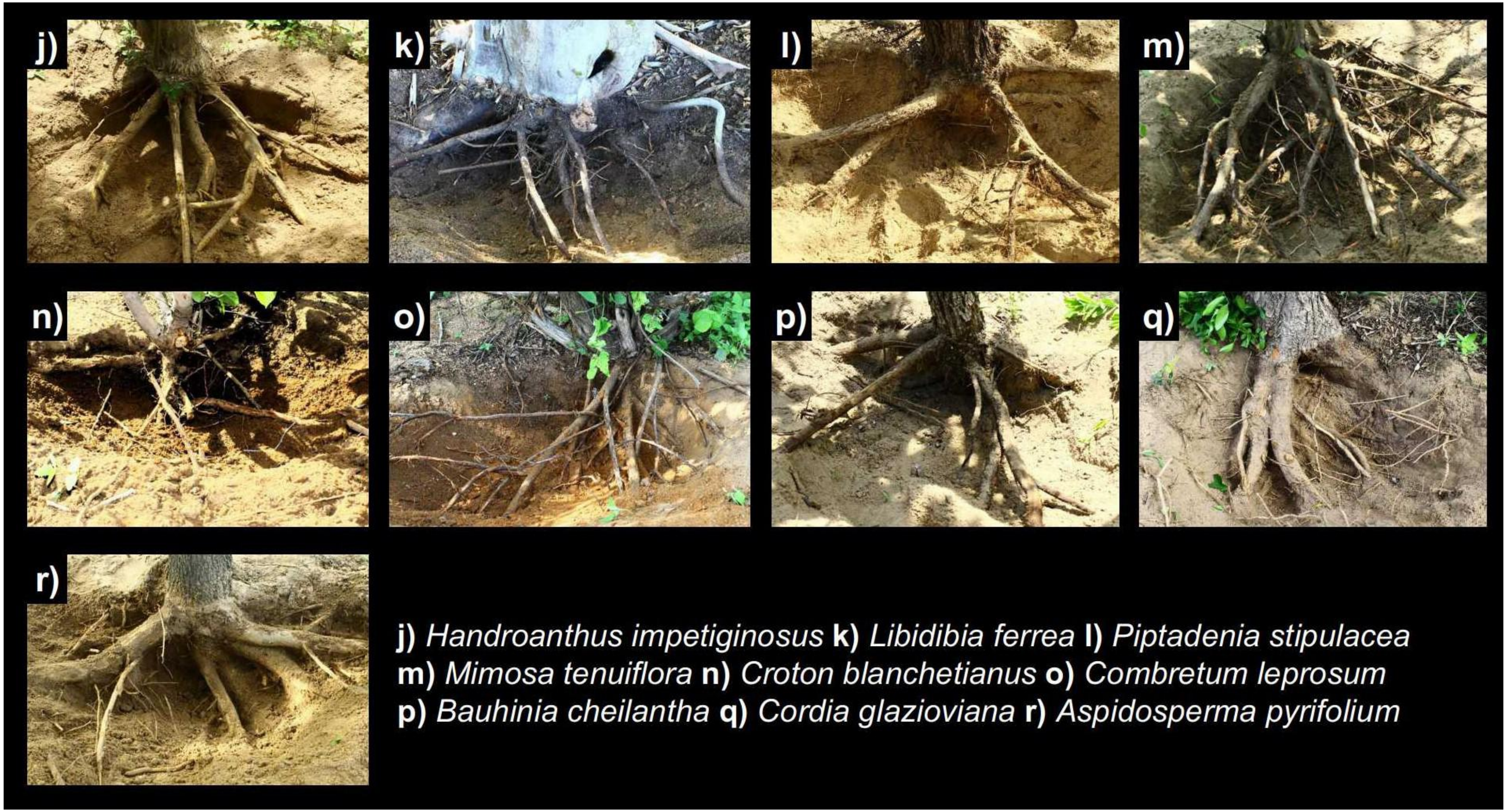


a) *Cochlospermum vitifolium* **b)** *Anandenanthera colubrina* **c)** *Sebastiania macrocarpa*
d) *Poincianella gardneriana* **e)** *Amburana cearensis* **f)** *Cynophala hastata*
g) *Pseudobombax marginatum* **h)** *Commiphora leptophloeos*
i) *Handroanthus impetiginosus* **j)** *Libidibia ferrea* **k)** *Piptadenia stipulacea*
l) *Combretum leprosum* **m)** *Bauhinha cheilanta* **n)** *Aspidospermum pyrifolium*
o) *Mimosa tenuiflora* **p)***Pityrocarpa moniliformis* **q)** *Croton blanchetianus*
r) *Cordia glazioviana* **s)***Spondias tuberosa* **t)** *Erythroxylum nummularia*

Arquitetura da raíz de espécies lenhosas da Caatinga



a) *Anadenanthera colubrina* **b)** *Sebastiania macrocarpa*
c) *Pityrocarpa moniliformis* **d)** *Poincianella gardneriana* **e)** *Amburana cearensis*
f) *Erythroxylum nummularia* **g)** *Cynophalla hastata*
h) *Pseudobombax marginatum* **i)** *Commiphora leptophloeos*



j) *Handroanthus impetiginosus* **k)** *Libidibia ferrea* **l)** *Piptadenia stipulacea* **m)** *Mimosa tenuiflora* **n)** *Croton blanchetianus* **o)** *Combretum leprosum* **p)** *Bauhinia cheilantha* **q)** *Cordia glazioviana* **r)** *Aspidosperma pyrifolium*