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Facilitation as a driver of plant assemblages in Caatinga

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ABSTRACT

Nurse plants reduce the environmental severity experienced by neighboring plants by providing shade, enabling nutrient accumulation or protection from herbivores within patches of vegetation. Nurse plants should preferentially promote the coexistence of ecologically dissimilar species with little niche overlap, and if ecological traits are conserved within evolutionary lineages, this should result in phylogenetic overdispersion. In contrast to competition, facilitation is expected to increase species richness. Therefore, to examine the role of facilitation as a driver of plant assemblages in Caatinga, we quantified the functional traits of nurse species and compared species richness, phylogenetic diversity, phylogenetic structure of the tree layer and of the herbaceous layer between patchy Caatinga and Caatinga with segregated plants. Results show that functional traits related to resilience and resistance against herbivory seem to be crucial for facilitation in Caatinga. Autochory occurs at a higher frequency in nurse plants than in Caatinga in general. The herbaceous layer of patchy Caatinga is richer in species than of Caatinga with segregated plants, and facilitation is the suggested cause. As the whole community of the 196 patches is phylogenetically overdispersed compared to the null expectations, facilitation seems to predominantly promote the coexistence of dissimilar species with little niche overlap.

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1. Introduction

Biological interactions such as facilitation, competition, herbivory and mutualism, are key ecological processes that influence community composition (i.e.), assembly rules, (Kraft et al., 2015). Facilitation is a positive interaction in which the presence of a nurse plant reduces the environmental severity experienced by neighboring plants (Jankju, 2013), increasing growth rate, recruitment, and survival as well as enhancing the reproductive success of these facilitated plants (Hierro and Cock, 2013). In contrast to competition, facilitation diversifies niches and increases the species richness of communities (Valiente-Banuet and Verdú, 2013, 2007). Therefore, facilitation is a key factor in ecosystem resilience and resistance (Pugnaire and Lázaro, 2000) that has further been recently recognized as a ubiquitous phenomenon in community assembly, especially in arid and semi-arid regions (Filazzola and Lortie, 2014).

Facilitation tends to group these plants into clumps or patches of

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http://dx.doi.org/10.1016/j.jaridenv.2017.03.006 0140-1963/© 2017 Elsevier Ltd. All rights reserved. vegetation dominated by the nurse plant, thus forming a characteristic mosaic of aggregated plants (Eccles et al., 1999), while plants in competition-dominated communities are likely to exhibit spatial segregation (Maestre et al., 2009). The benefits of nurse plants to facilitated plants may include the creation of favorable microclimates through shading or increases in nutrient content, organic matter, moisture and oxygenation of the soil (Filazzola and Lortie, 2014; McIntire and Fajardo, 2014). Additional facilitation mechanisms include protection from herbivores, increased pollination rates or seed recruitment and improved soil microbiota (Filazzola and Lortie, 2014).

To increase the species richness of communities and avoid niche overlap between nurse and facilitated plants, facilitation should promote the coexistence of ecologically dissimilar species (Castillo et al., 2010). By investigating this phenomenon, the analysis of phylogenetic community structure can offer valuable insights (Gastauer and Meira-Neto, 2013; Webb et al., 2002). If phylogenetically related species are ecologically more similar, i.e., their ecological traits are conserved within evolutionary niches, facilitation should promote phylogenetic overdispersion (Fig. 1A). Although facilitation would result in phylogenetic overdispersion or phylogenetic evenness if ecological traits are predominantly



Fig. 1. How facilitation, competition and environmental filtering influence phylogenetic community structure and species richness of a community. Species represented by the same symbols share functional traits; i.e., they are ecologically similar to each other. Contoured symbols represent species from the metacommunity that are not present within the community. Adapted from Sargent and Ackerly (2008).

convergent (Cavender-Bares et al., 2009; Valiente-Banuet and Verdú, 2007), it would never cause phylogenetic clustering (Fig. 1D).

In the case of conserved ecological niches within evolutionary lineages, competition would cause phylogenetic overdispersion (i.e., competitive exclusion of more related lineages due to competition for limited resources such as water or nutrients, Fig. 1B), while environmental filtering would cause phylogenetic clustering (i.e., filtering out of lineages lacking adaptative traits, for instance, against herbivore pressure, Fig. 1C, Webb et al., 2002). If traits are convergent, competition and environmental filtering would cause phylogenetic evenness, as with facilitation (Fig. 1E and F); however, competition and environmental filtering should decrease species richness (Fig. 1, Cavender-Bares et al., 2009; Gastauer and Meira-Neto, 2013).

The objective of this study is to analyze facilitation as a driver of plant assemblages in the semiarid savannas of the Caatinga in Brazil, where the plant community is structured in two main vegetation types: the patchy Caatinga and the Caatinga with segregated plants. Although other ecological and evolutionary processes may influence the phylogenetic structure of plant communities (Cavender-Bares et al., 2009; Sargent and Ackerly, 2008) we expect that coexisting species in patches of the patchy Caatinga founded by nurse plants will not be phylogenetically clustered and will show higher species richness than Caatinga with segregated plants. Therefore, the aims of this study are as follows: (i) we describe and quantify the functional traits of nurse plants in Caatinga patches to highlight their main functions and possible benefits to facilitated species. Next, (ii) we determine if the species coexisting within patches with nurse plants (i.e., under facilitation) show phylogenetic evenness or overdispersion, indicating a low niche overlap. Furthermore, (iii) we test whether patchy Caatinga is phylogenetically overdispersed, which would indicate niche diversification promoted by facilitation. Finally, (iv) we investigate whether patchy Caatinga shows higher species richness than Caatinga with segregated plants; nurse plants should ameliorate stressful environmental conditions, balance competitive exclusion and diversify niches.

2. Methods

2.1. Vegetation and study area

The Caatinga is a type of vegetation distributed in the biogeographical region that expands from 3° S to 17° S and from 35° W to 45° W with a tropical savanna-like, semi-arid vegetation that covers more than 800,000 km² in northeast Brazil (Veloso et al., 1991). The Brazilian Caatinga occurs on a wide range of soil types in the depressions between plateaus and on hills composed of sandstones, granite, gneiss and other metamorphic rocks (Menezes et al., 2012), and it represents the largest tropical semiarid vegetation type in South America, containing more than 300 endemic plant species. Overexploitation and endangerment of this unique vegetation has revealed its potential for ecological studies of facilitation, especially as a tool for restoration and conservation (Leger et al., 2014). However, Caatinga is often referred to as being a deeply disturbed and neglected vegetation type, so knowledge of facilitation in this system remains incipient (Silva et al., 2015).

Caatinga has been referred as dry forest (Dryflor et al., 2016), but its predominant physiognomy is savanna-like with segregated woody plants, here called Caatinga with segregated plants (Fig. 2). Patchy Caatinga differs from Caatinga with segregated plants because presents patches of clustered plants with few plants and bare soil in between patches (Fig. 2).

This study was carried out in Northern Bahia State, Brazil. Ten study sites were selected between the counties of Campo Alegre de Lourdes and Jeremoabo ($09^{\circ}29' - 10^{\circ}05'S$; $38^{\circ}16' - 43^{\circ}9'W$). The altitude varied from 289 m ASL in Jeremoabo to 556 m ASL in Canudos (Table 1).

According to the Köppen classification, this region has a semiarid steppe climate (BSh) with an annual rainfall of less than 800 mm, while the mean annual temperatures are higher than 18 °C. Although the ten study sites all belong to this single climate class, their precipitation regimes vary from 752 mm in Campo Alegre de Lourdes to 463 mm in Curaçá, one of the driest areas of Caatinga vegetation. Average annual temperatures are stable at approximately 24 °C (Alvares et al., 2013).

The plants on three of the study sites were segregated without

definite patches, while those on the other seven were clustered in patches (Fig. 2). A patch was defined as a discrete group of two or more plants growing together and surrounded by bare ground.

2.2. Data collection

To quantify the functional traits of the nurse plants and determine if the facilitated patches were phylogenetically overdispersed (aims i and ii), the composition of the patches within an area of $60 \text{ m} \times 90 \text{ m}$ were recorded for each of the seven study sites with patchy vegetation. Since height is directly related to diameter, canopy and age (Navarro-Cano et al., 2014), since shading is a main facilitation factor in hot conditions (McIntire and Fajardo, 2014) and because height is related to the plant position in the vertical light gradient (Pérez-Harguindeguy et al., 2013), we assumed that the tallest plant in each patch was the main nurse in this patch at the sampling moment. We, thus, measured the height of all plants within each patch, identified the potential nurse and next we classified nurse plants according to their life-forms (Pérez-Harguindeguy et al., 2013), dispersal mode (Pijl, 1982), capacity to



Fig. 2. Top: Caatinga with segregated plants in Campo Alegre de Lourdes, 08-04-2014 (09° 37' 22″ S, 42° 42' 25″ W). Bottom: patchy Caatinga; the patches are surrounded by bare soil with very few woody plants, in Juazeiro, 07-15-2014 (09° 29' 34″ S, 40° 12' 58″ W). Photos by JFCarrión.

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Table 1

Vegetation pattern, location and climatic characteristics of 10 study sites. Alt. is the altitude above sea level; Prec. is the mean annual precipitation; Temp. is the mean annu
temperature. Soil type by the Brazilian System of Soil Classification (EMBRAPA, 2006).

#	County	Vegetation pattern	Soil type	Location	Alt. [m]	Prec. [mm]	Temp. [°C]
1	Juazeiro	Patchy plants	Planosol	9.51882 S, 40.11998 W	440	472	24.4
2	Curaçá	Patchy plants	Luvisol	9.70714 S, 39.69572 W	484	463	24.3
3	Jeremoabo	Patchy plants	Litholic Neosol/Cambisol	9.89944 S, 38.83192 W	320	566	23.6
4	Canudos	Patchy plants	Litholic Neosol/Cambisol	9.97816 S, 38.99881 W	556	519	23.6
5	Canudos	Patchy plants	Litholic Neosol/Cambisol	9.95078 S, 39.01594 W	434	519	23.6
6	Canudos	Patchy plants	Litholic Neosol/Cambisol	9.94523 S, 39.00602 W	421	519	23.6
7	Canudos	Patchy plants	Litholic Neosol/Cambisol	9.95104 S, 39.00213 W	423	519	23.6
8	Remanso	Segregated plants	Latosol/Sandy Neosol	9.64851 S, 42.22878 W	411	644	24.6
9	Remanso	Segregated plants	Argisol	9.62291 S, 42.70718 W	439	644	24.6
10	Campo A. L.	Segregated plants	Argisol	9.49262 S, 43.16176 W	521	752	24.6

fix nitrogen, presence of thorns and/or spines and toxicity and/or urticancy. Nitrogen fixers were defined according to Sprent (2009), and all of the other traits were either observed during the field work or extracted from Soliveres et al. (2014).

Caatinga with segregated plants was chosen as control instead gaps between patches because almost all plants in gaps were gathered in small patches, with too few segregated plants (Table 1, Fig. 2).

In each of the ten study sites, a 20-m x 50-m plot was sampled. To compare species richness, phylogenetic diversity and community structure between segregated and patchy vegetation (aims iii and iv), all the angiosperm trees with stem circumferences equal to or greater than 10 cm (at ground level) and higher than 1 m were identified within the study plots. Furthermore, all smaller plants (i.e., individuals with diameter less than 3.18 cm at ground level or smaller than 1 m) in two 10-m x 10-m subplots arranged on two opposite plot corners, were sampled.

Individuals from all species were collected, in flowering or fruiting stages when possible, on first appearance during the surveys. The samples were treated according to conventional techniques before being deposited in the VIC Herbarium.

The identification of the botanical material was confirmed by comparison with specimens in the VIC and HUEFS Herbarium, and experts and specialized literature were consulted throughout the identification process. The classification of sampled species followed APG IV (The Angiosperm Phylogeny Group, 2016).

2.3. Richness, phylogenetic diversity and structure

All species found during the survey were inserted into the R20120829mod.new megatree (Gastauer and Meira-Neto, 2016) using the phylomatic function in the Phylocom-4.2 software package (Webb et al., 2002). The resulting phylogeny was calibrated based on node age estimates (Bell et al., 2010) using the 'bladj' algorithm embedded in Phylocom-4.2. The dated tree was pruned to the species occurring within the vegetation patches, and separate community trees were generated for the tree layer and the herbaceous layer in each test.

To determine the influence of the spatial configuration of the vegetation on species richness and phylogenetic diversity, individual-based accumulation curves were used to estimate species richness and phylogenetic diversity (Chao et al., 2015). Estimates for the effective number of species and their 95% confidence intervals were computed by rarefying and extrapolating species abundance data from plots using 'iNext' and 'iNextPD' in the iNEXT and iNextPD packages (Hsieh et al., 2015) in R Environment 3.1.0 (R Development Core Team, 2012).

To detect the phylogenetic community structures within distinct vegetation patches, the following parameters were computed: Faith's phylogenetic diversity - PD (Faith, 1992), the

mean pairwise distance - MPD, and the mean nearest taxon distance - MNTD (Webb et al., 2002). While MPD describes the entire phylogenetic structure of the community including deep evolutionary splits, the MNTD emphasizes more recent evolutionary events. The MPD and MNTD values were computed among different taxa as well as among individuals to obtain information about the structure of the entire community and the dominant species. Furthermore, the standard effect sizes (ses-transformations) of the indices PD, MPD and MNTD were calculated using the functions 'ses.mpd', 'ses.mntd' and 'ses.pd' from the picante package (Kembel, 2015). To do this, the community composition was randomized 10,000 times under the unconstrained null model so that all of the species that occurred at least once in a patch, plot or subplot had the same chance of entering randomized patches, plots or subplots. Positive values of the ses-transformed indices indicated phylogenetic overdispersion, while negative ones represented the coexistence of more phylogenetically related trees than expected by chance, i.e., phylogenetic clustering.

To test whether the ses-transformed index values were smaller than zero, i.e., demonstrate phylogenetic clustering, one-sided ttests were performed after testing and correcting for normality. Because the values of the ses. transformed indices may be negative or positive, we transformed all of the results into positive values by adding the largest absolute value to all of the computed values before carrying out a square-root or logarithmic transformation and then performing the tests using these corrected values.

To test if richness of herbaceous layer is different between Caatinga with segregated plants and patchy Caatinga in the 10-m x 10-m plots, we used generalized linear mixed models (GLMM) with the soil type as random variable, using the function 'glmer' of Lme4 package (Bates et al., 2014) in R statistical environment (R Development Core Team, 2012). Additionally, we used the GLMM with soil as random variable to test if decreased richness effects of standardized effect size (i.e., ses transformations) of PD, MPD and MNTD differed between Caatinga with segregated plants and patchy Caatinga. We repeated the same analyses for the tree layer sampled in the 20-m x 50-m plots.

3. Results

During the fieldwork, we identified 35 nurse species, five of which occurred with high frequency. The most common nurse species, i.e., species facilitating more than 10 patches each, were *Poincianella microphylla*, *Aspidosperma pyrifolium*, *Poincianella pyramidalis*, *Croton echioides* and *Tacinga palmadora* (Table 2).

Of the identified nurse species, 33 were phanerophytes; one was a camephyte; and one was a hemicryptophyte. Eighteen species were resprouters; nine had spines and/or thorns; five were urticant or toxic; and three were potentialy able to fix nitrogen due to associations with rhizobia. Sixteen species were autochoric; 13 were

Table 2

Species identified as potential nurse species. Life form according to Raunkiaer (1934), dispersal mode (Disp), ability to fix N₂ (N₂ Fix) according to Sprent (2009), presence of spines and/or thorns, presence of toxicity and/or urticancy (Tox./Urtic.) and number of patches facilitated by the nurse plants (n^o patches). PHAN is phanerophyte, CAM is camephyte and HEM is hemicryptophyte. ZOO is zoochoric species, ANE is anemochoric species and AUT is autochoric species. Those potential nurse species found in more than 10 patches across the study sites are indicated in bold.

Family	Species	Life Form	Disp	Resp	N ₂ Fix	Spines/thorns	Tox./Urtic.	n ^o patches
Acanthaceae	Harpochilus neesianus Mart. ex Nees	CAM	AUT	х				3
Annonaceae	Annona spinescens Mart.	PHAN	Z00			Х		2
Apocynaceae	Aspidosperma pyrifolium Mart.	PHAN	ANE	Х			Х	22
Bromeliaceae	Bromelia laciniosa Mart. ex Schult. & Schult.f.	HEM	Z00			Х		1
Burseraceae	Commiphora leptophloeos (Mart.) J.B.Gillett	PHAN	Z00					5
Cactaceae	Cereus jamacaru DC.	PHAN	Z00			Х		2
Cactaceae	Pilosocereus gounellei (F.A.C. Weber ex K. Schum.) Byles & G.D. Rowley	PHAN	Z00			Х		1
Cactaceae	Pilosocereus tuberculatus (Werderm.) Byles & G.D. Rowley	PHAN	Z00			Х		2
Cactaceae	Tacinga palmadora (Britton & Rose) N.P. Taylor & Stuppy	PHAN	Z00			Х		12
Capparaceae	Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	PHAN	Z00	Х				6
Euphorbiaceae	Acalypha brasiliensis Müll.Arg.	PHAN	AUT	Х				1
Euphorbiaceae	Cnidoscolus pubescens Pohl	PHAN	AUT	Х			Х	6
Euphorbiaceae	Cnidoscolus quercifolius Pohl	PHAN	AUT	Х			Х	1
Euphorbiaceae	Croton blanchetianus Baill.	PHAN	AUT	Х				7
Euphorbiaceae	Croton echioides Baill.	PHAN	AUT	Х				14
Euphorbiaceae	Croton grewioides Baill.	PHAN	AUT	Х				1
Euphorbiaceae	Jatropha mollissima (Pohl) Baill.	PHAN	AUT				Х	1
Euphorbiaceae	Jatropha mutabilis (Pohl) Baill.	PHAN	AUT				Х	9
Fabaceae	Calliandra depauperata Benth.	PHAN	AUT		Х	Х		4
Fabaceae	Copaifera martii Hayne	PHAN	Z00					3
Fabaceae	Cratylia mollis Benth.	PHAN	AUT	Х	Х			1
Fabaceae	Dahlstedtia araripensis (Benth.) M.J. Silva & A.M.G. Azevedo	PHAN	ANE	Х	Х			1
Fabaceae	Guibourtia hymenaeifolia (Moric.) J. Léonard	PHAN	ANE					3
Fabaceae	Pityrocarpa moniliformis (Benth.) Luckow & R. W. Jobson	PHAN	AUT					4
Fabaceae	Poincianella microphylla (Mart. ex G. Don) L.P. Queiroz	PHAN	AUT	Х				46
Fabaceae	Poincianella pyramidalis (Tul.) L.P. Queiroz	PHAN	AUT	Х				17
Fabaceae	Trischidium molle (Benth.) H.E. Ireland	PHAN	AUT	Х				2
Malpighiaceae	Banisteriopsis sp.	PHAN	ANE					2
Malpighiaceae	Byrsonima vacciniifolia A. Juss.	PHAN	Z00	Х				4
Malpighiaceae	Ptilochaeta sp.	PHAN	ANE	Х				2
Malvaceae	Pavonia glazioviana Gürke	PHAN	AUT	Х				5
Rhamnaceae	Ziziphus joazeiro Mart.	PHAN	Z00	Х		Х		1
Rubiaceae	Cordiera sp.	PHAN	Z00					1
Rutaceae	Balfourodendron molle (Miq.) Pirani	PHAN	ANE					5
Ximeniaceae	Ximenia americana L.	PHAN	Z00	Х		Х		1

zoochoric; and four were anemochoric. Nine species were Fabaceae; eight were Euphorbiaceae; four were Cactaceae; three were Malpighiaceae; and one nurse species belonged to each of the other families (Table 2).

Of a total of 196 individual nurse plants censused during the study, 141 (72%) were resprouters; 39 (20%) were urticant and/or toxic; 28 (14%) had spines and/or thorns; 6 (3%) were potential nitrogen fixers; 122 (62%) were autochoric; 41 (21%) were zoo-choric; and 33 (17%) were anemochoric (Table 2).

Individual-based rarefactions showed that both species richness and phylogenetic diversity of the herbaceous layer in patchy Caatinga were higher than in Caatinga with segregated plants. The species richness of the tree layer in patchy Caatinga was not significantly higher than in Caatinga with segregated plants. The phylogenetic diversity of the tree layer followed the same trend (Fig. 3).

A total of 2446 trees from 100 species were recorded in the 20m x 50-m pots, with a species composition that corresponded to a phylogenetic diversity of 4936 Myr (Table S1 from the Electronic Supplementary Material, hereafter ESM). Furthermore, 332 individuals were sampled from the herbaceous layer vegetation, belonging to 70 species, with a species composition representing 3603 Myr of phylogenetic diversity (Table S2).

From all 196 patches censused in this study, 4789 individuals belonging to 118 species from 38 families were found (Table S3 from ESM). The number of species per patch ranged from two to 18 for an average of 6.4. Among the different taxa within the Caatinga patches, the computed ses. MPD and ses. PD were greater

than zero (Fig. 4), while the ses. MNTD between taxa was not significantly different. Additionally, the ses. MPD and ses. MNTD computed among different individuals were both greater than zero (ESM Fig. S1). Therefore, the Caatinga patches were predominantly overdispersed and were not phylogenetically clustered.

Using the soil type as random factor, species richness of the herbaceous layer is higher in patchy Caatinga than in Caatinga with segregated plants. On contrast, ses. PD, ses. NRI and ses. NTI did not differ (Fig. 5). The tree layer does not differ in terms of richness, ses. PD, ses. NRI and ses. NTI (results not shown).

4. Discussion

The results from this study suggest plant-plant facilitation may be a driver of community assembly in Caatinga, and this is supported by the higher herbaceous richness in patchy Caatinga than in Caatinga with segregated plants. The phylogenetic diversity of the herbaceous layer in the patchy Caatinga is higher than Caatinga with segregated plants as an effect of the increased richness. Additionally, phylogenetic overdispersion is found in patches of patchy Caatinga. Those results are consistent with a facilitation scenario in which nurse plants favor species with distinct functional traits that are conserved within evolutionary lineages (Cavender-Bares et al., 2009; Valiente-Banuet and Verdú, 2013).

Almost all nurse plants were woody phanerophytes. More than 70% of the nurse plants and the four most common nurse species were resprouters, suggesting that the resilience promoted by resprouting (Meira-Neto et al., 2011; Pausas and Verdú, 2005) is an

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Fig. 3. Species richness and phylogenetic diversity of the tree and herbaceous layer layers of patchy Caatinga and Caatinga with segregated plants. Continuous lines are values interpolated from data, whereas dashed lines represent extrapolated data. Colored areas represent 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 4. Box-and-whisker plots of phylogenetic structure and diversity of Caatinga patches: standard effect sizes of the indices Mean Pairwise Distance (ses.MPD), Mean Nearest Taxon Distance (ses.MNTD) and Phylogenetic Diversity (ses.PD) calculated between different taxa from 196 Caatinga patches of patchy Caatinga, including the tree layer and herbaceous layer together. P-values indicate the level of significance at which the mean are larger than zero according to a one-tailed t-test; i.e., showing phylogenetic overdispersion. Points are outliers.

important functional trait that enables facilitation to occur in patchy Caatinga. Resprouting is considered the most important characteristic of resilience in woody plants in terrestrial ecosystems with fire disturbance regimes (Trabaud and Lepart, 1981). However, fire is not a widespread disturbance factor in Caatinga due to the absence of a continuous grassy layer, in contrast to tropical savannas (Simon et al., 2009), and the lack of fuel accumulation, in contrast to Mediterranean ecosystems (Trabaud and Lepart, 1981). Instead, herbivory by goats, sheep and cattle seems to be the most widespread disturbance factor in Caatinga (Vasconcelos et al., 2010) and has been observed in all sites of this study. The ability to resprout promotes shading more effectively than the germination response in bare soil following a disturbance (Pausas and Keeley, 2014). In addition to resilience in the form of resprouting after herbivory, resistance against herbivory is also important, as 19% of the nurse plants in this study were urticant and/or toxic and 14% had spines and/or thorns. Resistance and resilience are key responses that promote ecosystem stability (Mori, 2016) and play a central role in patchy Caatinga, so these functional traits are essential to promote facilitation among plants in Caatinga.

The four most frequent nurse species exhibit abiotic dispersal mechanisms; three are autochoric, and one is anemochoric. Of the 196 censused nurse plants, 61% are autochoric; 16% are anemochoric (77% have abiotic dispersal); and 20% are zoochoric. Therefore, abiotic dispersal, especially autochory, seems to be important for nursing in Caatinga because it occurred at a higher proportion (77%) in the patchy Caatinga than the 64% that has been

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Fig. 5. Box-and-whisker plots of species richness, standard effect sizes of the indices Phylogenetic Diversity (ses.PD), Mean Pairwise Distance (ses.MPD), and Mean Nearest Taxon Distance (ses.MNTD) on the herbaceous community within the 10-m x 10-m plots of Caatinga with segregated plants (Segregated) and patchy Caatinga (Patchy). P-values indicate the significance between differences of Segregated and Patchy means calculated by GLMM. Points are outliers.

reported for Caatinga in general (Griz and Machado, 2001). The observations that plants are clumped in patchy Caatinga and that autochory is the dispersal mechanism in 61% of nurse plants demonstrates an association between clumping and autochory, which disperses in shorter distances compared to zoochory and anemochory (Muller-Landau et al., 2008). The occurrence of autochory with secondary myrmecochory under a facilitation scenario in clumped Caatinga (Vasconcelos et al., 2010) would be an interesting research topic as ants may play an important role in seed dispersal in Euphorbiaceae, one of the two richest families among the nurse plants in this study.

In patchy Caatinga, the whole community is phylogenetically overdispersed in terms of standard effect size of Mean Pairwise Distance. This result suggests that plants within patches coexisting with nurse plants are less closely related than the null expectations within the metacommunity formed by all sampled species of this study, suggesting less niche overlap when and where functional traits are conserved within evolutionary lineages. Although the phylogenetic signal of the ecological niches within the Caatinga species pool has not yet been studied, the phylogenetic overdispersion observed might be due to trait conservatism within the evolutionary lineages. Findings of niche conservatism in plant communities of other arid and semi-arid regions, such as the desert near Puebla in Mexico (Valiente-Banuet and Verdú, 2007), the Mediterranean shrublands (Valiente-Banuet and Verdú, 2013) and perennial Mediterranean pastures (Soliveres et al., 2012) show that the average phylogenetic distances between nurse plants and facilitated species are significantly greater than the null expectation. However, in this study, there were no differences between the ses-transformed phylogenetic structures of the patchy Caatinga and the Caatinga with segregated plants, despite differences in species richness. Competitive exclusion of close relatives (Fig. 1) might explain the absence of differences in ses-transformed phylogenetic diversity and phylogenetic structure as well as the lower herbaceous richness in Caatinga with segregated plants compared to patchy Caatinga.

The species richness results suggest that facilitation is a major assembly rule in patchy Caatinga. The increased species richness of the herbaceous layer in patchy Caatinga is consistent with the results of other studies that analyzed the effects of facilitation in patchy vegetation in harsh environments (Pistón et al., 2016). Furthermore, those results are congruent to the increased herbaceous richness that has been found in other patches of Caatinga and also interpreted as a result of facilitation (Silva et al., 2015). Our results not only suggest that facilitation increases herbaceous richness in Caatinga but also that the plant communities within patches are more phylogenetically overdispersed in patchy Caatinga than the null expectations for the whole community.

The increased richness of herbaceous layer as well as the phylogenetic overdispersion of whole community in patchy 8

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Caatinga, compared to null expectations for the metacommunity, may be explained by niche diversification caused by facilitation (Valiente-Banuet and Verdú, 2013). This diversification might be due to increased environmental variation through shading, nutrient accumulation, reduced evapotranspiration and altered soil and air temperatures. As general trend, there is a buffering effect against severe environmental conditions in facilitation patches, even when environmental conditions become harsher (Pistón et al., 2016). Therefore, the higher species richness in herbaceous layer and phylogenetic overdispersion in patchy Caatinga suggest that facilitation enhances environmental conditions and niche diversification for the herbaceous layer of patchy Caatinga.

As our methods considered the highest plants in each patch as nurse plants, some primary nurse species might be underscored in number of facilitated patches. Thus, an interesting nurse species that deserves further attention is *Calliandra depauperata*, a small nitrogen-fixing and autochoric shrub with canopies forming cushions, a common plant architecture associated with facilitation (Butterfield et al., 2013).

The potential application of knowledge about facilitation to Caatinga restoration is promising (Moura et al., 2013), especially in the context of early succession. For instance, gypsite mining is an important economic activity in the Caatinga region, but studies of facilitation in association with succession are still lacking. Future research should link sterile gypsite application techniques in the region with facilitation information to restore gypsite quarries under the harsh environmental conditions of the Caatinga. Caatinga restoration remains an unexplored field of study in contrast to other, better-known arid ecosystems (Matesanz and Valladares, 2007). As facilitation studies in Caatinga are still incipient, there is an information gap about the effects of potential nurse species on essential factors in order to select candidates for ecological restoration. Studies about the effects of nurse species on abiotic factors (e.g., temperature, shading, humidity and mineral nutrients), on biotic factors (e.g., soil organic carbon, soil organic nitrogen, microbial activity, microbial diversity) as well as on ecological interactions (e.g., micorrhyzal associations, nitrogen fixation, dispersion, pollination, herbivory) would be fundamental to restore Caatinga disturbed areas.

The role of facilitation in the Caatinga does not seem critical only for ecological restoration. Northeastern Brazil is experiencing increasing aridity and temperature, according to most predictive models (IPCC, 2013). Despite the environmental amelioration promoted by facilitation (Pistón et al., 2016), patches in arid and semiarid environments might shift from facilitation to competition (Jankju, 2013), and, as a consequence, to competitive exclusion under extreme conditions. We still do not know the thresholds between facilitation and competition caused by herbivory, anthropogenic disturbances and climate change in Caatinga. Those thresholds would indicate how much Caatinga is resistant and resilient to global changes.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2017.03.006.

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