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Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance

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Summary

1. Tropical plant assemblages can be taxonomically and phylogenetically impoverished by chronic anthropogenic disturbance (CAD), such as firewood collection and extensive grazing. However, to what extent the functional dimension responds to CAD is still unclear. Such knowledge is urgently required for predicting, preventing or even reversing the impacts of CAD.

2. CAD may operate as an ecological filter by selecting functional trait values (e.g. low wood density), thereby altering the functional composition and diversity of plant assemblages. We tested this hypothesis using 29 woody plant assemblages across three ontogenetic stages (seedlings, saplings and adults) in a 220-km² landscape of the Caatinga, northeast Brazil. We adopted a CAD index consisting of four indicators (proximity to urban centre and houses, and the density of both people and livestock) and tested how well it explained functional diversity and effect sizes (richness, evenness and dispersion) and composition (community-weighted mean).
3. CAD affected several functional metrics across the three ontogenetic stages. However, CAD effects were stronger in adult communities by negatively affecting functional richness, dispersion and their effect sizes. CAD also altered the functional composition of leaf mass per area, woody density and leaf area of adult assemblages. Sapling communities were affected in terms of functional composition (leaf area, leaf dry matter and wood density), with positive and negative effects, while seedling assemblages responded positively to CAD only in terms of functional evenness and its effect size. Some changes in functional metrics were influenced by dominant Euphorbiaceae species across ontogenetic stages, especially in terms of leaf area and woody density.

4. Synthesis. CAD is an important driver of plant-community functional organization across ontogenetic stages in the Caatinga. Adult assemblages are particularly sensitive and tend to lose functional niche space and support more acquisitive rather than conservative strategies as CAD increases. The proliferation of Euphorbiaceae disturbance-adapted species can explain part of the community responses to CAD. Our findings highlight the ecological effects of CAD and show that it is a key influence on tropical biotas. Changes in plant functional traits associated with plant resource use is likely to affect ecosystem functioning and services provided by Caatinga.

Key-words: biodiversity loss, community assembly, functional plant traits, human disturbance, seasonally dry tropical forest, semi-arid ecosystem, wood plant assemblages.

Introduction

Chronic anthropogenic disturbance (CAD) is characterized by the continuous and gradual removal of small portions of forest biomass (e.g. frequent collection of firewood, exploitation of non-timber forest products, and extensive grazing by livestock), which, at low intensities,
is quite cryptic and difficult to detect (Singh, 1998). However, CAD represents a geographically widespread threat to tropical biodiversity, especially in areas where there are dense, forest-dependent human populations (Forest Peoples Programme, 2012). Although millions of livelihoods across the tropics are dependent on activities that contribute to CAD, its effects on tropical biotas are still poorly known, limiting our ability to propose conciliatory strategies for forest use and biodiversity conservation (Singh, Rawat, & Garkoti 1997; Schmidt & Ticktin, 2012). In this context, seasonally dry tropical forests (SDTFs) could be considered more vulnerable to CAD due to their lower productivity (e.g. 6-16 t/ha/yr, Murphy & Lugo, 1986) and the regeneration of the extant vegetation occurs almost exclusively during the wet season (Ray & Brown, 1994). In fact, recent studies have demonstrated that CAD in SDTFs causes negative impacts at the community level, such as biological impoverishment and biotic homogenization, particularly at the taxonomic level (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015; Ribeiro-Neto, Arnan, Tabarelli, & Leal 2016; Schulz et al., 2016; Rito, Tabarelli & Leal 2017).

Potentially, one of the major processes leading to community-level responses to disturbance are biological invasions, such as those by the exotic species Lantana camara L. in some forests in India (Sundaram & Hiremath, 2012), where CAD were the main cause of community-level reorganization; i.e. classical winner-loser replacement as proposed by McKinney and Lockwood (1999). However, the replacement of a diverse group of native disturbance-sensitive species by a less diverse group of disturbance-adapted native species has also been documented (Ribeiro-Neto, Arnan, Tabarelli & Leal, 2016), i.e. a native-driven winner-loser replacement sensu Tabarelli, Peres and Melo (2012). One example of such a winner group is the Euphorbiaceae family, as some species are considered aggressive colonizers of human-disturbed patches of vegetation, leading to shifts in community
taxonomic composition and even floristic homogenization (Carvalho, Araújo-Filho, Garcia, Pereira-Filho, & Albuquerque 2001; Rito, Tabarelli, & Leal 2017). For instance, increments in the abundance of *Jatropha mollisima* (Pohl) Baill. and *Croton sonderianus* Muell. Arg. (Euphorbiaceae) were paralleled by a decline in the abundance of disturbance-sensitive species such as the long-lived tree species *Fraunhofera multiflora* Mart. (Celastraceae), *Bauhinia cheilantha* (Bong.) Steud. (Fabaceae) and *Myracrodruon urundeuva* Fr. All. (Anacardiaceae) at most disturbed sites in a Brazilian SDTF (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015; Ribeiro-Neto, Arnan, Tabarelli, & Leal 2016; Rito, Tabarelli, & Leal 2017). Although some studies suggest that CAD has weak effects on plant functional diversity and composition (Mandle & Thicktin, 2015; Carreño-Rocabado et al., 2016), a consensus on this topic is still to emerge, which may be particularly challenging for SDTFs considering their myriad of physiognomies exposed to forest-dependent people. CAD effects at the community level have not only theoretical implications in relation to the drivers of species assembly (see review by Cavender-Bares, Kozak, Fine, & Kembel 2009), but also applied implications relative to ecosystem functioning, forest resilience and the provision of ecosystem services because community-level changes usually have cascading effects on ecosystem functioning such as patterns of carbon storage (Conti & Díaz, 2013; Mandle & Thicktin, 2015; Prado-Junior et al., 2016).

The Caatinga stretches over 912,529 km² of northeast Brazil and is considered the largest SDTF in the neotropics (Silva, Leal, & Tabarelli 2017). It has also been recognized as the most species-rich neotropical SDTF, supporting 950 genera, 3,150 species and 152 families of flowering plants; one third of which are endemic to the Caatinga (Queiroz, Cardoso, Fernandez, & Moro 2017). The Caatinga is also the most populated semiarid region globally, with 26 habitants per square kilometre (INSA, 2012). Similar to other SDTFs, Caatinga landscapes are dominated by family farms, for which the forest provides key
products and services for their livelihoods such as firewood, timber, forage for livestock, potable water and new sites for agriculture after forest slash-and-burn agriculture (Ramos, Medeiros, Almeida, Feliciano, & Albuquerque 2008; Albuquerque, Araújo, Castro, & Alves 2017). Thus, the Caatinga dry forest offers an interesting opportunity to assess how CAD affects the organization of biodiversity in STDFs at several ecological levels (from population to ecosystem) and the potential impacts on forest resilience and the livelihoods of local human populations (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli & Leal, 2015).

Here, we examine whether CAD can operate as an ecological filter by selecting a subset of functional trait values, thereby limiting/altering the functional diversity and composition of plant assemblages. We tested this hypothesis using 29 woody plant communities across three ontogenetic stages (seedlings, saplings and adults) in a 220-km² human-modified landscape of the Caatinga dry forest. We estimated CAD, using an index based on four chronic disturbance indicators (such as proximity to urban centre and houses, human population density and livestock density), and a wide set of functional diversity/composition metrics for each plant community based on four leaf traits (leaf area, leaf mass per area, leaf thickness and leaf dry matter), one stem trait (wood density), and two whole-plant traits (deciduousness and dispersal syndrome, Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter 2010), which have been proposed to be related to plant resource-use strategies (Chave et al., 2009; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter 2010).

In our focal landscape, some plant traits selected by local people are phylogenetically conserved (e.g. wood density; Chave et al., 2006) and often represent a mirror for leaf trait composition along the acquisitive-conservative resource-use spectrum exhibited by plants such as wood density (Reich, 2014; Díaz et al., 2015). Moreover, the continuous exploitation of hard-wood adults might reduce seed input, leading to an underrepresentation of
conservative species in sapling and seedling assemblages (Singh, Rawat, & Garkoti 1997). Finally, CAD is expected to create more open and illuminated habitats (Sundaram & Hiremath, 2012), likely favouring light-demanding, competitive species and their acquisitive leaf traits, such as low leaf mass per area, thin leaves, low dry matter content, and large leaf area. This is particularly true for some dominant species from the Euphorbiaceae family (Neves, Funch, & Viana 2010; Rito, Tabarelli, & Leal 2017), which have been documented to proliferate in response to CAD in the same Caatinga landscapes (Rito, Tabarelli, & Leal 2017). We thus expected CAD to reduce functional diversity and change functional composition towards more acquisitive strategies or trait values, with dominant Euphorbiaceae relative abundance expected to influence most community-level functional changes.

Materials and methods

STUDY AREA

This study was carried out in a 220-km² human-modified landscape covered by the Caatinga dry forest, in northeast Brazil (8°5’26’’ S; 39°34’ 41’’ W; Fig. 1). The local climate is classified as tropical semi-arid (BSh’w by the Köppen system), with average annual rainfall of 431 mm and temperature of 26°C (CPRM 2005). Soils are predominantly non-calcic brown soils (clay soil), regosols and planosols (sandy soils) (IBGE, 1985). The Caatinga dry forest in this landscape is considered hyper-xerophytic, consisting of small trees and shrubs, with an annual herbaceous layer during the four-month rainy season (from January to April; Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015). Since the 16th century, forest in our focal landscape has been converted for agricultural purposes, with only c. 45% of the original forest cover remaining (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015). The remaining forest is exposed to CAD, such as extraction of forest products for medicine,
food, firewood collection and grazing by livestock (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015).

**CHRONIC ANTHROPOGENIC DISTURBANCE INDEX**

We established 29 50 x 20-m plots in a 220-km² landscape (Figure 1) that is exposed to CAD and has no sign of prior clear cutting. Plots were placed at least 300 m apart (μ = 7269 m ± 4632 m) and located across flat lands exposed to the same level of precipitation, geomorphological basement (crystalline) and soil type group (intermediate levels of clay content) in order to control baseline variables. Four indicators of CAD (Sagar, Raghubanshi, & Singh 2003; Martorell & Peters, 2005; Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015) were recorded in each plot as follow: (i) proximity to the nearest house; (ii) proximity to the nearest urban centre; (iii) density of people living near the plot; and (iv) density of livestock. For more information about how these indicators may affect plant diversity, see Table S1. We opted for proxies instead of direct measures of logging, hunting, fuel-wood harvesting and overgrazing because these disturbances are not easily quantified at the landscape scale (Acharya & Dangi, 2009). Moreover, the indicators we adopted have been demonstrated to impact taxonomic (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015; Ribeiro-Neto, Arnan, Tabarelli, & Leal 2016; Rito, Arroyo-Rodríguez, de Queiroz, Leal, & Tabarelli 2017) and phylogenetic (Ribeiro et al., 2016) diversity of plant assemblages in the Caatinga.

Proximity to the nearest house and urban centre was considered as the reciprocal distance from the centre of each plot using satellite imagery from the Advanced Land Observing Satellite (ALOS). To estimate the density of people and livestock near each plot, we first identified all active dwellings in the focal region via ALOS satellite imagery. We

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visited the dwellings and, through 40 interviews, we collected data on the number of inhabitants and the number of domestic animals (livestock) managed by each household. To estimate the density of people and livestock near each plot we took a 2-km radius around the centre of each plot and summed the numbers of inhabitants and livestock that fell within this buffer (i.e. within an area of 1256 ha; see Fig. 1). According to the local household representatives, this 2-km radius encompasses the maximum walking distance of grazing animals.

Following Martorell and Peters (2005) and Ribeiro et al. (2016), we collapsed the four chronic disturbance indicators into a single disturbance index through a principal component analysis (PCA; see Appendix S1), using the package ‘stats’ for R (R core Team 2017). The CAD index was based on the scores of the first PCA axis, which explained 50.2% of the variation of these indicators and was positively and significantly correlated with the density of people and of livestock, and the proximity to the nearest urban centre (mean correlation coefficients: \( r = 0.69, P < 0.05 \)). The CAD index was rescaled from 0 to 100, representing the least and most disturbed sites, respectively (Martorell & Peters, 2005; Ribeiro et al., 2016). This approach offers an accurate/feasible descriptor of CAD in the region as previously demonstrated (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015).

PLANT COMMUNITY SAMPLING

Adult plants (diameter at soil height > 3 cm and height > 1.5 m; Rodal, Sampaio, & Figueiredo 1992) were recorded across the whole plot. Saplings (diameter at soil height, DSH < 3 cm and height between 1 and 1.5 m) were recorded in three 5 × 5-m subplots (75 m²) located in the centre of each 50 × 20-m plot and separated by 10 m. Seedlings (height < 1 m) of woody species were recorded in three 2 × 2-m subplots (12 m²) located in the centre of each 5 × 5-m sapling subplot. All plant ontogenetic stages were sampled during the rainy...
seasons of 2012 and 2013. We identified all plants to species level by comparing the sampled species with samples from the Federal University of Pernambuco herbarium.

FUNCTIONAL TRAITS AND METRICS

A total of 51 woody plant were recorded across the 29 plots. For 48 species (excluding three Cactaceae species) we measured four leaf traits [leaf area (cm²); leaf mass per area (mg cm⁻²); leaf dry matter content (mg g⁻¹) and leaf thickness (mm)], one stem trait [wood density (g cm⁻³)], one whole-plant trait [deciduousness (0 = evergreen; 1 = deciduous)] and one regenerative trait [dispersal syndrome (0 = abiotic; 1 = biotic)]. We selected these traits because they provide valuable information about plant resources-use strategies that may be related to changes caused by disturbance. For example, leaf mass per area reflects leaf construction costs per unit leaf area (Westoby & Wright, 2006), while leaf thickness is related to sensitivity to heat and drought (Pérez-Harguindeguy et al., 2013) and leaf dry matter content reflects ability to conserve nutrients and resistance to herbivores (Hodgson et al., 2011). Wood density indicates mechanical strength and drought resistance (Chave et al., 2009), and deciduousness, reflecting whether leaves are shed during dry periods—which is an important indicator of drought resistance (Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter 2010). Biotic dispersal is related to the investment in fleshy fruits that attract local fauna (Eriksson, 2008). For more information about the adopted traits and their ecological meaning see Appendix S2.

We measured traits exclusively for adult individuals following standard protocols (Pérez-Harguindeguy et al., 2013). We adopted the mean trait value of adults for saplings and seedlings to have a species value across all ontogenetic stages as there is no evidence for considerable cross-ontogenetic variation in trait values for the Caatinga flora. Trait data was locally measured and some were obtained from several publications (e.g. wood density,
deciduousness and biotic dispersal; see trait values recorded for each species and publications consulted in Ribeiro et al., 2018 database in Data Accessibility section). Leaf traits were recorded on randomly selected fully expanded leaves from branches at a height of 1.5 m from at least five adult individuals. Stem traits were measured on the same individuals. We considered deciduousness as a binary variable because information about leaf phenology as a continuous measure is scarce and hard to collect. We thus considered species that lose their leaves in the dry season as deciduous and those that maintain their leaves throughout the year as evergreen. We are aware that species intraspecific variation would play an important role in species adaptation along disturbance gradients such as that in our focal landscape. Sfair, de Bello, França, Baldauf & Tabarelli (2017) recently documented that CAD explains a considerable amount of trait intraspecific variation for some species in the Caatinga dry forest. However, due to logistic limitations, we have not considered intraspecific variation and have adopted average trait values in our analyses (Rozendaal, Hurtado, & Poorter 2006).

Three multi-trait functional diversity indices (functional richness, functional evenness and functional dispersion) and single-trait community-weighted means based on each of the traits mentioned above were estimated for the 29 communities (Villéger, Mason, & Mouillot 2008). The three multi-trait functional indexes are based on a functional trait space approach, which considers the position occupied by a species in functional trait space (Villéger, Mason, & Mouillot 2008). Functional richness (FRic) represents the amount of functional space filled by the community; in multi-trait studies it corresponds to the volume of a multidimensional space filled by the focal community (Villéger, Mason, & Mouillot 2008; Laliberté, Legendre, Shipley, & Laliberté 2014). Lower FRic values indicate less niche space occupied and environmental filtering (Mouchet, Villéger, Mason, & Mouillot 2010). Functional evenness (FEve) illustrates the evenness of abundances in functional trait space (Mason, de Bello, Mouillot, Pavoine, & Dray 2013). Small values of FEve indicate that some parts of the
functional trait space are unevenly occupied and underutilized (Mason, de Bello, Mouillot, Pavoine, & Dray 2013). Functional dispersion (FDis) describes the average functional distance between the species and is calculated as the mean distance of a species to the centroid of all species in multi-dimensional space (Laliberté & Legendre, 2010). FDis is recommended to analyse patterns of trait convergence and divergence, and small values of this metric suggest greater influences from environmental filtering (Ricotta & Moretti, 2011).

As two of our variables (deciduousness and dispersal syndrome) are binary, we calculated distances between species using the Gower dissimilarity index (Laliberté & Legendre, 2010). To compute FEve and FDis values, species abundances were included as a weighting factor. The community-weighted mean (CWM) is a metric of functional composition that represents the mean of species trait values weighted by their relative abundance; often understood as the dominant trait value in a community (Laliberté, Legendre, Shipley, & Laliberté 2014). According to Ricotta and Moretti (2011), this metric can be adequately used to summarize shifts in mean trait values within communities due to environmental filtering.

To infer the presence of environmental filtering in the most disturbed sites and remove potential effects of species richness, a null model was adopted, and the values contrasted with the observed functional diversity metrics (FRic, FEve and FDis). We used the independent swap null model to randomize our community data matrix, maintaining total species occurrence across all plots in the study and site richness (Kembel et al., 2016). This method is recommended for measuring alpha functional diversity indices (Swenson, 2014), and is useful for detecting environmental filtering (Götzenberger et al., 2016). First we replicated the null model function 999 times, and latter combined the observed output with these 999 random values per community (Swenson, 2014). We quantified the standardized effect size (SES) for each functional diversity metric by the subtracting null distribution means from the observed value and dividing them by the standard deviation of the null
distribution (Swenson, 2014) for both the observed and null model values. Positive SES values indicate that the observed value is higher than the average random expectation and thus community is more diverse than the randomly generated communities, while negative values indicate the opposite (Swenson 2014). Functional diversity indices and CWM were obtained using the package ‘FD’, and null model analyses were done using the ‘picante’ package for R (R core Team 2017).

DATA ANALYSIS

Multiple linear regression models were adopted to examine the relationship between the CAD index and each observed functional metric (FRic, FEve, FDis and CWM) and the standardized effect size of functional diversity (FRic, FEve and FDis) across the three ontogenetic stages. To infer the underlying mechanisms of functional changes, we included in these models the relative abundance of the most dominant species from the Euphorbiaceae family as a predictor variable — Croton sonderianus, Cnidoscolus quercifolius Pohl, Jatropha mollissima and Jatropha ribifolia — as these species have been considered aggressive colonizers on human-modified landscapes of the Caatinga dry forest (Carvalho, Araújo-Filho, Garcia, Pereira-Filho, & Albuquerque 2001; Rito, Tabarelli, & Leal 2017). Analyses were done separately for all ontogenetic stages. All statistics were performed in R using the package ‘stats’ (R core Team 2017). For all response variable errors we confirmed normality with Shapiro-Wilk tests. As suggested by Kissling and Karl (2008), we tested whether our model errors presented autocorrelation at short spatial distances using the ‘nfc’ and ‘spdep’ packages for R (R core Team 2017). For these analyses, we adopted 20 lag-distance classes, searched for significant values of spatial autocorrelation (p values > 0.05) and observed Moran I correlograms (Kissling & Karl, 2008). Spatial autocorrelation was not
observed in the errors of any of our models, confirming that our plots can be considered as independent replicates.

**Results**

A total of 10,260 adult plants belonging to 48 species, and 716 saplings and 257 seedlings belonging to 40 species were recorded across the 29 plots. Communities of all ontogenetic stages exhibited large variations in functional diversity and functional composition metrics across all plots (Table S2). However, the way communities responded to CAD varied according to ontogenetic stage. For adults, CAD was responsible for changes in two out of three functional diversity metrics, and three out of seven functional composition metrics (CWMs) (Table 1). More specifically, CAD had a negative impact on functional richness and dispersion and community-weighted mean leaf mass per area and wood density, while at the same time having a positive impact on community-weighted mean leaf area (Table 1; Fig. 2). Effect sizes of functional richness and dispersion were also negatively affected by disturbance (Table 1; Fig. 2). These sets of responses/effects indicated a reduction in functional trait space, underdispersion of functional traits and shifts in functional composition towards more acquisitive trait strategies for adult communities in more disturbed sites.

The effect of CAD on functional diversity and composition of saplings and seedling communities were generally weaker compared to adults, but with many similar responses (Table 1; Fig. 2). In the case of saplings, CAD negatively affected the effect sizes of functional dispersion, and wood density and leaf dry matter community-weighted means. However, leaf area community-weighted mean was positively affected by CAD (Table 1; Fig. 2). Seedling communities were only affected in terms of functional evenness, including its effect size, implying more regular distribution of species abundances and dissimilarities in
This response represented the major quantitative difference between adults and earlier ontogenetic stages.

The relative abundance of dominant Euphorbiaceae species accounted for 56.9% of all recorded individuals in adult plant assemblages, 53.3% and 52.1% for sapling and seedling communities, respectively, demonstrating the importance of this group in our studied flora. Across the three ontogenetic stages, the relative abundance of most dominant Euphorbiaceae was related positively with community-weighted mean of leaf area but negatively with wood density community-weighted mean (Table 1). Specifically in the case of adults and saplings, the relative abundance of most dominant Euphorbiaceae also caused a reduction in functional dispersion, while in seedling communities it was correlated positively with (1) the observed values of functional evenness, (2) the effect size of functional dispersion, and (3) community weighted leaf thickness (Table 1).

Discussion

Here, we assessed the effects of chronic anthropogenic disturbance (CAD) on functional diversity and composition of woody plant assemblages in the Caatinga dry forest—a species-rich (3150 species of flowering plants, of which 23% are endemic; Queiroz, Cardoso, Fernandez, & Moro 2017) and threatened seasonally dry tropical forest with 64% of its area composed by anthropogenic disturbed ecosystems (Silva, Leal, & Tabarelli 2017).

Our results suggest that CAD affects a wide spectrum of functional diversity and compositional traits of woody plant assemblages across multiple ontogenetic stages, with adults being the most sensitive and seedlings the least. Moreover, responses to CAD seem to be consistent across plant stages, particularly the responses exhibited by adult and sapling communities. In adults, CAD reduces functional richness and dispersion (i.e. functional impoverishment), while it benefits particular traits: plant assemblages subject to a higher
disturbance level tend to be dominated by individuals bearing a subset of trait values that
describe a more acquisitive resource-use strategy (e.g. softer wood, larger leaves and lower
leaf mass per area). Thus, CAD appears to favour a particular combination of traits (i.e. trait
replacement) or even a plant strategy in terms of resource use (i.e. water and nutrients). Such
a functional convergence is moderately influenced by the relative abundance of
Euphorbiaceae species (a locally dominant taxa), particularly in the case of leaf area and
wood density traits.

CAD (e.g. biomass extraction and livestock grazing) have already been documented
to alter the taxonomic and phylogenetic composition of woody plant assemblages in
seasonally dry tropical forests (e.g. Sagar, Raghubanshi, & Singh 2003; Ribeiro, Arroyo-
Rodríguez, Santos, Tabarelli, & Leal 2015; Ribeiro et al., 2016; Rito, Arroyo-Rodríguez, de
Queiroz, Leal, & Tabarelli 2017). However, few studies have examined the effect of CAD on
functional diversity/composition and potential cascades on ecosystem functioning (but see
Mandle & Thickett, 2015; Carreño-Rocabado et al., 2016; Sfair, de Bello, França, Baldauf &
Tabarelli 2017). Thus, we offer additional support for the notion that CAD can be an
important driver of species assembly and the structure/organization of native communities in
human-modified landscapes. In fact, we have expanded the relevance of CAD by
documenting its effects on the functional dimension of communities across multiple
ontogenetic stages. Briefly, CAD affects the assembly of woody plant species in the Caatinga
— from the early seedling stage of recruitment through the sapling and adult stages, with
increasingly pervasive effects (i.e. a higher number of affected attributes). Adult assemblages
(the most sensitive) lose functional diversity in terms of niche occupation (functional
richness) and divergence (functional dispersion), while they experience trait replacement
toward more acquisitive strategies — which is evidence of community-level convergence
(Ricota & Moreti, 2011).

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It is also worth mentioning that CAD effects documented in our focal landscape appear to be stronger than those documented for selectively logged semideciduous forests (Carreño-Rocabado et al., 2012) and for biomass extraction, livestock grazing and ground fires in tropical savannas (Mandle & Thicktin, 2015). Such differences in sensitivity to CAD might result from the biota exposure to previous disturbance. For instance, it is well-known that paleotropical biotas have had a longer history of CAD than Neotropical ones and thus effects of current disturbance are weaker because they have already reorganized themselves in response to CAD (Cole, Bhagwat, & Willis 2014; Mandle & Thicktin, 2015). Differences in CAD intensity among ecosystems can also explain contrasting findings in different studies. For instance, in a Bolivian semideciduous forest exposed to selective logging, few plant traits were affected by CAD (Carreño-Rocabado et al., 2012), while in Caatinga stands exposed to a suite of disturbances (from selective logging to browsing by livestock), several plant traits can be affected, as demonstrated here.

Although we did not explicitly address the baseline mechanisms for community-level changes in response to CAD and cross-ontogenetic state variation in our focal landscape, we can offer some working hypotheses. Overall, the mechanisms encompass both direct and indirect CAD effects on plant recruitment and mortality. We refer to population-level processes driven by changes in the physical environment imposing filters (as suggested by changes in functional diversity), with benefits some species, in addition to direct exploitation of plants by humans. Seedling recruitment, sapling and adult performance and plant trait expression may be affected due to increased abiotic stress under higher CAD levels (Singh, 1998; Sfair, de Bello, França, Baldauf & Tabarelli 2017). The continual removal of forest biomass in concert with other forms of chronic anthropogenic disturbances can alter vegetation structure (e.g. reduced stem density, increased canopy openness; Sagar, Raghubanshi, & Singh 2003; Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015) and
microclimatic conditions (e.g. drier and hotter environments with more degraded soils
Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter 2010; Lohbeck et al., 2013; Schulz et al., 2016). Although empirical evidence is still lacking, disturbed forest patches appear to be much more open and desiccated as compared to undisturbed ones (Sagar, Raghubanshi, & Singh 2003). These conditions can cause environmental filters that may limit the recruitment/reproduction of some plant functional groups (Endress, Gorchov, & Noble 2004), while other plant functional groups may experience increases in recruitment and performance across all ontogenetic stages; i.e. winner-loser replacement (Tabarelli, Peres, & Melo 2012).

In fact, some exotic and native species proliferate — due to decreased mortality and increased recruitment and growth — in disturbed hotter and drier habitats (Marvier, Kareiva, & Neubert 2004; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter 2010). This is the case for many native Euphorbiaceae species, such as Cnidoscolus quercifolius, Croton sonderianus, Jatropha mollissima and J. ribifolia, which usually proliferate in more disturbed sites in the Caatinga (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015; Ribeiro et al., 2016; Ribeiro-Neto et al., 2016; Rito, Tabarelli & Leal 2017) and can be defined as local winner species. By assessing the relationship between CAD, functional changes in plant community and the abundance of dominant Euphorbiaceae species we were able to confirm that Euphorbiaceae species proliferate in disturbed areas of the Caatinga (Ribeiro et al. 2016; Ribeiro-Neto, Arnan, Tabarelli, & Leal 2016; Rito, Tabarelli & Leal 2017), and that the dominance of these species impacts the functional composition of plant assemblages and their responses to CAD. Accordingly, these disturbance-adapted Euphorbiaceae species have low wood density (0.33 to 0.60 g cm⁻³) and large leaves (24.43 to 75.59 cm²; Ribeiro et al., 2018; see database in Data Accessibility section). Although large leaf area and low wood density are unexpected traits for hotter and drier habitats (Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter 2010; Lohbeck et al., 2013), in the Caatinga, euphors with these traits

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are able to store more water, initiate vegetative and reproductive phenophases during the dry season, and drop their leaves in the transition period between the rainy and dry seasons, thereby tolerating drought (Lima & Rodal, 2010). Proliferation of disturbance-adapted species benefiting from environmental changes in parallel to the filters imposed to other trait sets apparently constitutes one of the baseline mechanisms supporting community-level changes imposed by CAD.

In addition to environmental filters, overexploitation can result in population declines in target species (Marvier, Kareiva, & Neubert 2004; Goetsch, Wigg, Royo, Ristau, & Carson 2011; Ordonez et al., 2014). Species negatively affected by CAD, such as *Myracrodruon urundeuva*, show relatively higher wood density and smaller leaf area (0.97 g cm$^{-3}$ and 14.06 cm$^2$, see Ribeiro et al. 2018 database in Data Accessibility section). This implies that CAD favours a combination of acquisitive trait values (e.g. higher leaf area and softer wood), while disfavouring conservative trait values (i.e. lower leaf area and higher wood density, Chave et al., 2009; Reich, 2014). In addition to the general effects of CAD we have documented here, the combined effects of prolonged exposure to environmental filters plus direct plant exploitation by humans probably explain why adult communities are more sensitive and negatively affected by CAD, while seedlings exhibit slight but positive responses; i.e. intermediate disturbance increasing evenness as suggested elsewhere (Svensson, Lindgarth, Jonsson, & Pavia 2012; Rito, Arroyo-Rodríguez, de Queiroz, Leal, & Tabarelli 2017).

We thus argue that in the Caatinga dry forest, CAD reduces forest biomass, and favours disturbance-adapted species with acquisitive resource-use traits through soil and microclimate-mediated environmental filtering (Carreño-Rocabado et al., 2012). This is likely to operate in parallel with population decline among exploited species such as those with higher biofuel quality (e.g. high wood density and little wood water content; Ramos, Medeiros, Almeida, Feliciano, & Albuquerque 2008). This has been already documented in
our focal landscape (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal 2015; Ribeiro et al., 2016), and contributes to community-level functional changes. Direct exploitation can also be considered as a management filter, which operates according to human preferences (Ordonez et al., 2014) and may result in a complete functional reorganization of plant assemblages (Cadotte, Carscadden, & Mirochnick 2011) and affect ecosystem functioning. For example, the reduction of trees and shrubs with high wood density can affect ecosystem services, such as climate control by carbon storage and biomass productivity (Conti & Díaz, 2013; Prado-Junior et al., 2016). It also limits provisioning services such as wood used for firewood and poles (Ramos, Medeiros, Almeida, Feliciano, & Albuquerque 2008). Moreover, as species with acquisitive traits are more vulnerable to drought (Lopez-Iglesias, Villar, & Poorter 2014), shifts in functional composition may limit the resilience of the Caatinga ecosystem to increasing aridity predicted by climate change models (IPCC, 2014).

In synthesis, CAD can be considered one of the major drivers of plant species assembly and community organization in the Caatinga dry forest by causing functional impoverishment and convergence due to favouring/disfavouring different groups of species and trait values via a combination of both environmental and management filters. Furthermore, by favouring acquisitive trait values (e.g. soft wood, large leaves with low leaf mass per area), CAD is likely to alter patterns of ecosystem functioning, forest resilience and ecosystem services. Similar to the Caatinga, most of SDTFs are experiencing increasing levels of pressure by forest-dependent people and some of their biotas are considered extremely vulnerable to climate change (Tabarelli, Leal, Scarano, & Silva 2017). This reinforces the relevance and importance of a CAD research agenda, not only for the potential to address fundamental questions on community organization, but also questions on the drivers of forest dynamics and threats to sustainability in human-modified landscapes.
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Author Contributions

EMSR, ML, BAS, VAR, IRL and MT conceived the ideas and designed methodology. EMSR collected the data, analysed the data, and led the writing of the manuscript. All authors contributed critically to all drafts and gave final approval for publication.

Data accessibility

The database used in this study is available at Dryad Digital Repository http://dx.doi.org (Ribeiro et al. 2018).

References


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Table 1. Results of linear regressions evaluating the relationships between our chronic anthropogenic disturbance (CAD) index and observed values and standard effect sizes (SES) of functional diversity (richness, evenness and dispersion), and composition (CWM, community-weighted mean for seven different traits) of adult, sapling and seedling plant assemblages in the Brazilian Caatinga. D.f. = 1, 26 in all cases.

<table>
<thead>
<tr>
<th>Functional metrics</th>
<th>Chronic anthropogenic disturbance index</th>
<th>Relative abundance of dominant Euphorbiaceae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>T</td>
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<tr>
<td>Adults</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Functional richness</td>
<td>-0.180</td>
<td>-3.139</td>
</tr>
<tr>
<td>Functional evenness</td>
<td>-0.000</td>
<td>-1.157</td>
</tr>
<tr>
<td>Functional dispersion</td>
<td>-0.005</td>
<td>-2.406</td>
</tr>
<tr>
<td>SES.FUNCTIONAL richness</td>
<td>-0.075</td>
<td>-2.210</td>
</tr>
<tr>
<td>SES.FUNCTIONAL evenness</td>
<td>0.001</td>
<td>0.227</td>
</tr>
<tr>
<td>SES.FUNCTIONAL dispersion</td>
<td>-0.017</td>
<td>-2.478</td>
</tr>
<tr>
<td>CWM – Leaf mass per area (g cm²)</td>
<td>-0.001</td>
<td>-4.216</td>
</tr>
<tr>
<td>CWM – Leaf thickness (mm)</td>
<td>0.000</td>
<td>0.529</td>
</tr>
<tr>
<td>CWM – Leaf area (cm²)</td>
<td>0.074</td>
<td>4.786</td>
</tr>
<tr>
<td>CWM – Leaf dry matter content (g/g)</td>
<td>0.008</td>
<td>1.644</td>
</tr>
<tr>
<td>CWM – Wood density (g cm³)</td>
<td>-0.001</td>
<td>-2.610</td>
</tr>
<tr>
<td>CWM – Deciduousness</td>
<td>0.000</td>
<td>1.483</td>
</tr>
<tr>
<td>CWM – Biotic dispersal</td>
<td>0.001</td>
<td>0.897</td>
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### Saplings

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<tr>
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<tbody>
<tr>
<td>Functional richness</td>
<td>-0.049</td>
<td>-1.669</td>
<td>0.108</td>
<td>-8.891</td>
<td>-0.228</td>
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<tr>
<td>Functional evenness</td>
<td>0.000</td>
<td>0.578</td>
<td>0.568</td>
<td>-3.341</td>
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<td>1.671</td>
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<td>CWM – Leaf mass per area (g cm²)</td>
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<td>-0.110</td>
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<td>0.000</td>
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<td>0.016*</td>
<td>157.060</td>
<td>2.609</td>
<td>0.015*</td>
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<tr>
<td>CWM – Leaf dry matter content (g/g⁻¹)</td>
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<td>-2.191</td>
<td>0.038*</td>
<td>238.612</td>
<td>0.437</td>
<td>0.666</td>
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<td>CWM – Wood density (g cm⁻³)</td>
<td>0.001</td>
<td>-2.517</td>
<td>0.018*</td>
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<td>-2.575</td>
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<td>2.527</td>
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<td>0.056</td>
<td>0.956</td>
<td>1.872</td>
<td>0.777</td>
<td>0.444</td>
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### Seedlings

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<td>-0.002</td>
<td>0.313</td>
<td>0.758</td>
<td>-11.627</td>
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<td>0.002</td>
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<td>0.021*</td>
<td>-1.392</td>
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<td>0.128</td>
<td>0.900</td>
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<td>Coefficient</td>
<td>Standard Error</td>
<td>t-Value</td>
<td>P-value</td>
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<td>0.022</td>
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<td>-13.781</td>
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<td>0.885</td>
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<td>0.553</td>
<td>-0.001</td>
<td>-1.283</td>
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<td>CWM – Leaf thickness (mm)</td>
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<td>0.643</td>
<td>0.171</td>
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<td>-0.488</td>
<td>0.629</td>
<td>571.682</td>
<td>5.756</td>
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<td>CWM – Leaf dry matter content (g/g⁻¹)</td>
<td>-0.076</td>
<td>-0.125</td>
<td>0.901</td>
<td>-254.976</td>
<td>-2.800</td>
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<td>CWM – Wood density (g cm⁻³)</td>
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<td>0.762</td>
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<td>-5.827</td>
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<td>1.590</td>
<td>0.123</td>
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<td>CWM – Biotic dispersal</td>
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<td>0.322</td>
<td>1.797</td>
<td>1.308</td>
<td>0.202</td>
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*Significant P values (< 0.05).