

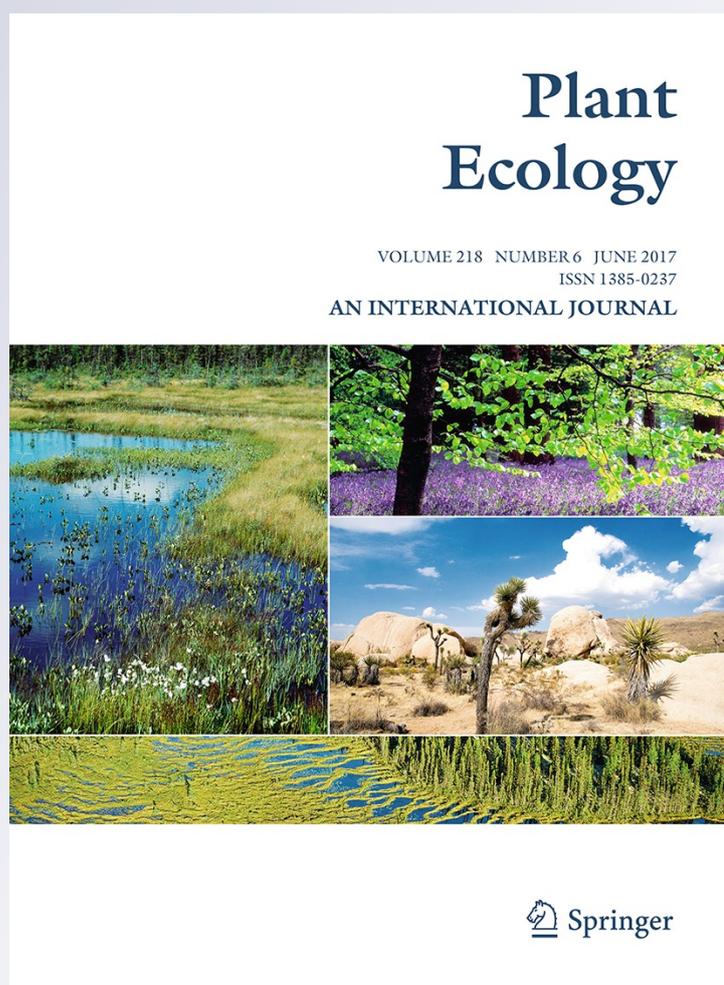
Euphorbiaceae responses to chronic anthropogenic disturbances in Caatinga vegetation: from species proliferation to biotic homogenization

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Euphorbiaceae responses to chronic anthropogenic disturbances in Caatinga vegetation: from species proliferation to biotic homogenization

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Abstract Chronic anthropogenic disturbances (CAD) have posed tangible threats to biodiversity-relevant tropical biotas, but community- and ecosystem-level impacts still remain poorly understood. Here we address a 152 km² Caatinga landscape in northeast Brazil in order to investigate how Euphorbiaceae species and these seasonally dry tropical plant assemblages respond to a CAD gradient. Woody plant

species were recorded across 26 0.06 ha spatially independent plots exposed to CAD. Euphorbiaceae species accounted for 78.9% of all plants and 21.5% of all species, with some species reaching up to 283 individuals per 0.06 ha or 92% of all recorded plants. Despite such contributions, Euphorbiaceae total and relative abundance, as well as total and relative richness, did not correlate with disturbance intensity at plot scale. At species level, some Euphorbiaceae species responded positively to disturbance, while others declined or did not exhibit a consistence response (i.e., positive, negative, and neutral responses). CAD intensity affected patterns of community similarity considering the whole plant assemblage as follow: first, plot-level disturbance correlated positively with NMDS scores; second, *C. sonderianus* experienced a 100% increment in terms of relative abundance along the disturbance gradient, and its plot-level abundance correlated positively with NMDS scores; and finally, cross-plot similarity correlated positively with cross-plot geographical distance. Among others, our results suggest that CAD may favor some particular species (i.e., proliferating taxa), leading to community-level changes, including biotic homogenization as disturbance increases.

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Introduction

Habitat loss and fragmentation (i.e., acute human disturbance), particularly the elimination of old-growth forest stands and the expansion of edge-affected habitats in human-modified landscapes, has drastically altered both the availability and quality of tropical forest habitats (Foley et al. 2005; Hansen et al. 2013; Laurance et al. 2014). Such acute disturbances represent a major threat to tropical biodiversity by leading many species to population collapse at multiple spatial scales (Tscharntke et al. 2012); particularly, disturbance-sensitive species bearing particular life-history traits, such as immense trunks or large seeds in the case of tropical flora (Laurance et al. 2001). Other species, however, may experience a contrasting trajectory relative to population size and range (i.e., winner species sensu McKinney and Lockwood 1999). Both winners and losers tend to belong to particular ecological groups, suggesting that biodiversity erosion in human-modified landscapes is not a random process (Laurance et al. 2006).

In contrast to acute human disturbances, chronic anthropogenic disturbances (CAD; sensu Singh 1998) are subtler because they usually involve regular, frequent, and long-term removal of small amounts of biomass. In the case of tropical forests, the collection of firewood, fodder and other non-timber forest products (NTFP), and biomass removal by livestock are considered CAD (Singh et al. 1984). As rural human populations trying to meet their basic needs (i.e., forest dependent people), CAD are not expected to be negligible or cease in the presence of environmental regulations (Shahabuddin and Prasad 2004; Kumar and Shahabuddin 2005; Karanth and DeFries 2010), and may also threaten the ecological integrity of protected areas (Kumar and Shahabuddin 2005). Depending on their intensity, CAD can also threaten biodiversity from population to ecosystems level. Briefly, CAD have been reported to impose negative effects from population (recruitment failure, local extinction and proliferation) to ecosystem level as they can drive shifts in soil, hydrology, and microclimatic conditions (Mishra et al. 2004; Portilla-Alonso and Martorell 2011). The demographic shifts experienced by some cactus species in Mexico (Martorell and Peters 2005; Martorell et al. 2012) and the

replacement of Himalayan forests by shrub-dominated vegetation (Mehta et al. 2008) are illustrative cases.

Caatinga vegetation is a mosaic of seasonally dry tropical forests and xerophytic, deciduous thorn scrubs (Pennington et al. 2009) that occupies ca. 800,000 km² of northeastern Brazil (10% of the territory, Portillo-Quintero and Sánchez-Azofeifa 2010). This semiarid region has been more densely occupied since the mid-sixteenth century with European colonization, and currently is home to over 23 million people (11.8% of the Brazilian population) and is one of the most populous semiarid regions globally, with 26.03 hab/km² (Ab'Sáber 1999; Medeiros et al. 2012). Cattle-ranching, wood extraction and subsistence agriculture have imposed a continuum of degradation varying from biomass reduction to complete desertification (Leal et al. 2005; MMA 2011). To worsen this scenario of high human pressure, strictly protected areas encompass less than 1% of Caatinga vegetation (Leal et al. 2005). Finally, the role played by CAD in vegetation and plant community structure has only recently started to be examined (Sánchez-Azofeifa et al. 2005; Santos et al. 2011; Ribeiro et al. 2015, 2016; Ribeiro-Neto et al. 2016), which limits our ability to propose conservation guidelines and regulations (Leal et al. 2005; Lôbo et al. 2011).

In this study, we address Euphorbiaceae species and woody plant communities in a 152 km² Caatinga landscape in order to examine the potential effects imposed by CAD, particularly firewood collection and browsing by livestock, on plant species abundance and community-level taxonomic composition. We adopted Euphorbiaceae species as a biological model because they are a highly diverse group in the Caatinga biota (Silva et al. 2003), with some species positively responding to CAD (Ribeiro et al. 2015, 2016; Ribeiro-Neto et al. 2016). First, we offer family-level-related scores across a set of plots covering a CAD gradient. Second, we examine individual species responses to the CAD gradient and correlate them with levels of cross-plot taxonomic similarity. We expected Euphorbiaceae species to increase their abundances in areas experiencing high levels of disturbance, with tangible effects on patterns of species similarity. Finally, we speculate about potential mechanisms responsible for the observed patterns and address theoretical implications of the CAD context.

Methods

Study site

This study was carried out in a continuous patch of Caatinga vegetation near Parnamirim city (8°5'S; 39°34'W; 393 m asl) in Pernambuco state, northeast Brazil. The climate is semiarid with most of the 550 mm mean annual rainfall occurring between January and May (IBGE 1985). The wet season is highly variable in its length, with the dry season lasting for 7–11 months (Nimer 1972; Prado 2003). The predominant soils are non-calcic brown soil, regosols, planosols and podzolic yellow soils (EMBRAPA 2001). The vegetation includes patches of seasonally dry tropical forest and scrub vegetation (Sampaio 1995; Prado 2003). Parnamirim city was founded in the nineteenth century, and its origin is related to livestock farming, a common economic activity in semiarid regions of Brazil. Nowadays, the local economy also includes smallholder agriculture, and the human population in Parnamirim is around 20,000 people, with 11,000 living in rural areas (IBGE 2011).

Measurement of anthropogenic disturbance

We established 26 0.06-ha plots (30 × 20 m each, separated by at least 4 km) on two soil types (15 on sand and 11 on clay) in a 152 km² landscape dominated by old-growth vegetation exposed to chronic anthropogenic disturbances. Areas that had experienced acute rather than chronic disturbance, such as slash-and-burn agriculture, were not included. For each plot we recorded five indicators of chronic disturbance that have been described in tropical forests studies as important drivers of chronic human disturbances (Sagar and Singh 2003; Martorell and Peters 2005; Leal et al. 2014; Ribeiro et al. 2015): (1) distance to Parnamirim city center; (2) distance to nearest property; (3) distance to nearest road; (4) density of livestock (goats and cattle combined) near the plot; and (5) density of people living near the plot. We opted for proxies instead of direct measures of logging, hunting, cutting, and overgrazing because these disturbances are not easily quantified and accessed at the landscape scale (Martorell and Peters 2005; Acharya and Dangi 2009).

We quantified distance to Parnamirim city center, distance to nearest property and distance to nearest road as the reciprocal distance from the center of each plot using satellite imagery from the Advanced Land Observing Satellite (ALOS). To estimate the densities of livestock and people, we identified in the satellite imagery all dwellings near the plots. We identified 34 dwellings, and we collected information on the number of people living in, and the number of stock managed through interviews done with each householder (i.e., one interview per householding). We then used the ALOS satellite imagery to estimate densities of livestock and people considering the interview data in a 2 km buffer area from the center of each plot (i.e., within an area of 1256 ha). We used this buffer size because local households informed that the maximum dispersal distance of browsing animals falls within 2 km.

A previous study has demonstrated that all these five indicators of disturbance negatively affect plant assemblage of Caatinga vegetation in the same region (Ribeiro et al. 2015). We then used a synthetic index to collapse all these indicators into a single figure in order to simplify the analysis of the effects of CAD. To classify plot disturbance level, we categorize each indicators of disturbance into four categories (as adopted by Leal et al. 2014). For the three distance indicators, categories ranged from one (highest distance value) to four (lowest distance value), and, for densities of livestock and people, from one (lowest) to four (highest). We thus summed the values of each indicator to obtain an overall disturbance score for each site, with higher scores representing higher disturbance levels. Finally, the scores obtained were rescaled from 0 to 100, representing the least and most disturbed sites, respectively (Electronic supplementary material Table S1).

Plant species surveys

Euphorbiaceae species form a monophyletic group, which have been referred to in the literature as a common component of degraded Caatinga areas (Andrade et al. 2005; Ribeiro et al. 2015, 2016; Ribeiro-Neto et al. 2016), thereby offering an interesting opportunity to address CAD. In order to examine Euphorbiaceae individual species responses to the CAD gradient and correlate them with levels of

cross-plot taxonomic similarity, we marked and identified all individuals of all woody plant species with diameter at soil level ≥ 3 cm and total height ≥ 1 m (Rodal et al. 1992) in each plot. In addition to total Euphorbiaceae relative abundance and richness in each plot, we calculated the relative abundance of Euphorbiaceae species that were present in at least 50% of sites.

Data analysis

To test the effect of CAD on each response variable, we used generalized linear models. As soil type may influence Euphorbiaceae species richness and abundance (Ribeiro-Neto et al. 2016), we added this factor as a covariate. We fixed a Gaussian error distribution for continuous response variables (i.e., relative data). For total richness and abundance data, we fixed a Poisson error distribution, as recommended for count-dependent variables (Crawley 2007). To correct for the overdispersion associated with count data, we used quasi-poisson error distributions in the models when necessary (Crawley 2007).

We then performed a nonmetric multidimensional scaling (NMDS) ordination of all 26 sites using a Bray–Curtis dissimilarity matrix of species composition (Krebs 1999), considering all plant species present in the plots. To avoid any bias resulting from highly abundant species and differences in sample sizes, species abundance data were square root transformed. To examine if there was a relationship between the floristic similarity and any changes in the Euphorbiaceae group, we plotted the first NMDS axis against the relative abundance of those Euphorbiaceae species that benefitted from disturbance. Additionally, we tested if there is a relationship between floristic similarity and CAD by plotting the first NMDS axis against our synthetic chronic disturbance index. We tested these relations with linear regressions and performed all analyses with the *stats* and *ecodist* packages in R (R Core Team 2015; Goslee 2007). Additionally, we evaluated the effect of variation in Euphorbiaceae abundance in plant composition by means of a Mantel test between the composition distance matrix and a matrix of geographical distances between pairs of plots. This analysis was performed with the *vegan* package in R (R Core Team 2015).

Results

Stands of Caatinga vegetation were submitted to a wide spectrum of CAD intensity with plot-level scores ranging from 5 to 20 (i.e., a gradient of CAD intensity rescaled from 0 to 100%). However, plots were located no farther than 3 km from roads, household farms, and cities, with plots exposed to over 600 farm animals (Table S1). A total of 5554 plant individuals, distributed among 51 species and 18 families were recorded across the 26 plots. Euphorbiaceae accounted for 4383 individuals (167.88 ± 61.88 ; mean \pm SD; 78.9% of all plants), followed by Fabaceae (732 individuals) and Apocynaceae (98 individuals). Euphorbiaceae plants were distributed between 11 species (21.5% of all species) from six genera; *Croton* (88.8% of individuals), *Jatropha* (5.1%), and *Cnidoscolus* (4.1%) were the most abundant genera. *Croton sonderianus* was the most abundant species reaching up to 283 individuals per 0.06 ha or 92% of all recorded plants.

Despite such large contributions, Euphorbiaceae total abundance (168.6 ± 62.9 ; $t = -0.63$, $df = 23$, $p = 0.53$), relative abundance ($77.9\% \pm 10.51$; $t = 1.48$, $df = 23$, $p = 0.15$), total ($z = 0.80$, $df = 23$, $p = 0.42$) and relative ($t = 1.92$, $df = 23$, $p = 0.07$) species richness were not affected by disturbance level at plot scale. Moving to species level, five species were recorded in more than 50% of all plots: *Croton sonderianus*, *Croton adamantinus*, *Jatropha mollissima*, *Cnidoscolus quercifolius*, and *Sapium glandulosum*. Among these frequent species, relative abundance of *C. sonderianus* and *J. mollissima* increased with disturbance (Table 2; Fig. 1b, f), while the total and relative abundance of *C. adamantinus* decreased (Tables 1, 2; Fig. 1c, d). *Cnidoscolus quercifolius* and *Sapium glandulosum* did not exhibit any trend (Tables 1, 2; Fig. 1g–j).

CAD intensity affected patterns of species similarity considering the whole plant assemblage. Firstly, NMDS scores were slightly and positively correlated with plot-level disturbance ($R = 0.15$, $df = 24$, $p = 0.03$; Fig. 2). Secondly, *C. sonderianus* experienced a 100% increment in terms of relative abundance along the disturbance gradient and its plot-level abundance correlated positively with NMDS scores ($R = 0.74$, $df = 24$, $p < 0.0001$; Fig. 3a). On the other hand, *J. mollissima* did not influence the similarity among plots ($R = 0.01$, $df = 24$,

Fig. 1 Euphorbiaceae species total and relative abundance in relation to different anthropogenic disturbance levels in 26 0.06 ha plots in a continuous patch of Caatinga vegetation, Parnamirim City, northeast Brazil. Graphs in the right column are total abundances and graphs in the left column are relative abundances

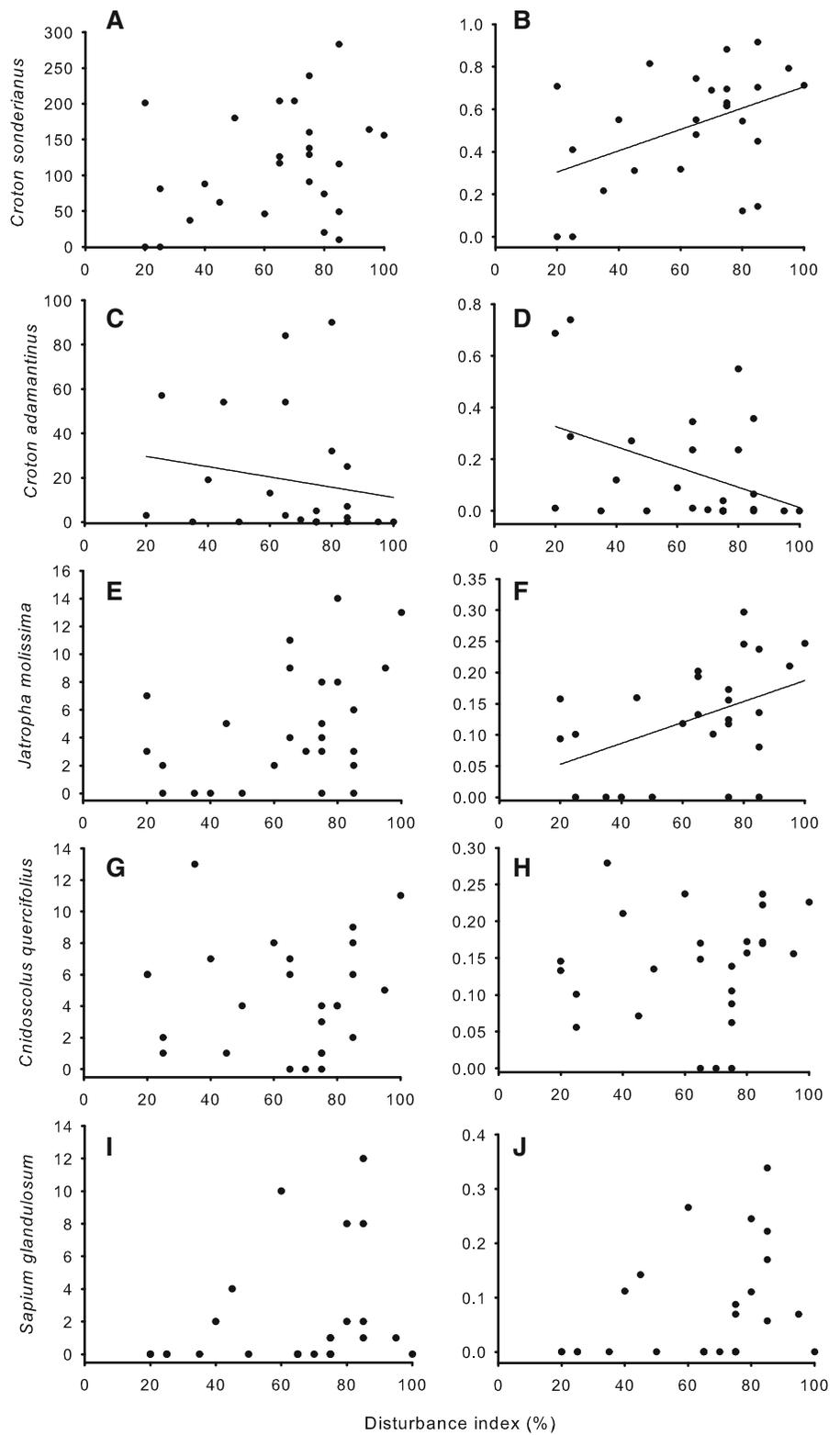


Table 1 Total abundance (mean \pm SD) of five Euphorbiaceae woody species in 26 0.06 ha plots along a gradient of chronic anthropogenic disturbance in a continuous patch of Caatinga vegetation, Parnamirim City, northeast Brazil

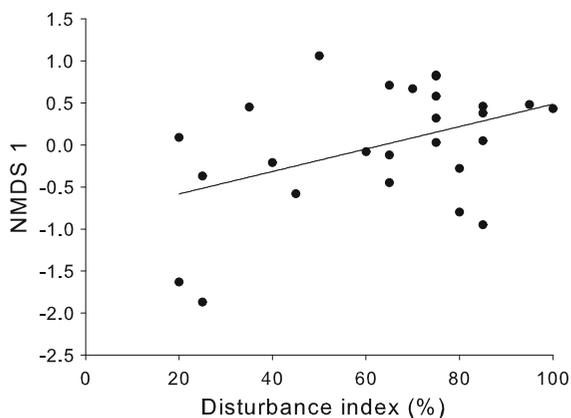
Euphorbiaceae species	Abundance	Disturbance		Soil	
		<i>t</i>	<i>p</i>	<i>t</i>	<i>P</i>
<i>Croton sonderianus</i>	144.42 \pm 76.69	1.63	0.12	-1.32	0.20
<i>Croton adamantinus</i>	35.56 \pm 65.02	-2.94	0.01	-0.81	0.43
<i>Jatropha molissima</i>	4.75 \pm 4.14	2.10	0.05	-0.60	0.55
<i>Cnidoscolus quercifolius</i>	4.68 \pm 3.50	0.01	0.99	0.97	0.34
<i>Sapium glandulosum</i>	2.00 \pm 3.56	1.76	0.09	1.97	0.06

Values in bold denotes a significant difference

Table 2 Relative abundance of five Euphorbiaceae woody species (mean \pm SD) in 26 0.06 ha plots along a gradient of chronic anthropogenic disturbance in a continuous patch of Caatinga vegetation, Parnamirim City, northeast Brazil

Euphorbiaceae species	Abundance	Disturbance		Soil	
		<i>t</i>	<i>p</i>	<i>t</i>	<i>P</i>
<i>Croton sonderianus</i>	0.79 \pm 0.33	2.55	0.02	-0.58	0.57
<i>Croton adamantinus</i>	0.30 \pm 0.33	-2.18	0.03	0.71	0.49
<i>Jatropha molissima</i>	0.13 \pm 0.09	2.36	0.03	-0.25	0.80
<i>Cnidoscolus quercifolius</i>	0.14 \pm 0.08	0.35	0.73	1.95	0.06
<i>Sapium glandulosum</i>	0.07 \pm 0.10	1.76	0.09	2.94	0.01

Values in bold denote a significant difference

**Fig. 2** Relation between the nonmetric multidimensional scaling (NMDS) ordination (axis 1) on the basis of floristic similarity and different anthropogenic disturbance levels of 26 0.06 ha sites in a continuous patch of Caatinga vegetation, Parnamirim City, northeast Brazil

$p = 0.58$; Fig. 3b). Finally, cross-plot similarity correlated positively with cross-plot geographical distance (Mantel test; $R = 0.20$, $p = 0.01$).

Discussion

Although CAD has been argued to cause impacts on multiple levels of ecological organization, from population to ecosystem (Singh 1998), few biotas have been examined so far, with most studies addressing the effects on plant population level, particularly of species exploited for NTFP (Shahabuddin and Prasad 2004). Despite the relative simplicity and arbitrariness, we adopted to measure/describe CAD in our focal landscape, there is no evidence that in our case CAD correlates with other environmental variables driving plant distribution (e.g., precipitation), and thereby, we assume that our uncovered patterns describe CAD effects. Precisely, our findings suggest that Euphorbiaceae species represent a dominant element across disturbed stands of Caatinga vegetation (i.e., 2/3 of all stems), but although this taxon is considered a monophyletic group, species do not respond similarly to CAD in terms of species abundance, even if we consider congeneric species (e.g.,

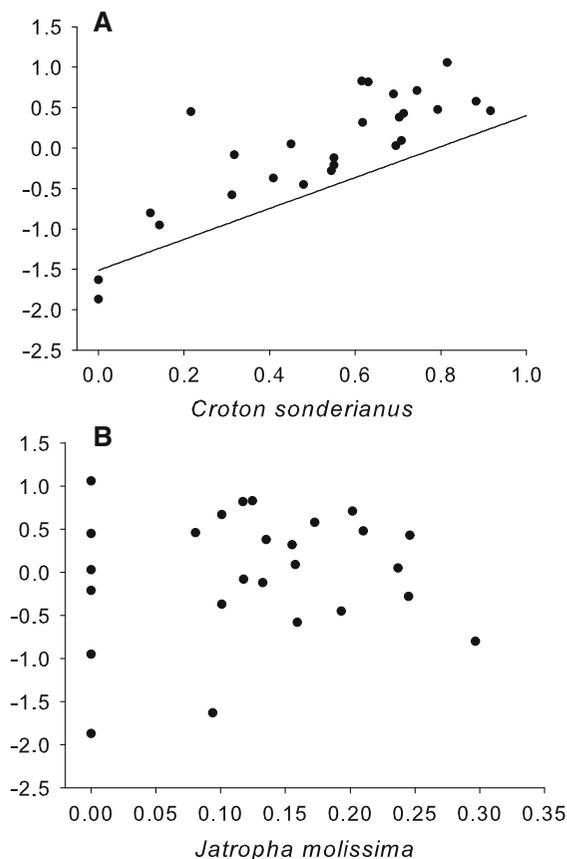


Fig. 3 Relation between nonmetric multidimensional scaling (NMDS) ordination (axis 1) of 26 0.06-ha sites on the basis of their floristic similarity and *Croton sonderianus* (a) and *Jatropha mollissima* (b) in a continuous patch of Caatinga vegetation, Parnamirim City, northeast Brazil

Croton species). In fact, some species responded positively and could potentially dominate plant assemblages in intensively disturbed sites, while others declined or did not exhibit a consistence response. These taxa-dependent responses including positive, negative, and neutral responses resulted into similar scores of Euphorbiaceae species richness along our CAD gradient and refuted our main hypothesis. As CAD intensity is slight correlated with increments in community-level species similarity, CAD may result in biotic homogenization.

These findings offer interesting contributions relative to CAD impacts on tropical biotas at population and community level, and we shall start by those recognized as more general and potentially able to trigger cascades effects. We refer to the notion that (1) some species are able to benefit from CAD, such as

some ‘ruderal’ Cactaceae species in Mexico (Martorell et al. 2012), and those Euphorbiaceae species already documented in the Caatinga vegetation (Ribeiro et al. 2015, 2016; Ribeiro-Neto et al. 2016), and (2) proliferation of native plant taxa in response to human disturbances represent a more general pattern as it is not restricted to acute disturbance (see Tabarelli et al. 2012). Species that benefit from anthropogenic disturbance have been referred to as weedy (Tilman and Lehman 2001), ruderal (Martorell et al. 2012), ecological winners, or proliferating species (Tabarelli et al. 2012), including both exotic and native species (McKinney and Lockwood 1999; Tabarelli et al. 2012). Furthermore, species proliferation is not a random process since proliferating species bear particular traits or life-history strategies which confer increased fitness in particular disturbance scenarios (Laurance et al. 2001; Tabarelli et al. 2008). A well-documented example is that of some small-seeded, pioneer plant species proliferating across human-modified landscapes in the Atlantic forest region (Lôbo et al. 2011).

Population reduction or collapse among native plant species across biotas exposed to CAD have been proposed to result from a combination of drivers, including reduced fitness due to biomass collection (e.g., fodder), overbrowsing, changes in environmental conditions (soil nutrients and microclimate) causing increased stress and competition with exotic plant species (McKinney and Lockwood 1999; Olden et al. 2004). On the other hand, changes in environmental conditions and reduced competition with negatively affected species can favor disturbance-adapted species via increased recruitment and population growth (Martorell et al. 2012). We refer to physically stressful environments (Sagar and Singh 2003) causing compensatory dynamics (Gonzalez and Loreau 2009), at least until habitat degradation (e.g., aridization) limits the recruitment of such species.

These previous findings permit us to speculate about underlying mechanisms driving the responses we documented in the Caatinga, although we did not explicitly address them in our study design. We particularly refer to processes mediated by the absence/presence of plant traits related to (1) human potential use, (2) tolerance to stressful environments, (3) dispersal/colonization ability, and (4) foliage palatability for livestock. For example, *Jatropha mollissima* has a low wood density (0.29 g/cm³;

Vitorio 2013)—thus it is not used by local human communities as firewood or for fence construction (Ribeiro et al. 2015; also reported in our set of interviews). Moreover, the low wood density implies a high water reserve that may be used in the production of fruits and leaves (Borchert 1980; Rivera et al. 2002) and consequently contributes to plant maintenance in disturbed areas. *Jatropha mollissima* also bears flowers throughout the whole year; it is self-compatible, and in natural conditions, the percentage of fruit production is 85% (Santos et al. 2005). Thus, high reproductive success and low use pressure would contribute to its proliferation as documented here.

Similarly, *C. sonderianus* seems to be favored for its: (1) resprouting ability, (2) production of viable seeds via agamospermy (Araujo 1998) and (3) low foraging value for goats, sheep and cattle; the main herbivores in these areas of Caatinga vegetation (Cândido 1998; Moreira et al. 2006; Santana et al. 2011), reaching 10–45 thousand individuals per hectare in successional areas (Carvalho et al. 2001). Note that in the Caatinga vegetation, slash-and-burn agriculture leading to soil degradation, firewood collection and overbrowsing by livestock have been reported to be the main drivers of habitat degradation (Leal et al. 2005; MMA 2011; Ribeiro et al. 2015). In this ecological context, resprouting ability and unpalatable foliage represent key traits (Bond and Midgley 2001).

As a complementary force organizing species distribution along CAD gradients, we shall also consider the possibility of competition-mediated species displacement, particularly in the case of congeneric species (see Milla and Iriondo 2011; He et al. 2012). We refer to the replacement of *C. adamantinus* by *C. sonderianus* as CAD intensifies as suggested by their abundances in our focal gradient. In this perspective of trait-mediated responses to CAD every Euphorbiaceae species bear more than a single trait-suite mediating neutral, negative, or positive response to CAD and packages differ among species, although closely related species are frequently assumed to be ecologically similar (Burns and Strauss 2011).

Finally, we offer a slight evidence for the emergence of taxonomically more similar plant assemblages at landscape level, and in this study, we argue that it is probably due to both the proliferation (*Croton sonderianus* and *Jatropha mollissima*) and the

collapse (*Croton adamantinus*) of particular taxa in response to increasing disturbance as discussed earlier, although some species exhibit neutral responses. Similar findings have been reported to both woody plant species and ants in the Caatinga vegetation (Ribeiro et al. 2015; Ribeiro-Neto et al. 2016). Note that biotic homogenization is an expected response in cases where disturbance increments both physical stress and environmental filtering (Tilman and Lehman 2001). In this context, we offer additional evidence for causal relationship between species proliferation and biotic homogenization as an integrated effect of CAD. As a note of alert it is worth informing that in addition to biotic homogenization, proliferation of disturbance-adapted species may be associated with or represents the first step towards more profound changes in vegetation structure and the nature of plant assemblages (Singh 1998). More precisely, as disturbance intensity exceeds certain thresholds and radically alters the physical environment, trees are replaced by shrubs (in the case of forests), vegetation biomass, and structure collapse, and plant communities become impoverished and may experience increasing levels of invasion (Mishra et al. 2004; Mehta et al. 2008). Such trajectories as experienced by temperate and tropical dry forests in India suggest that CAD may drive targeted vegetation towards transitional plant assemblages between two extremes: old-growth forest and shrub-dominated vegetation (Singh et al. 1984; Mehta et al. 2008). This phenomenon adds new insights and confirms the degradation potential of CAD and reinforces the notion that biotic homogenization is a more generalized response to human disturbance than previously advocated (Tabarelli et al. 2012).

In synthesis, chronic anthropogenic disturbances have been reported in the literature as being as degrading as acute forms of disturbance such as habitat loss and fragmentation (Singh 1998). This may be particularly true in the case of environmental-dependent human communities (sensu Millennium Ecosystem Assessment 2005) as seen today across many regions covered by tropical dry forests and savannas (Davidar et al. 2010; Gaoue et al. 2013; Blackie et al. 2014; Ribeiro et al. 2015). In this study, we offer evidence for species-level responses to CAD, including both abundance decline and increment. Although population decline represents a direct threat to biodiversity persistence when this results in

species extirpation, proliferation of disturbance-adapted species may also represent a threat, because it is apparently associated with community-level homogenization driven by CAD, as is the case with Euphorbiaceae-dominated plant assemblages. This human-driven degrading force requires attention, since like other tropical biotas with significant conservation value, Caatinga vegetation will continue to experience the immense challenges posed by poverty, increasing human populations and climate change, that make it imperative to reconcile biodiversity conservation and the meeting of human needs (Karanth and DeFries 2010). Accordingly, much more information is needed to examine the generality and the consistence of the patterns documented/proposed here, as well as the underlying mechanisms responsible for species proliferation and biotic homogenization to offer effective guidelines for conciliating appropriate human livelihoods and ecosystem integrity.

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