

# Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation

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## Summary

1. In addition to acute transformations of ecosystems caused by deforestation, old-growth forests world-wide are being increasingly altered by low-intensity but chronic human disturbance. Overgrazing and the continuous extraction of forest products are important drivers of chronic disturbance, which can lead to the gradual local extinction of species and the alteration of vegetation structure.

2. We tested this hypothesis in the Brazilian Caatinga vegetation, one of the most species-rich and populated semi-arid regions of the world. Using a multimodel averaging approach, we examined the impact of five recognized indicators of chronic disturbance (i.e. proximity to urban centre, houses, roads, density of people and livestock) on the diversity, abundance and evenness of 30 woody plant communities. We separately tested the response of seedlings, saplings and adults to identify the ontogenetic stages that are most susceptible to chronic disturbance.

3. We recorded over 11 000 individuals belonging to 51 plant species. As expected, most indicators of chronic disturbance were negatively related to species diversity and stem abundance, with a variable effect on community evenness. The density of people and density of livestock were the main factors driving changes in plant communities, with a stronger negative impact on seedling and sapling diversities. Species composition also varied significantly with disturbance indicators, irrespective of ontogeny.

4. Our results show the potential negative impact that chronic disturbance can have on Caatinga plant assemblages and highlight the fact that disturbance resulting from an extractivism-based and subsistence economy are probably driving old-growth forest stands towards shrub-dominated secondary stands.

5. *Synthesis and applications.* These findings indicate that chronic disturbance should not continue to be neglected and we argue for: (i) research and rural programmes able to support better practices in terms of land use and sustainable exploitation of forest resources, (ii) improved governance and law enforcement to shift extractivism towards sustainable standards, and (iii) expanding the coverage and effective implementation of strictly protected areas.

**Key-words:** biodiversity crisis, chronic human disturbance, multi-model inference approach, plant assemblages, seasonally dry tropical forests, semi-arid vegetation, species diversity

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## Introduction

Changes in land use have drastically decreased forest cover world-wide, with research emphasizing habitat loss and fragmentation as the main threats to tropical biodiversity and services provided by this irreplaceable ecosystem (Laurance, Sayer & Cassman 2014). However, old-growth and secondary forest patches are experiencing increasing levels of human-related disturbance that do not result in habitat loss and fragmentation, but also have negative impacts on the biological integrity of tropical biota (Singh 1998; Laurance & Peres 2006). We refer, for example, to continuous poaching, extraction of firewood and non-timber forest products, as well as the damage caused by livestock, which overall result in a subtle but permanent removal of small fractions of forest biomass (Martorell & Peters 2005; May-Tobin 2011). In contrast to large-scale habitat loss and fragmentation, chronic disturbance is (i) usually diffuse, more frequent and operate at a small spatial scale, (ii) not detected via traditional resources such as satellite imagery (Laurance & Peres 2006), and (iii) not expected to cease even in those countries where habitat loss is now regulated.

Chronic regimes in fact represent a global pervasive source of disturbance that operates as complementary sources of habitat degradation and species erosion in human-modified landscapes (Mahiri & Howorth 2001; FAO 2011). Reductions in stem density, basal area, species richness and community evenness and changes in plant demographic structure and proliferation of disturbance-adapted species, which all cause detrimental effects to forest-dependent and long-lived plant species, have been reported (Sagar, Raghubanshi & Singh 2003; Smart *et al.* 2006; Wiegmann & Waller 2006). Plant–animal interactions, such as seed dispersal, can also be altered in sites experiencing livestock, hunting and firewood collection (Leal, Andersen & Leal 2014), but our general understanding on the impacts that chronic disturbance may have on plant species diversity and vegetation structure is still limited (Álvarez-Yépez *et al.* 2008).

The Caatinga vegetation of Brazil consists of broad mosaics of seasonally dry tropical forest and scrub vegetation (Veloso, Sampaio & Pareyn 2002). This semi-arid region sustains over 23 million people (11.8% of the Brazilian population) and is one of the most populated semi-arid regions globally, with 26 inhabitants km<sup>-1</sup> (INSA 2012). Nearly 10 million m<sup>3</sup> per year of firewood and charcoal are obtained via exploitation of native vegetation (Gariglio *et al.* 2010), and historically goat herds can exceed 16 million animals (IBGE 2010a). Collectively, slash-and-burn agriculture, overgrazing by livestock and firewood collection impose a continuum of degradation varying from reduced biomass to complete desertification (Leal *et al.* 2005). Despite this alarming scenario, the role played by chronic disturbance on plant community structure in the Caatinga has been poorly examined (Leal *et al.* 2005; Santos *et al.* 2011). The Caatinga vegetation thus

offers an interesting opportunity to address how seasonally dry tropical forest and semi-arid biotas respond to small-scale land use (as opposed to commercial land use) in order to provide conservation guidelines and better practices.

We assessed how Caatinga plant assemblages are affected by small-scale but frequent disturbance, such as extensive browsing by livestock, selective tree removal, firewood collection and hunting. Because human disturbance usually favours a small group of disturbance-tolerant species that ultimately become locally dominant (Smart *et al.* 2006; Wiegmann & Waller 2006), we expected that all indicators of chronic disturbance would be negatively related to stem abundance, species diversity and community evenness. These relationships, however, were expected to be stronger in seedling and sapling assemblages, as these ontogenetic stages are often more vulnerable to chronic disturbance (Singh, Rawat & Garkoti 1997).

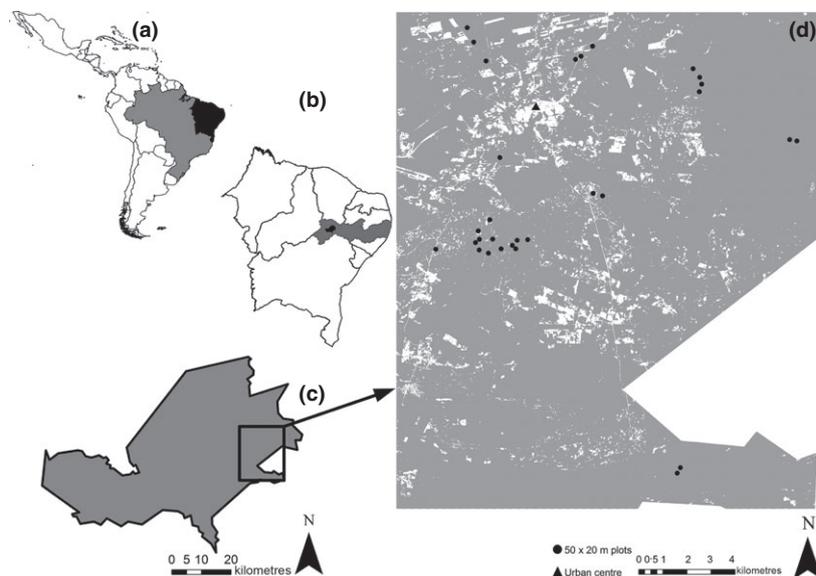
## Materials and methods

### STUDY AREA

The Caatinga encompasses 826 411 km<sup>2</sup> of seasonally dry tropical forests and scrub vegetation restricted to Brazil (MMA & IBAMA 2011). The studied area is located in the Parnamirim municipality, Pernambuco state, north-east Brazil (8°5'26"S; 39°34'41"W; Fig. 1). The climate is semi-arid, with an average temperature of 26 °C and most of the 431 mm mean annual rainfall is received between January and May (IBGE 1985; CPRM 2005). Soils are predominantly non-calcic brown soils (clay soil), regosols and planosols (sandy soils) (IBGE 1985). The Caatinga vegetation has undergone deforestation since the sixteenth century for extensive livestock and temporary farming (Leal *et al.* 2005; IBGE 2010b). Parnamirim municipality has approximately 55% of the original Caatinga forest cover. Forest products extracted for medicinal purposes, animal and human food, and wood collection are also common within the forest remnants.

### STUDY SITES

We established 30 50 × 20 m plots (Fig. 1) within a 220 km<sup>2</sup> landscape dominated by old-growth vegetation exposed to chronic disturbance. We considered old-growth vegetation to be forest stands not exposed to slash-and-burn agriculture in the last 50 years (Leal, Andersen & Leal 2014). Because the response of tree species to chronic disturbance may be affected by soil characteristics (Pinheiro, Rodal & Alves 2010), we located 15 plots on brown non-calcic soils and 15 on regosols. We adopted a landscape scale perspective to obtain a gradient of chronic disturbance intensity. We used five indicators of chronic disturbance that have been described as important drivers of human disturbance in tropical forests studies. They are (i) proximity to the nearest house (Proximity to house) (Sagar, Raghubanshi & Singh 2003; Martorell & Peters 2005; Leal, Andersen & Leal 2014), (ii) proximity to the nearest road (Proximity to road) (Sagar, Raghubanshi & Singh 2003; Leal, Andersen & Leal 2014), (iii) proximity to Parnamirim city (Proximity to city) (Sagar, Raghubanshi &



**Fig. 1.** (a) Study area in north-eastern Brazil, (b) the Parnamirim municipality (in black) within the Pernambuco state (in grey), (c) the study landscape in which we located 30  $50 \times 20$  m plots and (d) the urban centre of Parnamirim (black triangle) (the white areas in (d) represent deforested areas).

Singh 2003; Leal, Andersen & Leal 2014), (iv) density of people living near the plot (People) (Leal, Andersen & Leal 2014), and (v) density of livestock (Livestock) (Leal, Andersen & Leal 2014). We opted for proxies instead of direct measures of logging, hunting, cutting and overgrazing because disturbance is not easily quantified at the landscape scale (Acharya & Dangi 2009). Thus, plots covered a wide range of disturbance level (see Table S1 in Supporting Information).

We used satellite imagery from the Advanced Land Observing Satellite (ALOS) to estimate the indicators 'Proximity to house', 'Proximity to road' and 'Proximity to city' as the reciprocal distance from the centre of each plot. To estimate 'People' and 'Livestock', we first identified all occupied dwellings near the plots. Through 40 interviews, we collected information on the number of people living in, and the number of stock managed by, each dwelling. We later used the ALOS satellite imagery to localize all dwellings in a 2-km buffer area from the centre of each plot and then estimated 'People' and 'Livestock' in terms of density taking into account the interview data and an area of 1256 ha. We selected this buffer size because local people reported that the maximum dispersal distance of herd animals is 2 km.

#### SURVEY OF PLANT COMMUNITIES

We sampled plant assemblages in each plot during the rainy seasons of 2012 and 2013. We considered three stages (adults, saplings and seedlings) to identify the ontogenetic stages that are most susceptible to chronic disturbance, as well as to predict compositional change in plant communities. Adults were defined as individuals with diameter at soil height (DAS)  $>3$  cm and height  $>1.5$  m; saplings were individuals with DAS  $<3$  cm and height between 1 and 1.5 m; and seedlings were defined as individuals with height  $<1$  m (Rodal, Sampaio & Figueiredo 1992; Felfili, Carvalho & Haidar 2005). We recorded all adults found in each  $50 \times 20$  m plot. Saplings were sampled in three  $5 \times 5$  m subplots located in the centre of each  $50 \times 20$  m plot and separated by 10 m. Seedling communities were sampled in  $2 \times 2$  m subplots located in the centre of each  $5 \times 5$  m subplot. We identified all plants at species level by comparing the sampled species with samples from the Federal University of Pernambuco herbarium and the botanical nomenclature followed APG III (2009).

#### STRUCTURE OF PLANT COMMUNITIES

We first calculated the inventory completeness for each site and ontogenetic class using the coverage estimator recommended by Chao & Shen (2010), which is a less biased estimator of sample completeness:

$$\hat{C}_n = 1 - \frac{f_1}{n} \left[ \frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right],$$

where  $f_1$  and  $f_2$  are the number of species represented by one (singletons) and two (doubletons) individuals, respectively, and  $n$  is the total number of individuals in each sample.

Because sample coverage was variable among plots and ontogenetic classes (ranging from 20% to 99%), our estimates of species richness could be biased by differences in sample completeness (Chao & Jost 2012), particularly because species richness is sensitive to variations in the number of singletons and doubletons (Jost 2006). Thus, following Chao & Jost (2012), we estimated the species richness of adults, saplings and seedlings in each plot using coverage-based extrapolations with the iNEXT software (Hsieh, Ma & Chao 2013). In particular, we considered 99% completeness as a reliable estimator of richness for all plots (Chao & Jost 2012).

In addition to estimating species richness (or  ${}^0D$ ), we estimated the inverse Simpson concentration (or  ${}^2D$ ) (Jost 2006). Both  ${}^0D$  and  ${}^2D$  are in the same units and satisfy the replication principle (Jost 2006), which is required in biodiversity assessments as it considers the uniqueness of each species that compose an assemblage (Gotelli & Chao 2013). The formulas of  ${}^0D$  and  ${}^2D$  are detailed elsewhere (Jost 2006).  ${}^0D$  is not sensitive to species abundances and so gives disproportionate weight to rare species (Jost 2006). In contrast,  ${}^2D$  favours abundant species and can be interpreted as the number of 'very abundant' or 'dominant' species in the community (Jost 2006).

To assess changes in community structure, we also considered stem abundance in each plot and the evenness factor ( $EF$ ) proposed by Jost (2010).  $EF$  represents the proportion of dominant species in the community, and it is derived from the measures of effective number of species ( $EF = {}^2D/{}^0D$ ) (Jost 2010).  $EF$  ranges between 1 (when the community is perfectly even) and nearly

$1/{}^0D$  (when the community is dominated by one species; Jost 2010).

#### DATA ANALYSES

First, we ran a Mantel test to check for spatial independence of our samples before testing our hypothesis (see Appendix S1, Supporting information). Then, for each ontogenetic class (i.e. adults, saplings and seedlings) and each response variable (i.e.  ${}^0D$ ,  ${}^2D$ , abundance and  $EF$ ), we built generalized linear models including five continuous explanatory variables ('Proximity to house', 'Proximity to road', 'Proximity to city', 'People' and 'Livestock'). To avoid multicollinearity problems between the predictor variables, we first estimated the variance inflation factor (VIF) of each predictor using the *car* package for R version 3.0.1 (R Core Team 2013). All VIF values found were lower than 3.1, indicating that none of our predictors were collinear (Neter, Wasserman & Kutner 1990), allowing us to include all of them in generalized linear models.

To test (and control for) the effect of soil type on each response variable, we included this categorical factor in the models as a fixed factor, as variations in continuous covariables were independent from variations in soil type. Then, using a multi-model inference approach (Burnham & Anderson 2002), we identified the subset of models with stronger empirical support. We ranked the models from the best to the worst based on the Akaike's information criterion corrected for small samples (AICc). The set of models with a difference in AICc (i.e.  $\Delta AICc$ )  $< 2$  was considered to have strong empirical support and similar plausibility, explaining most of the variation in the response variable (Burnham & Anderson 2002).

To evaluate the importance of each predictor and produce model-averaged parameter estimates, we used Akaike weights ( $w_i$ ), which represent the probability that a particular model is the best model for the data. Thus, we summed  $w_i$  of ranked models until the total was  $> 0.95$  (Whittingham *et al.* 2005). The set of models for which  $\Sigma w_i$  was 0.95 represents the models for which we have 95% confidence that the set contains the best approximating model to the true model (Burnham & Anderson 2002; Whittingham *et al.* 2005). The relative importance of each predictor was assessed based on the sum of Akaike weights ( $\Sigma w_i$ ) of

each candidate model in which the predictor appeared (Burnham & Anderson 2002).

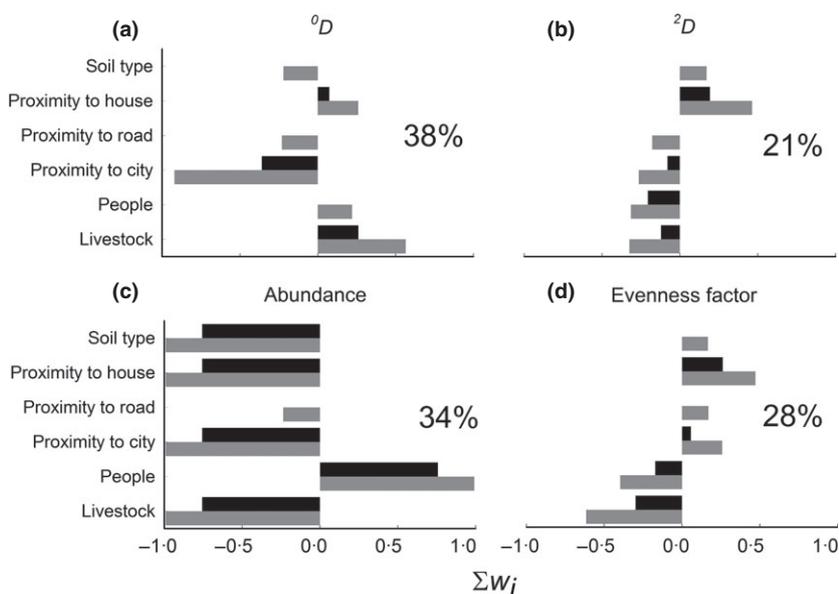
As recommended for count response variables, when analysing stem abundance, we constructed generalized linear models with a Poisson error and a log-link function (Crawley 2007). To correct for overdispersion associated with models with Poisson errors (Crawley 2007), we used QAICc values instead of AICc in such models (Calcagno & Mazancourt 2010). Models for  ${}^0D$ ,  ${}^2D$  and  $EF$  were tested using a Gaussian error structure, after testing that they showed a Gaussian distribution (Shapiro–Wilk test). All models were built using the package *glmulti* for R version 3.0.1 (Calcagno & Mazancourt 2010). We also estimated the goodness-of-fit of the models by estimating the percentage of deviance explained by the complete model compared with the null model (Crawley 2007).

To assess how species composition in each ontogenetic stage was related to disturbance indicators, we used a partial canonical correspondence analysis (CCA), controlling for the effect of soil type. To prevent spurious effects caused by low species abundance and to minimize the risk of type II statistical errors, CCA was performed excluding rare species (those with  $< 5$  individuals) with the package *vegan* for R version 3.0.1 (R Core Team 2013). We used a two-way ANOVA to test for CCA model and axes significance.

#### Results

We recorded 10 862 adult plants ( $362 \pm 92.1$  stems per plot; mean  $\pm$  SD) belonging to 51 species ( $18.5 \pm 3.6$ ). For the sapling assemblage, we recorded 732 stems ( $11.6 \pm 6.5$ ) from 40 species ( $6.7 \pm 2.2$ ). In the seedling community, we recorded 314 stems ( $10.6 \pm 3.5$ ) from 34 species ( $5.1 \pm 1.8$ ). Among the three ontogenetic classes, the most representative families were Euphorbiaceae and Fabaceae, with 10–13 species per ontogenetic class.

In all model sets, the single best model received limited support relative to alternative models (see Table S2, Supporting information). In general, the associations between explanatory and response variables were notably stronger in the adult (21–38% of explained deviance; Fig. 2) and



**Fig. 2.** Predictor variables included in the  $\Delta AICc < 2$  set of models (black bars) and 95% set of models (grey bars) for (a) the species richness  ${}^0D$ , (b) inverse Simpson concentration  ${}^2D$ , (c) stem abundance and (d) community evenness of adult plant communities in the Caatinga forest, Brazil. The importance of each variable is shown by the sum of Akaike weights (axis  $x$ ). The sign ( $\pm$ ) of Akaike weights represents the effect (positive or negative) of each predictor on each response variable based on the model-averaged parameters shown in Table 1. We also indicate the percentage of explained deviance within each panel.

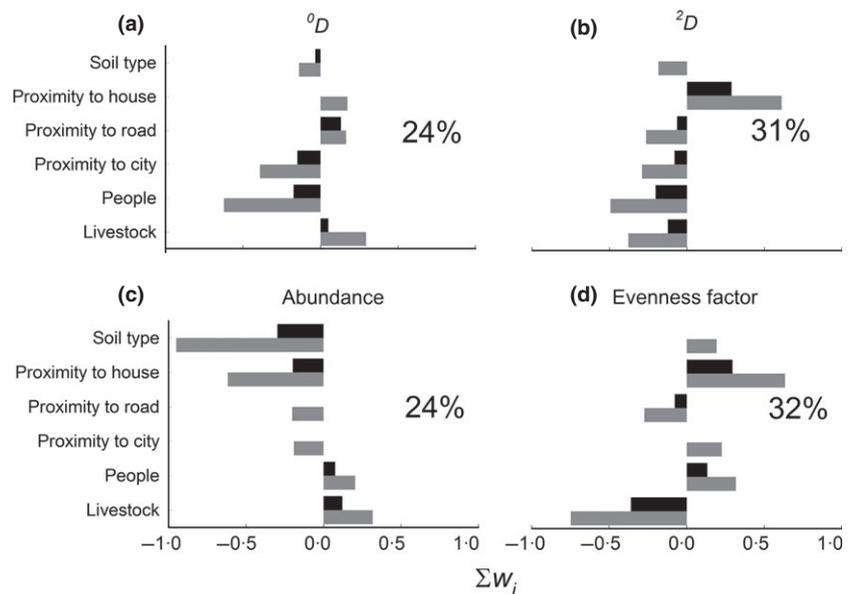
sapling communities (24–32%; Fig. 3) than in the seedling communities, in which models explained less than 24% of total deviance (Fig. 4). In most cases, the indicators of chronic disturbance showed negative associations with  ${}^0D$ ,  ${}^2D$  and stem abundance (Table 1). In fact, considering only the cases in which the explanatory variables appeared in at least one model of the set of best models (i.e. those with a  $\Delta AICc < 2$  indicated with † and ‡ in Table 1, see also Table S2), most associations (16 out of 22, 73%) were negative. This pattern was consistent in all ontogenetic classes. The few positive, but strong associations were found when evaluating the evenness factor, particularly within the adult and sapling assemblages (Table 1).

The indicators of chronic disturbance that best predicted changes in diversity, abundance and evenness of plant communities were ‘People’ (included in 20 out of 56

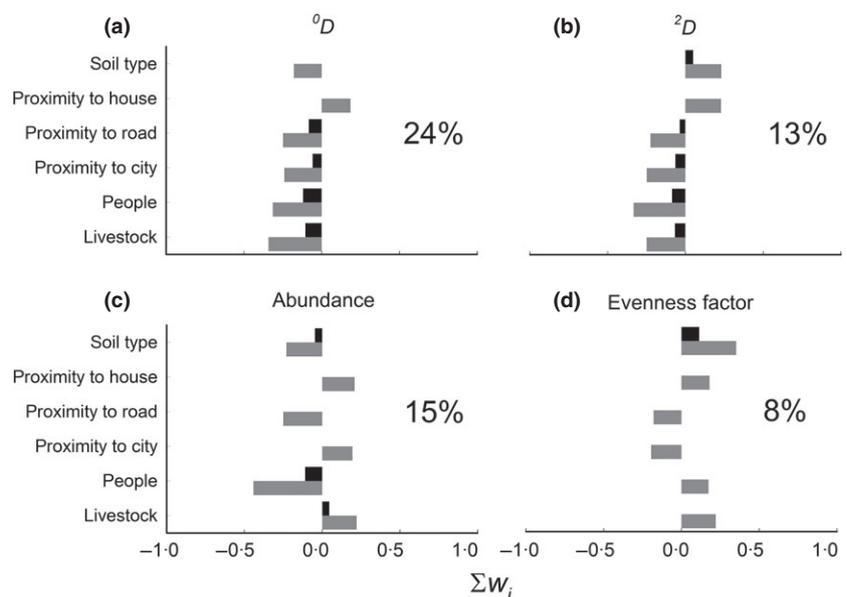
best models, 36%), ‘Livestock’ (36%) and ‘Proximity to house’ (34%) (see Table S3, Supporting information). The high sum of Akaike weights for these three variables further demonstrated their importance to plant communities (Figs 2–4). Yet, the predictive power of each explanatory variable varied across response variables, particularly when considering different ontogenetic classes (Figs 2–4).

In particular, ‘People’ and ‘Livestock’ showed similar impacts on the diversity and evenness of plant communities (Table 1). They were both strongly and negatively related to the number of dominant species ( ${}^2D$ ) in the adult (Fig. 2), sapling (Fig. 3) and seedling (Fig. 4) communities. When considering adults, they were both positively related to species richness ( ${}^0D$ , Table 1), and as a consequence, these two factors were negatively related to community evenness (Fig. 2). However, when assessing the seedling community, both factors were negatively

**Fig. 3.** Predictor variables included in the  $\Delta AICc < 2$  set of models (black bars) and 95% set of models (grey bars) for (a) the species richness  ${}^0D$ , (b) inverse Simpson concentration  ${}^2D$ , (c) stem abundance and (d) community evenness of sapling communities in the Caatinga forest, Brazil. The importance of each variable is shown by the sum of Akaike weights (axis  $x$ ). The sign ( $\pm$ ) of Akaike weights represents the effect (positive or negative) of each predictor on each response variable based on the model-averaged parameters showed in Table 1. We also indicate the percentage of explained deviance within each panel.



**Fig. 4.** Predictor variables included in the  $\Delta AICc < 2$  set of models (black bars) and 95% set of models (grey bars) for (a) the species richness  ${}^0D$ , (b) inverse Simpson concentration  ${}^2D$ , (c) stem abundance and (d) community evenness of seedling plant communities in the Caatinga forest, Brazil. The importance of each variable is shown by the sum of Akaike weights (axis  $x$ ). The sign ( $\pm$ ) of Akaike weights represents the effect (positive or negative) of each predictor on each response variable based on the model-averaged parameters shown in Table 1. We also indicate the percentage of explained deviance within each panel.



**Table 1.** Values of model-averaged parameter estimates ( $\beta$ ) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference for species richness ( ${}^0D$ ), inverse Simpson concentration ( ${}^2D$ ), stem abundance and community evenness for each ontogenetic plant community sampled in the Caatinga forest, Parnamirim municipality, Pernambuco, Brazil

Predictors	${}^0D$		${}^2D$		Abundance		Evenness factor	
	$\beta$	UV	$\beta$	UV	$\beta$	UV	$\beta$	UV
<b>Adults</b>								
Soil type	-0.242	0.774	0.000	0.099	-0.202	4.589	0.003	0.000*
Proximity to house	0.590	2.379	0.835	1.314	-0.207	1.300	0.032	0.002*‡
Proximity to road	-0.132	0.145	-0.010	0.017	-0.002	3.488	0.000	0.000*
Proximity to city	-27.90	159.25	-1.255	10.904	-0.569	2.608	0.045	0.017*
People	0.365	0.027*	-0.077	0.014*‡	0.020	2.305	-0.003	0.000*‡
Livestock	0.506	0.317*‡	-0.085	0.032*‡	-0.050	7.311	-0.109	0.001*‡
<b>Saplings</b>								
Soil type	-0.287	0.798	-0.077	-0.104	-0.281	6.447	0.009	0.001*
Proximity to house	0.015	1.153	1.062	1.255	-0.147	2.073	0.133	0.016*‡
Proximity to road	0.211	0.205*‡	-0.006	7.314	-0.004	3.162	-0.008	0.000*†
Proximity to city	-5.356	78.311	-0.844	0.027*†	-0.011	7.773	0.095	0.103
People	-0.153	0.061*‡	-0.084	0.014*‡	0.000	6.569	0.005	0.000*‡
Livestock	0.126	0.139	-0.150	0.042*‡	0.010	4.371	-0.038	0.000*‡
<b>Seedlings</b>								
Soil type	-0.008	0.226	0.112	0.128*	-0.189	0.004*	0.028	0.002*
Proximity to house	0.426	0.526	0.110	0.250	0.010	0.008*	0.007	0.002*
Proximity to road	-0.896	0.073*‡	-0.041	0.020*†	-0.009	0.000*	-0.001	0.000*
Proximity to city	-1.180	16.935	-0.714	5.653	0.009	0.000*	-0.028	0.041
People	-0.624	0.017*‡	-0.039	0.006*†	-0.012	0.000*	0.000	0.000*
Livestock	-0.135	0.071*†	-0.039	0.013*†	0.000	0.000*†	0.002	0.000*

\*Values with an asterisk indicate cases where the unconditional variance was smaller than the model-averaged parameter estimates, suggesting safety in interpretation of  $\beta$  (Burnham & Anderson 2002). For each response variable and ontogenetic stage, we also indicate the explanatory variables that appeared in one (†) or more (‡) models within the set of best models (see Table S2).

related to species richness, but positively related to evenness (Table 1). This pattern of lower  ${}^0D$ , lower  ${}^2D$  and higher evenness was also observed when assessing the impact of 'People' on the sapling communities (Table 1, Fig. 3).

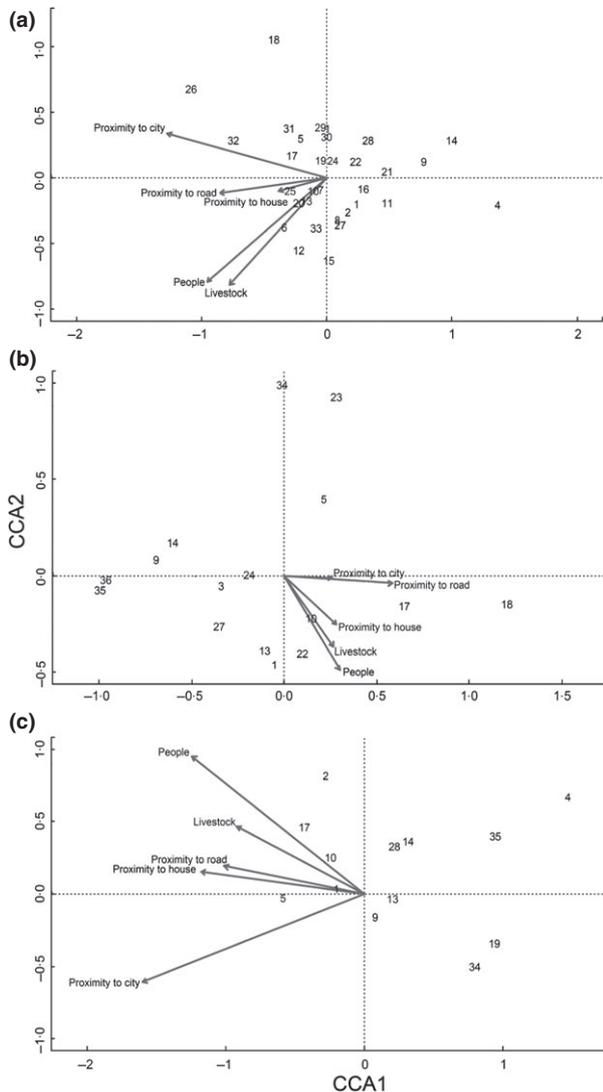
'Proximity to house' was positively associated with the evenness factor of the three ontogenetic classes, with a stronger effect on the adult (Fig. 2) and sapling (Fig. 3) assemblages. Although weaker, 'Proximity to road' was positively related to  ${}^0D$ , but negatively associated with the evenness factor of sapling communities. However, when considering the seedling community, plots closer to roads showed lower  ${}^0D$  and  ${}^2D$ . Interestingly, stem abundance was poorly explained by these indicators of chronic disturbance, although the explained deviances of 'Proximity to house' and 'Proximity to road' were relatively high when considering adult and sapling communities (Figs 2 and 3). In these cases, the unconditional variances were greater than the model-averaged parameter estimates. This suggests caution in the interpretation of such model-averaged parameter estimates, as it indicates that parameter estimates were very spread out around the mean. Only when assessing the seedling community, we found model-averaged parameter estimates higher than the unconditional variances (Table 1).

The first two CCA axes explained 42% and 21%, respectively, of the variation in adult communities species composition under the disturbance indicators (Fig. 5a). In

the sapling communities, these percentages were 36% and 31% (Fig. 5b), whereas in the seedling assemblage, they reached 40% and 32% (Fig. 5c). In all cases (adults, saplings and seedlings), species composition varied significantly with the disturbance predictors ( $P < 0.05$ ). Species such as *Croton sonderianus* and *Jatropha mollissima* were positively related to disturbance indicators in all ontogenetic stages, whereas *Bauhinia cheilantha*, *Fraunhoferia multiflora*, *Myracrodruon urundeuva* and *Senna macranthera* were negatively related to such indicators of disturbance (Fig. 5).

## Discussion

As expected, the indicators of chronic disturbance evaluated in this study showed a negative impact on plant species diversity (both  ${}^0D$  and  ${}^2D$ ) and stem abundance leading to a generalized impoverishment of plant communities across all ontogenetic classes, despite the fact that some species may respond positively to increased disturbance. Furthermore, degradation of plant communities increased with density of people and livestock within the stands of Caatinga vegetation (i.e. additive impacts), supporting a causal connection between rural human populations and the degradation of Caatinga vegetation. Although Caatinga degradation (including desertification) has been widely discussed in the literature (Leal *et al.* 2005; Santos *et al.* 2011), here we offer tangible quantitative



**Fig. 5.** CCA ordination diagrams displaying the plant–species relationships, in distinct ontogenetic stages (a – adults; b – saplings and c – seedlings), with the indicators of chronic disturbance (arrows) recorded at old-growth Caatinga forest sites in Parnamirim municipality, Pernambuco, Brazil. Each arrow points in the direction of maximum change of each disturbance indicator across the diagram, and its length is proportionate to the rate of change in this direction (i.e. disturbance indicators with longer arrows are more closely related to the pattern of species distribution shown in the ordination diagram). Plant species: 1. *Amburana cearensis* (Allemão) A.C. Sm., 2. *Anadenanthera colubrina* (Vell. Brenan), 3. *Aspidosperma pyriforme* Mart., 4. *Bauhinia cheilantha* (Bong.) Steud., 5. *Cnidocolus quercifolius* Pohl, 6. *Cnidocolus vitifolius* (Mill.) Pohl, 7. *Cochlospermum vitifolium* (Willd.) Spreng., 8. *Commiphora leptophloeos* (Mart.) J.B. Gillett, 9. *Croton adamantinus* Müll. Arg., 10. *Croton sonderianus* Müll. Arg., 11. *Cynophalla hastata* (Jacq.) J. Presl, 12. *Dalbergia cearensis* Ducke, 13. *Erythroxylum pungens* O.E. Schulz, 14. *Fraunhoferia multiflora* Mart., 15. *Guapira graciliflora* (Mart. ex J.A. Schmidt) Lundell, 16. *Guettarda angelica* Mart. ex Müll. Arg., 17. *Jatropha mollissima* (Pohl) Baill., 18. *Jatropha ribifolia* (Pohl) Baill., 19. *Manihot pseudoglaziovii* Pax & K. Hoffm., 20. *Mimosa tenuiflora* Benth., 21. *Myracrodruon urundeuva* Allemão, 22. *Piptadenia stipulacea* (Benth.) Ducke, 23. *Poinciana microphylla* (Mart. ex G. Don) L.P. Queiroz, 24. *Poinciana pyramidalis* (Tul.) L.P. Queiroz, 25. *Sapium glandulosum* (L.) Morong, 26. *Schinopsis brasiliensis* Engl., 27. *Senegalia polyphylla* (DC.) Britton, 28. *Senna macranthera* (DC. Ex Collad) H. S. Irwin & Barbeby, 29. *Cordia trichotoma* (Vell.) Arráb. ex Steud., 30. *Ziziphus joazeiro* Mart., 31. *Cereus jamacaru* DC., 32. *Pilosocereus gonunellei* (F.A.C. Weber) Byles & G.D. Rowley, 33. *Pilosocereus pachycladus* F.Ritter, 34. *Varronia leucocephala* (Moric.) J.S. Mill., 35. *Ditaxis desertorum* (Müll. Arg.) Pax & K. Hoffm., 36. *Combretum monetaria* Engl. & Diels, 37. *Jatropha mutabilis* Benth.

evidence (although indirect) for an important ecological impact that has gone unmeasured and little appreciated until now.

These findings reinforce the notions that (i) chronic disturbance can impose gradual (and hence unappreciated) but rather measurable degradation impacts on tropical forests, particularly in socio-ecological contexts marked by poverty in rural populations (Singh 1998; Sagar, Raghubanshi & Singh 2003; Martorell & Peters 2005), (ii) although human density has been considered an important driver of habitat loss in tropical countries (see Aide *et al.* 2013; Laurance, Sayer & Cassman 2014), it should be also considered a proxy of habitat degradation (Leal, Andersen & Leal 2014), and (iii) livestock is able to impose deleterious impacts on plant communities, particularly in dry forests (Carmel & Kadmon 1999; Leal, Vicente & Tabarelli 2003). Finally, as already demonstrated in the case of habitat loss and creation of forest edges in tropical forests (Lôbo *et al.* 2011; Tabarelli *et al.* 2012), few plant species benefit and may eventually proliferate in

chronically disturbed habitats. This is particularly true for species with vegetative spread and high resprouting ability, such as *Croton sonderianus*.

Several processes seem to synergistically operate and underlie the simplification and homogenization of old-growth Caatinga stands under chronic disturbance. First, the potential combination of lower seed availability (Singh, Rawat & Garkoti 1997), failed seed dispersal by wild frugivores (Leal, Andersen & Leal 2014), lower germination rates and higher herbivory by livestock (Papa-christou & Platis 2011; Marcora *et al.* 2013) could explain the lower diversity and simplification of seedling and sapling communities in more populated sites. In addition to bovines, goats are farmed extensively in the Caatinga, with stocking rates frequently exceeding governmental agency technical recommendations aimed at avoiding habitat degradation, as native plants (i.e. leaves, flowers, buds, fruits and bark) represent the main diet component of the goats (Pereira-Filho, Silva & Fontes 2013). Secondly, the replacement of disturbance-intolerant species, such as *B. cheilantha*, *S. macranthera*, *M. urundeuva* and *F. multiflora*, by disturbance-adapted species, such as *C. sonderianus*, *Mimosa tenuiflora* and *J. mollissima*, may permanently alter the structure and composition of plots with higher densities of people and livestock. Finally, local people have been reported to intensively collect plant resources for multiple purposes from medicine to famine

alleviation (Lucena *et al.* 2008). We shall briefly discuss the collection of long-lived, hardwood species for rural fences and constructions (e.g. *M. urundeuva*, *F. multiflora*, *Anadenanthera colubrina*, *B. cheilantha* and *Piptadenia stipulacea*; Ramos *et al.* 2008), and vegetation harvesting for domestic and commercial firewood. In north-east Brazil, 25% of total energy demand is supplied by fuelwood and charcoal; nearly 10 million m<sup>3</sup> year<sup>-1</sup> of fuelwood and charcoal are obtained via deforestation of native vegetation (80%) and managed patches of Caatinga vegetation (1.6%), among other sources (Gariglio *et al.* 2010). Such permanent exploitation of forest resources by one of the largest human populations (in terms of density) living in a semi-arid region is likely to result in plant population collapses and the impoverishment of plant assemblages. On the other hand, disturbance-adapted but not useful species tend to proliferate and cause vegetation biomass decline due to reduced stem density.

#### CONSERVATION AND MANAGEMENT IMPLICATIONS

In many aspects, the Caatinga biota illustrates the multiple values and the challenges experienced by seasonally dry tropical forests and some semi-arid biotas. First, they are frequently recognized as Hotspots, Global Wilderness (Gil 2002) or important centres of endemism (Pennington, Lavin & Oliveira-Filho 2009). Secondly, they have been neglected in terms of conservation efforts and public policies devoted to sustainable development (Sanchez-Azofeifa *et al.* 2005; Santos *et al.* 2011). Most seasonally dry tropical forests still lack an effective network of protected areas (e.g. <2% of Caatinga territory is protected), with many strictly protected areas experiencing subsistence and economic activities, including low-input farming, livestock production, wood harvesting and plant collection (Leal *et al.* 2005). Thirdly, dry forests support a large density of increasing and usually poor human populations, which are heavily dependent on forest resources for their livelihoods (Blackie *et al.* 2014). Thereby, they are experiencing gradual, but persistent degradation processes, ranging from the extinction of endemic and emblematic species (e.g. the Spix's macaw in the Caatinga region) to alarming rates of desertification (Leal *et al.* 2005; MMA & IBAMA 2011). Finally, this fragile ecosystem is expected to confront drastic shifts in patterns of rainfall in response to global warming, thus scaling-up poverty-driven degradation (IPCC 2007; Blackie *et al.* 2014).

This research demonstrates the potential negative impacts caused by human-imposed chronic disturbance on Caatinga vegetation and reinforces the notion that disturbance resulting from an extractivism-based and subsistence economy is probably driving old-growth forest stands towards shrub-dominated secondary stands (Leal *et al.* 2005). These chronic, small-scale human disturbances might accumulate into major ecological impacts, ranging from biological impoverishment, as suggested here, to desertification. This possibility requires further

investigation as it poses drastic challenges to reconcile human needs, biological conservation and provision of ecosystem services considering the current socio-ecological context experienced by tropical biotas. In many situations, the taxonomic impoverishment of tropical plant assemblages is associated with extirpation of key ecological plant groups (e.g. old-growth flora), reduced functional diversity and collapse of ecosystem services (Tabarelli, Lopes & Peres 2008).

Assuming increasing pressure on forest resources worldwide (Laurance, Sayer & Cassman 2014), chronic disturbance should not continue to be neglected across initiatives devoted to biodiversity conservation and rural development. Basically, we argue for (i) research and rural programmes able to support better practices in terms of land use and sustainable collection of forest resources, particularly in terms of livestock management and wood collection (i.e. improved land sharing via adaptive and mitigative approaches), (ii) improving governance and law enforcement in order to move forest extractivism towards sustainable standards, and (iii) expanding the coverage and effective implementation of strictly protected areas, that is the elimination of livestock and collection of forest products inside protected areas. Such commitment appears to be feasible in the face of increasing local and global concerns relative to the socio-ecological problems (see Melo *et al.* 2014). Unless issues of land sharing and land sparing are appropriately addressed in the Caatinga, human exploitation and habitat degradation will unavoidably lead to desertification and loss of this irreplaceable biome.

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#### Data accessibility

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.m7d8m> (Ribeiro *et al.* 2015).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Detailed Mantel test results description.

**Table S1.** Predictors of chronic disturbance measured and their range.

**Table S2.** Complete results of information-theoretic-based model selection and multimodel inference.

**Table S3.** Frequency of occurrence of each explanatory variable within the set of best models.