

Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation

Kátia F. Rito^{*,1,2}, Víctor Arroyo-Rodríguez², Rubens T. Queiroz³, Inara R. Leal⁴ and Marcelo Tabarelli⁴

¹Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, 50690-901 Pernambuco, Brazil; ²Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, 58190 Michoacán, Mexico; ³Department of Systematics and Ecology, Universidade Federal da Paraíba, João Pessoa, 58051-900 Paraíba, Brazil; and ⁴Department of Botany, Universidade Federal de Pernambuco, Recife, 50670-901 Pernambuco, Brazil

Summary

1. Seasonally dry tropical forests (SDTFs) are one of the most threatened forests world-wide. These species-rich forests not only cope with several acute (e.g. forest loss) and chronic (e.g. overgrazing and firewood extraction) human disturbances but also with climate change (e.g. longer and more severe droughts); yet, the isolated and combined effects of climate and acute and chronic human disturbances on SDTF vegetation are poorly known.

2. Given the environmental filter imposed by drought in SDTFs, the composition and structure of vegetation is expected to be strongly associated with annual precipitation, and thus the effects of human disturbances on vegetation may also depend on precipitation (i.e. interacting effect).

3. We tested these hypotheses in the Brazilian Caatinga – a SDTF threatened by climate change and human disturbances. We evaluated the isolated and combined (both additive and multiplicative) effect of precipitation, a chronic disturbance index and acute disturbance (landscape forest cover) on the diversity, stem density, evenness, taxonomic composition and above-ground biomass of adult trees and shrubs across 19 0.1-ha plots distributed along a disturbance and precipitation gradients.

4. We recorded 5541 stems from 129 species. Precipitation showed a stronger (positive) effect on species diversity than acute and chronic disturbances and, as expected, the effect of disturbance depended on precipitation (interacting effect): that is, species diversity (especially the number of rare species) was negatively related to forest loss but positively related to chronic disturbance in wetter sites, whereas in drier sites, species diversity was weakly related to forest cover, but strongly and negatively related to chronic disturbance. Contrary to species diversity, community evenness, stem density and biomass were weakly related to all predictors.

5. *Synthesis.* Precipitation appears to be a strong environmental filter determining the distribution of water-demanding plant species. Chronic disturbance in wetter (high-productive) forests may favour species diversity by increasing ecosystem heterogeneity (intermediate disturbance hypothesis). Yet, the biodiversity costs of chronic disturbance are higher in drier (low-productive) forests; that is, there is a co-limitation imposed by drought and disturbance in drier forests. Overall, our findings indicate that rapid climatic changes in the region will probably have strong negative effects on this seasonally dry tropical forest.

Key-words: anthropogenic disturbance, biodiversity loss, climate change, seasonally dry tropical forest, semi-arid ecosystem, woody flora

Introduction

Anthropogenic disturbances encompass a large array of phenomena, from local habitat loss and perturbation to global

climate change, and are important drivers of biodiversity loss in the tropics (Malhi *et al.* 2014). This is particularly true in the case of seasonally dry tropical forests (SDTFs), which has become one of the most threatened ecosystems in the world due to massive deforestation (Miles *et al.* 2006). Biodiversity persistence in SDTFs can also be threatened by climate

*Correspondence author. E-mail: rito_pereira@yahoo.com.br

change, as climate extremes impose strong environmental filters within this ecosystem (Moro *et al.* 2015). Dry forests will face an increase in evaporation and temperature by 2100 (Burkett *et al.* 2014), leading to longer and more severe droughts that can limit biodiversity persistence by (i) reducing primary net production (Zhao & Running 2010), (ii) inducing changes in annual population growth (Ureta *et al.* 2012) and (iii) increasing the probability of species extinction (Araújo & Rahbek 2006). In fact, drought can limit tree recruitment and survival in dry forests, potentially leading these ecosystems to new stable states, such as shrublands or grasslands (Anderson-Teixeira *et al.* 2013).

In addition to deforestation (acute disturbance) and climate change, most SDTFs historically support low-income rural populations widely dependent on forest resources for proper livelihood, such as fodder, firewood and timber (Singh 1998; Davidar *et al.* 2010; Ribeiro *et al.* 2015). Such a frequent and continuous removal of small portions of forest biomass is known as 'chronic anthropogenic disturbance' (Singh 1998). Yet, the impacts of chronic disturbance on biodiversity persistence and on the provision of ecosystem services have just started to be addressed globally (Ribeiro *et al.* 2015; Arroyo-Rodríguez *et al.* 2015; Barlow *et al.* 2016). We refer, for instance, to decreases in plant population densities (Hernández-Oria, Chavez & Sánchez 2006), limited seedling establishment and disrupted forest regeneration (Singh, Rawat & Garkoti 1997), decreases in tree species diversity and stem abundance (Ribeiro *et al.* 2015), and changes in forest structure, species composition (Kumar & Shahabuddin 2005) and tree phylogenetic diversity and structure (Ribeiro *et al.* 2016). Furthermore, there have been increasing evidence that climate change and disturbance can have complex (sometimes synergistic) effects on biodiversity (Travis 2003; Ponce-Reyes *et al.* 2013; García-Valdés *et al.* 2015), with hot and arid environments likely to be at greatest risk (Anderson-Teixeira *et al.* 2013; Gibb *et al.* 2015). Yet, to our knowledge, the isolated and combined effects of climate and acute and chronic human disturbances on SDTF biodiversity have never been explored.

Like other SDTFs, the Brazilian Caatinga vegetation is a diverse and threatened biota (Leal *et al.* 2005). This dry forest and scrub vegetation region stretches over 800 000 km², supporting one of the most populous semi-arid regions globally (i.e. 26 inhabitants km⁻²; 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 & IBAMA 2010). Unfortunately, the region will probably face the most impressive increase in temperature among Brazilian regions (1.8 °C to 4 °C in A2 and B2 scenarios; IPCC – Intergovernmental Panel on Climate Change 2001) and a reduction in rainfall of –22% by 2100 (Magrin *et al.* 2014). These climatic changes may threaten local populations because of low tolerance of agricultural cultures to climatic variations (Barbieri *et al.* 2010). Exposed to chronic anthropogenic disturbance and covering a large range of climatic variation (e.g. mean annual precipitation ranges between 240

and 1500 mm; Sampaio 1995), the Caatinga vegetation offers an interesting opportunity to examine potential effects on biodiversity emerging from relationships between local human disturbance and climate change.

To address this issue, we examined a 21 430-ha Caatinga landscape with a long history of human disturbance and naturally exposed to a rainfall gradient. In particular, we examined the isolated and combined (both additive and multiplicative) effect of precipitation, three predictors of chronic disturbance (i.e. distance to nearest farm, distance to nearest road, total goats' and cattle' faeces) combined in an index, and one predictor of acute disturbance (i.e. forest loss in the local landscape surrounding the plot) on the composition and structure of woody plant assemblages. Given the well-known environmental filter imposed by drought to vegetation (Esquivel-Muelbert *et al.* 2016), specially in SDTFs (Choat *et al.* 2012; Crowther *et al.* 2015; Rugemalila, Anderson & Holdo 2016) and the global effect that annual precipitation is known to have on species diversity and vegetation structure (e.g. Gentry 1988; Esquivel-Muelbert *et al.* 2016; Poorter *et al.* 2016), we expect that the composition and structure of vegetation is strongly associated with annual precipitation, being the species diversity (especially the number of rare species), stem density and tree biomass higher in wetter plots than in drier plots (Gentry 1988; Esquivel-Muelbert *et al.* 2016). We also hypothesized that the effect of human disturbance on vegetation depends on precipitation (i.e. interacting effect), being stronger in wetter plots, where we expect to record higher species richness. Alternatively, the effect of disturbance would be stronger in drier plots because of the co-limitation imposed by drought and disturbance on vegetation (synergistic effect). This study contributes to improve our understanding of the effects of human disturbances and precipitation on the structure and diversity of vegetation in SDTFs, thus allowing to predict (and possibly mitigate) future changes in vegetation within this vanishing biome.

Materials and methods

STUDY AREA

The Caatinga is a mosaic of SDTFs and scrubby vegetation (Pennington, Lavin & Oliveira-Filho 2009) that is restricted to Brazil. Annual temperature averages 25 °C, and average annual precipitation ranges from 240 to 1500 mm, being an important driver of plant composition and structure in the region (Sampaio 1995). The majority of rainfall is concentrated in 3 months year⁻¹ and there is a high interannual variability in rainfall with severe droughts, which may extend for years (Sampaio 1995; Chiang & Koutavas 2004).

Caatinga has suffered deforestation since the sixteenth century for agriculture and livestock creation (Leal *et al.* 2005; IBGE – Instituto Brasileiro de Geografia e Estatística 2010). In addition, Caatinga region supports a low-income rural population, which depends on different forest products for medicinal purposes, animal and human food, and fuelwood (Albuquerque *et al.* 2007; Nascimento *et al.* 2012; Ramos & Albuquerque 2012). Hunting and overgrazing by stock (goats and cattle) also represent important drivers of chronic disturbances in the region (Ribeiro *et al.* 2015, 2016).

STUDY SITES

We studied the Caatinga vegetation of the Catimbau National Park, Pernambuco state, Brazil (8°24'00" and 8°36'35" S; 37°0'30" and 37°1'40" W). This park has an area of c. 60 000 ha, and shows a high variation in relief and precipitation (i.e. 480–1100 mm year⁻¹). Approximately 70% of the park is dominated by litosols. Although the Park was created in 2002, people living inside its area still use Caatinga resources for their livelihood, specially firewood collection and extensive livestock.

Based on the RapidEye satellite imagery, maps of soil, precipitation and field explorations, we selected 19 areas to cover a wide range of disturbance and precipitation levels (Fig. 1). We established 19 20 × 50-m plots with a minimum 2-km distance within a 21 430-ha area dominated by old-growth vegetation exposed to chronic disturbance. Mean temperature within the plots only varied between c. 20 to 22 °C, and mean temperature was not related to precipitation ($r = -0.25$, $P = 0.52$). To control for the potential effects of terrain slope and soil characteristics on species responses (Pinheiro, Rodal & Alves 2010), all plots were located in areas with the same soil type (sand soil) and similar slope (flat terrain).

PREDICTORS OF DISTURBANCES AND PRECIPITATION DATA

We adopted a landscape perspective to obtain a gradient of chronic disturbance intensity. We assessed three metrics of chronic disturbance that have been used in previous studies of tropical forests, including: (i) distance to nearest farm (Sagar, Raghubanshi & Singh 2003; Martorell & Peters 2005; Leal, Andersen & Leal 2014); (ii) distance to nearest road (Sagar, Raghubanshi & Singh 2003; Leal,

Andersen & Leal 2014; Ribeiro *et al.* 2015); and (iii) total goats' and cattle's faeces within each plot (Martorell & Peters 2005). All metrics are proxies of human pressure (e.g. logging, cutting and hunting) and overgrazing by livestock and goat. Following previous studies (Martorell & Peters 2005; Leal, Andersen & Leal 2014; Ribeiro *et al.* 2015), we opted for these proxies because chronic disturbances are very difficult to quantify directly in the field. We used a RapidEye satellite imagery in ArcGIS 10.1 software to assess the metrics of distance and calculated them considering the relief cost. We used the *CostDistance* tool of ArcGis, which uses an elevation raster to calculate the shortest weighted distance (or accumulated travel cost) considering variations in elevation (<http://pro.arcgis.com/en/pro-app/tool-reference/spatial-analyst/understanding-cost-distance-analysis.htm>). According to Martorell & Peters (2005) and Ribeiro *et al.* (2016), all chronic disturbance indicators were combined in a single chronic disturbance index using a principal component analysis (PCA) performed with the *stats* package for R (R Core Team 2016). The first axis of PCA explained 58% of data variance and was used as the chronic disturbance index.

We also assessed landscape-scale vegetation cover (VC) – an important indicator of acute disturbance (Gould 2000; Fahrig 2013). VC was assessed within a 1-km radius (buffer) from the centre of each plot. We considered this buffer size to avoid overlap among buffers and thus increase the independence among samples (Eigenbrod, Hecnar & Fahrig 2011). VC data were obtained from a vegetation classification map. This map was performed from RapidEye satellite imagery by unsupervised classification based on clusters of statistically different sets of multiband data (radiance expressed by their radiance averaged over each spectral interval). Classification accuracy was assessed with 172 field observations points, and was very high (c. 80% of correctly classified points).

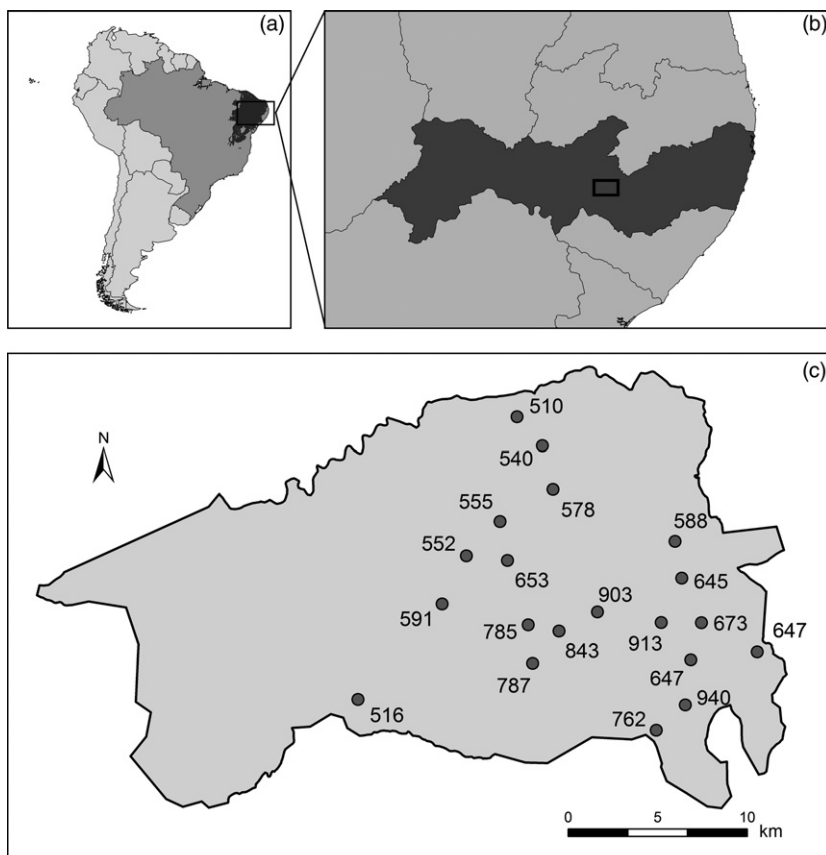


Fig. 1. Location of the study region in Northeastern Brazil (a), and the study landscape (rectangle) in the Pernambuco state (shaded area in b). The Catimbau National Park and the location of all 0.1-ha plots ($n = 19$) is also indicated (c). Numbers in (c) represent the mean annual precipitation in each plot.

Regarding the environmental variables related to water availability within the plots, we considered: (i) mean annual precipitation; (ii) mean annual climatic water deficit; (iii) precipitation of driest quarter; and (iv) precipitation of driest month. Yet, they were all strongly correlated among each other ($r > 0.85$, $P < 0.001$, in all cases), and when assessing the variance inflation factor (VIF) [i.e., $VIF = 1/(1 - R^2)$] of all pairwise comparisons, we found that all VIF values were >10 , thus indicating strong collinearity among variables (Jou, Huang & Cho 2014). We therefore focused the study on mean annual precipitation, which is widely used to measure climate change (Houghton *et al.* 2001), and is an important driver of species richness (Gentry 1988) and performance (Weltzin *et al.* 2003). In fact, in the Caatinga ecosystem (Prado 2003) and other SDTFs (Hirota *et al.* 2011; Choat *et al.* 2012; Rugemalila, Anderson & Holdo 2016), annual precipitation can have a strong influence on vegetation composition and structure, and is the principal factor influencing tree density in STDFs when compared to other climatic variables (Crowther *et al.* 2015). Mean annual precipitation within each plot was obtained from the updated WorldClim global climate data repository (Hijmans *et al.* 2005), with 30-arc second resolution or about 1-km spatial resolution along the equator (www.worldclim.org), using the *maptools* package for R (Bivand & Lewin-Koh 2015). Mean annual precipitation in the plots ranged from 510 to 940 mm.

PLANT SURVEY AND COMMUNITY STRUCTURE

We sampled all shrubs and trees with diameter at soil height (DAS) ≥ 3 cm and total height ≥ 1 m (Rito *et al.* 2016). We identified all individuals to the species level, and measured the DAS and total height to calculate the stem density and total plant above-ground biomass per plot. Total above-ground biomass was calculated using an allometric equation for Caatinga vegetation ($Biomass_{kg} = 0.173 DAS_{cm}^{2.295}$) as proposed by Amorim, Sampaio & Araújo (2005), which is based on basal area and height (Rito *et al.* 2016).

We used the coverage estimator recommended by Chao & Jost (2012) to estimate the accuracy of diversity inventories:

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

where f_1 and f_2 are the number of species with one individual and with two individuals in the sample, respectively, and n is the number of individuals. Sample coverage was very high ($>93\%$) in all sites (Table S1, Supporting Information), indicating that our sampling effort was adequate, and that our diversity estimates were not biased by differences in sample coverage among sites (Chao & Jost 2012; Chao *et al.* 2014). To assess changes in species diversity, we used Hill numbers of order 0 (0D , species richness), 1 (1D , exponential Shannon entropy) and 2 (2D , inverse Simpson concentration) (Jost 2006, 2007), calculated with the *entropart* package for R (Marcon, Zhang & Hérault 2014). 0D is not sensitive to species abundances and thus gives disproportionate weight to rare species (Jost 2006). 1D weighs each species according to its abundance in the community, being interpreted as the number of 'common' or 'typical' species in the community (Jost 2006). Finally, 2D favours abundant species, and is actually interpreted as the number of 'very abundant' or 'dominant' species in the community. Jost (2006) details the formulas for calculating these diversity measures. We also assessed changes in community evenness with the evenness factor (EF) proposed by Jost (2010): $EF = {}^2D/{}^0D$. We selected this index because it is based on Hill numbers, and is very easy to interpret. EF simply represents the proportion of dominant species in the community. It ranges between 1

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

DATA ANALYSIS

To test the isolated and combined (both additive and multiplicative) effect of precipitation and each predictor of chronic and acute disturbances on each response variable, we used generalized linear models. We fixed a Gaussian error distribution for continuous response variables (i.e. 1D , 2D , EF and total above-ground biomass), and a Poisson error distribution for count-dependent variables (0D and stem density) (Crawley 2007). To assess the independency of predictor variables we assessed the collinearity among predictors with the VIF using the *car* package for R. All VIF values were ≤ 1.06 (vegetation cover = 1.06; chronic disturbance index = 1.06; precipitation = 1.03), suggesting independence among predictors (Jou, Huang & Cho 2014). We also tested the correlation among pairs of predictor variables and all correlation values were very low ($r < 0.24$; $P > 0.33$, in all cases).

We evaluated the relative effect of each predictor on each response variable with a multimodel inference approach (Burnham & Anderson 2002) using the *glmulti* package for R. Although we considered five different terms in the models (i.e. VC, vegetation cover; CDI, chronic disturbance index; PREC, precipitation; and two interaction terms, PREC:VC and PREC:CDI), we limited the maximum number of terms in the models to three to avoid overfitting. Thus, for each response variable we constructed 26 models, which included the isolated and combined (both additive and multiplicative) effect of chronic and acute disturbances and precipitation to a maximum of three predictive terms per model (Tables S2–S7). We computed the Akaike's information criterion corrected for small samples (AICc) for each model, and obtained model-averaged parameter estimates using Akaike weights (w_i). To correct for overdispersion associated with count data, 0D and stem density were assessed with qAICc instead of AICc values (Calcagno & Mazancourt 2010). The set of models for which Σw_i was 0.95 represents a set that has 95% probability of containing the best model (Burnham & Anderson 2002). To be more conservative, a given explanatory variable was considered an important predictor for a given response variable if the following three criteria were met: (i) it showed a high Σw_i (i.e. considering all candidate model in which it appeared); (ii) it was present in at least one of the most plausible models; and (iii) the model-averaged parameter estimate was higher than its unconditional variance (i.e. it did not include zero). The most plausible models were those that, compared to the best model [i.e. the one with lowest (q)AICc value], showed a difference in (q)AICc < 2 (Burnham & Anderson 2002). We calculated the percentage of explained deviance by each model compared with the deviance explained by the null model (Crawley 2007). We then considered the mean percentage of explained deviance by the most plausible models [i.e. those with $\Delta(q)AICc < 2$] as a measure of goodness-of-fit of the best models (i.e. a proxy of the effect size of the most important explanatory variables on each response variable). To assess whether the study plots can be considered independent samples, we tested for autocorrelation patterns of residuals for each response variable model using the *acf* (autocorrelation function estimator) function in the *stats* package for R (R Core Team 2016). Because after a visual inspection of the autocorrelation function plots we did not detect any autocorrelation pattern in the data set residuals, we considered the plots as independent samples in our analyses.

Finally, we performed a canonical correspondence analysis (CCA) to identify the predictor variables with highest impact on species composition. Following Garmendia *et al.* (2013) and Russildi *et al.*

(2016) we excluded rare species (i.e. those with <5 stems) to prevent spurious effects caused by the distribution of rare species and to minimize risk of type II statistical error. The CCA analysis was carried out with the *vegan* package for R (Oksanen *et al.* 2016).

Results

We recorded 5541 stems belonging to 129 species (25.1 ± 8.9 species per plot; mean \pm SD) and 31 families. The most speciose family was Fabaceae (28% of species), followed by Euphorbiaceae (14%) and Myrtaceae (8%). The stem density per plot varied from 139 to 440 stems/1000 m² (292 ± 87 stems/1000 m²), and total above-ground biomass per plot varied from 4 962.7 to 43 588.2 kg ($14 690.8 \pm 9 676.2$ kg).

Considering the mean percentage of explained deviance by the most plausible models, all diversity measures (${}^0D = 50.8\%$, ${}^1D = 46.9\%$, ${}^2D = 41.1\%$) were strongly related to precipitation and human disturbance (Fig. 2a–c; Tables S2–S4). Yet, community evenness, stem density and biomass were weakly related to all predictors (Fig. 2d–f; Tables S5–S7). Precipitation (PREC) showed a stronger effect on all diversity measures than human disturbance (VC and CDI), as it showed a relatively high Σw_i (Fig. 2a–c), it was present in at least one of the best models (Fig. 2a–c; Tables S2–S4), and it showed parameter estimates different from zero (Table 1), thus meeting our three criteria for

important variables. In particular, 0D , 1D and 2D increased with PREC, especially 0D , thus indicating that such increase is particularly important for rare species. Species richness (0D) was also positively related to vegetation cover (VC) and negatively related to chronic disturbance (CDI) (Fig. 2a; Table 1). Nevertheless, 1D and 2D were weakly related to both metrics of human disturbance (VC and CDI) (Fig. 2b and c), as (i) VC was not included in the set of best models for 1D and 2D (Table S3 and S4); and (ii) parameter estimates (β) for CDI included zero (Table 1).

Supporting the hypothesis that precipitation mediates the effect of human disturbance on plant assemblages, both interaction terms (PREC:VC and PREC:CDI) were strongly related to 0D , 1D and 2D (Fig. 2a–c), being these interaction terms included in the set of best models for these three response variables (Table S2–S4). In particular, the positive relationship between VC and each diversity measure (0D , 1D and 2D) tended to be more pronounced at high precipitation levels (Fig. 3b, d and f), particularly when considering 0D , thus indicating that such interacting effect of PREC and VC is particularly strong on rare species. The effect of CDI on 0D , 1D and 2D also depended on precipitation, with a negative effect on species diversity in drier plots, but a strong positive effect in wetter plots (Fig. 3a, c and e). Based on the Cook's distance test, we did not find evidence that these trends were driven by data outliers (Table S8).

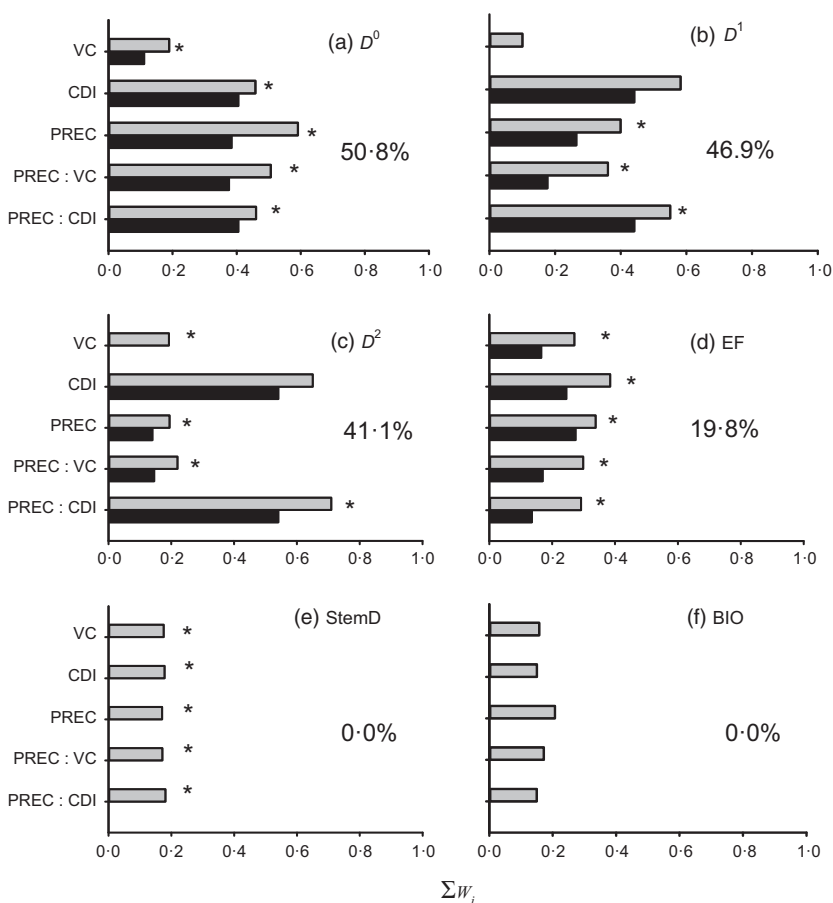


Fig. 2. Response of species diversity (Hill numbers of order 0, 1 and 2; panels a, b, c), community evenness (d), stem density (e) and above-ground biomass (f) of woody plant assemblages to five explanatory variables in the Catimbau National Park, Brazil: VC (vegetation cover), human chronic disturbances (CDI), precipitation (PREC) and two interaction terms (PREC:VC and PREC:CDI). The explanatory variables included in the $\Delta AIC_c < 2$ set of models (black bars) and 95% set of models (grey bars) are indicated. The sum of Akaike weights (Σw_i) is a proxy of the importance of each variable. We indicate the parameters that were more accurate, that is, those higher than the unconditional variance with asterisks (see Table 1). The mean percentage of deviance explained by the most parsimonious models for each response variable is included as a proxy of goodness-of-fit.

Table 1. Results of information-theoretic-based model selection and multimodel inference for assessing additive and multiplicative effects of precipitation (PREC) and anthropogenic disturbance predictors on species diversity (Hill numbers of order 0, 1 and 2), community evenness (EF), stem density (StemD) and above-ground biomass (BIO) in 19 plots located within the Catimbau National Park, Brazil. Disturbance predictors included chronic disturbance index (CDI) and acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot). The model-averaged parameter estimates (β) and the unconditional variance (UV) are indicated. The sign (+/−) of each parameter represents the effect (positive or negative) of each predictor on each response variable (summarized in Fig. 2). The β values that are more accurate (i.e. those that were higher than the UV) are indicated in boldface

	⁰ D		¹ D		² D		EF		StemD		BIO	
	β	UV	β	UV	β	UV	β	UV	β	UV	β	UV
VC	2.28 × 10⁻²	0.43 × 10⁻²	7.09 × 10 ⁻²	1.54 × 10 ⁻¹	5.41 × 10⁻²	3.91 × 10⁻²	1.52 × 10⁻³	2.41 × 10⁻⁵	8.96 × 10⁻⁴	5.93 × 10⁻⁴	−3.23 × 10¹	8.26 × 10⁴
CDI	−2.81 × 10⁻¹	1.34 × 10⁻¹	−6.74	52.67	−5.68	27.89	−3.85 × 10⁻²	6.55 × 10⁻³	7.05 × 10⁻⁴	4.98 × 10⁻⁴	1.29 × 10 ²	3.82 × 10⁶
PREC	3.67 × 10⁻³	0.07 × 10⁻³	1.17 × 10⁻²	2.46 × 10⁻³	2.29 × 10⁻³	4.38 × 10⁻⁴	−1.24 × 10⁻⁴	3.06 × 10⁻⁷	−5.36 × 10⁻⁶	3.76 × 10⁻⁸	3.19	9.86 × 10²
PREC:	−2.15 × 10⁻⁵	7.76 × 10⁻⁹	3.19 × 10⁻⁹	2.66 × 10⁻⁷	5.67 × 10⁻⁶	4.78 × 10⁻⁸	−4.78 × 10⁻⁸	3.19 × 10⁻¹¹	3.02 × 10⁻⁷	4.15 × 10⁻¹²	2.43 × 10⁻²	1.04 × 10⁻¹
VC	3.41 × 10⁻⁴	1.96 × 10⁻⁷	7.94 × 10⁻³	7.70 × 10⁻⁵	6.61 × 10⁻³	4.04 × 10⁻³	3.60 × 10⁻⁵	9.04 × 10⁻⁹	1.01 × 10⁻⁵	9.49 × 10⁻¹⁰	−1.43 × 10⁻¹	5.83
PREC:												
CDI												

When assessing variations in species composition associated with each environmental metric, the first and second CCA axes explained 47% and 30% of the variation in species composition respectively (Fig. 4). No predictor variable was significantly associated with species composition, but precipitation showed a stronger effect ($\chi^2 = 0.37$, $P = 0.06$) than human disturbances (VC: $\chi^2 = 0.26$, $P = 0.44$; CDI: $\chi^2 = 0.25$, $P = 0.52$). The CCA analysis shows some species more strongly related to sites with high precipitation (e.g. *Guapira graciliflora*, *Pilosocereus pachycladus*, *Strychnos rubiginosa*) and low precipitation (e.g. *Croton heliotropifolius*, *Pilosocereus gounellei*, *Croton argyrophyloides*, *Ziziphus joazeiro*, *Evolvulus linoides*, *Cnidocolus obtusifolius*; Fig. 4). Other species seem to be positively associated with sites surrounded by higher vegetation cover (e.g. *Lippia grata*, *Eugenia spl.*, *Psidium brownianum*) and another species with sites with higher chronic disturbance level (e.g. *Senegalia polyphylla*, *Croton grewoides*, *Croton nepetifolius*).

Discussion

Our results suggest that annual precipitation and human disturbances are emerging forces shaping woody plant assemblages in the Brazilian Caatinga vegetation, particularly affecting species diversity. As expected for a SDTF, precipitation shows a strong positive effect on species diversity, even stronger than the effect of acute (i.e. forest loss in the local landscape surrounding the plot) and chronic disturbances (i.e. three predictors of chronic disturbance combined in an index). In fact, the effects of disturbances on species diversity seem to be mediated by precipitation (interacting effect). In particular, species diversity (especially the number of rare species) is negatively related to forest loss but positively related to chronic disturbance in wetter sites, whereas in drier sites, species diversity is weakly related to forest cover, but strongly and negatively related to chronic disturbance. Contrary to species diversity, community evenness, stem density and above-ground biomass are weakly related to precipitation and human disturbance. Although these associations should be viewed with care (note that our sample size is relatively small and we do not have a wide range of variation in forest cover), we describe below some potential mechanisms that can explain these findings, as well as some important ecological and conservation implications.

The importance of precipitation for species diversity is not surprising. Both direct and indirect measures of water availability, such as average precipitation, are known to affect plants across multiple levels of biological organization (Engelbrecht *et al.* 2007; Gutiérrez *et al.* 2014; Crowther *et al.* 2015; Seiler *et al.* 2015; Hiltner *et al.* 2016). The 'dry tolerance' hypothesis actually predict that tree taxa are nested along precipitation gradients, with a larger number of taxa (including many rare species) restricted to wet areas, and those tolerant to seasonal drought occurring along a wider portion of the precipitation gradient (Esquivel-Muelbert *et al.* 2016). Our findings are in agreement with this hypothesis

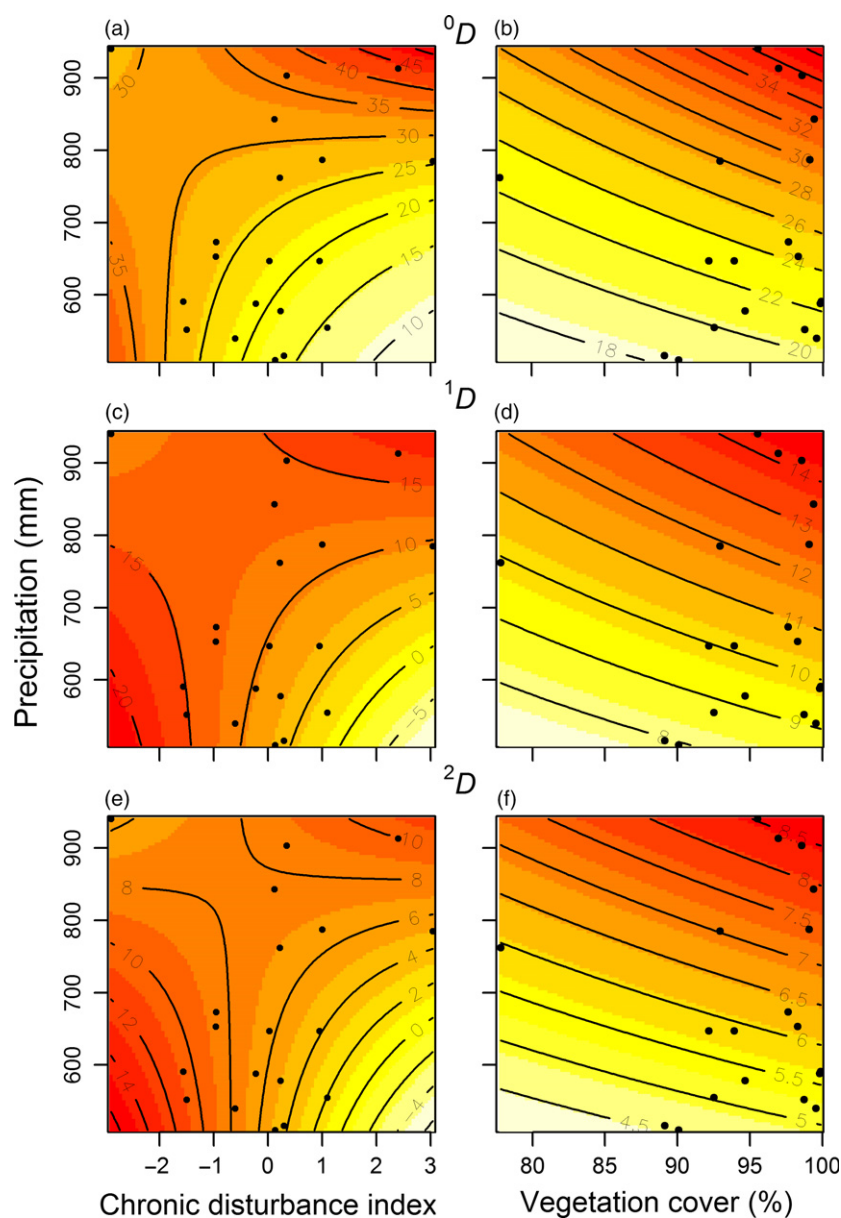


Fig. 3. Contour plots showing model predictions for the additive and interactive effect of precipitation and acute and chronic anthropogenic disturbances on species diversity [Hill numbers of order 0 (a and b), 1 (c and d) and 2 (e and f)] of woody plant assemblages in the Brazilian Caatinga. The original data sets are included within each panel. [Colour figure can be viewed at wileyonlinelibrary.com]

(see Table S9), and suggest that water availability represents a strong environmental filter that limits the occurrence of water-demanding plant species (Grime, Hodgson & Hunt 1988; Prentice *et al.* 1992; Seiler *et al.* 2015). The decrease in water availability increases the physiological stress of plants, limiting biomass production and fitness, potentially leading to the death of stress-sensitive species (Engelbrecht *et al.* 2007; Santos *et al.* 2014; Figueiredo *et al.* 2015). We refer, for example, to large trees from rare species that occur principally in wetter sites (e.g. *G. graciliflora*, *Sapium glandulosum*, *Handroanthus impetiginosus*, *Libidibia ferrea*; Table S9).

More interestingly, our findings add to an increasing line of evidence suggesting that the effects of human disturbance on biodiversity depend on climatic variables, such as annual precipitation (Mantyka-Pringle, Martin & Rhodes 2012; Gibb *et al.* 2015; Mantyka-Pringle *et al.* 2015). For example, in a

meta-analysis of different biological groups, Mantyka-Pringle, Martin & Rhodes (2012) find that habitat disturbance shows weaker effects on populations and assemblages in regions where climate change has increased the average rainfall over time. However, Gibb *et al.* (2015) demonstrate that ant species richness is higher in disturbed than in undisturbed areas, especially under high precipitation scenarios. Our results support Gibb *et al.* (2015)'s findings, once we also find that in wetter forests chronic disturbance increases species diversity, especially the number of rare species. This pattern is consistent with the intermediate disturbance hypothesis (Grime 1973), as chronic disturbance in wetter (and more productive) forests may contribute to increase ecosystem heterogeneity and limit the proliferation of strong competitors, thus favouring the persistence of a larger number of inferior competitors (Orrock & Watling 2010). In contrast to wet forests, drier forests maintain impoverished assemblages, especially when

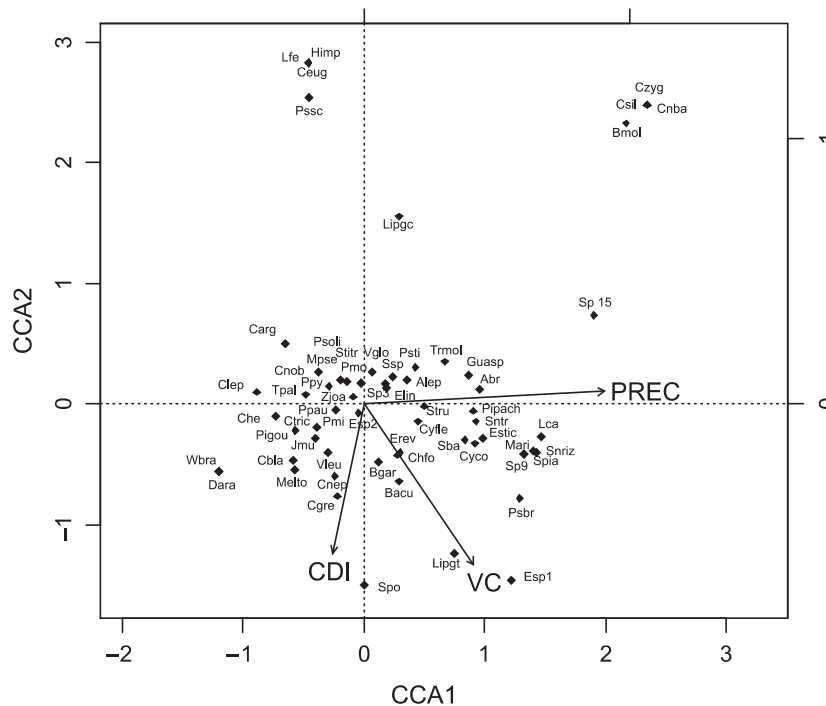


Fig. 4. Canonical Correspondence Analysis showing the plant species recorded in the Catimbau National Park, NE Brazil, and its association with annual precipitation and indicators of acute (VC = vegetation cover) and chronic disturbances (CDI). Plant species: Abr = *Acalypha brasiliensis*, Alep = *Annona leptopetala*, Bmol = *Balfourodendron molle*, Bacu = *Bauhinia acuruana*, Bgar = *Byrsonima gardneriana*, Ceug = *Campomanesia eugenioides*, Csil = *Casearia silvestris*, Cziyg = *Chamaecrista zygodiphyloides*, Chfo = *Chloroleucon foliolosum*, Cnba = *Cnidocolus bahianus*, Cnob = *Cnidocolus pubescens*, Cyco = *Colicodendron yco*, Clep = *Commiphora leptophloeos*, Ctric = *Cordia trichotoma*, Carg = *Croton argyrophyloides*, Cbla = *Croton blanchetianus*, Che = *Croton heliotropifolius*, Cnep = *Croton nepetifolius*, Cgre = *Croton grewoides*, Cyfle = *Cynophalla flexuosa*, Dara = *Dahlstedtia* sp., Erev = *Erythroxylum revolutum*, Esp1 = *Eugenia* sp1, Esp2 = *Eugenia* sp2, Estic = *Eugenia stictopetala*, Elin = *Evolvulus linoides*, Guasp = *Guapira graciliflora*, Himp = *Handroanthus impetiginosus*, Jmu = *Jatropha mutabilis*, Lca = *Lantana camara*, Lfe = *Libidibia ferrea*, Lipgc = *Lippia gracilis*, Lipgt = *Lippia grata*, Mpsp = *Manihot pseudoglaziovii*, Mari = *Maytenus rigida*, Melto = *Melochia tomentosa*, Sp3 = *Sp3*, Ppau = *Peltogyne pauciflora*, Pigou = *Pilosocereus gounellei*, Pipach = *Pilosocereus pachycladus*, Psti = *Piptadenia stipulacea*, Pmo = *Pityrocarpa moniliformis*, Pmi = *Poincianella microphylla*, Ppy = *Poincianella pyramidalis*, Psbr = *Psidium brownianum*, Psoli = *Psidium oligospermum*, Pssc = *Psidium schenckianum*, Sba = *Senegalia bahiensis*, Sp9 = *Senegalia polyphylla*, Spia = *Senegalia piauhiensis*, Ssp = *Senegalia* sp., Snriz = *Senna rizzinii*, Snttr = *Senna trachypus*, Sp 15 = *Sp 15*, Stitr = *Stillingia trapezoides*, Stru = *Strychnos rubiginosa*, Tpal = *Tacinga palmadora*, Trmol = *Trichidium molle*, Vglo = *Varronia globosa*, Vleu = *Varronia leucocephala*, Wbra = *Waltheria brachypetala*, Zjoa = *Ziziphus joazeiro*.

increasing disturbance (Fig. 3), which suggest that the biodiversity costs of disturbance are higher in forests with lower productivity (Mantyka-Pringle, Martin & Rhodes 2012; Gibb *et al.* 2015); that is, there is a co-limitation imposed to species diversity by drought and disturbance.

The weak effect of precipitation and disturbance on stem density and biomass is related to the widespread distribution of dominant species along environmental gradients (Tables S9 and S10, Fig. S1). Although most rare species are restricted to wet areas (Table S9), they show a poor contribution to total stem density and above-ground biomass. These two variables rather depend on the distribution of common and dominant species, which occur along the entire precipitation and disturbance gradient (Tables S9 and S10, Fig. S1). Therefore, the loss of rare species in drier and more disturbed plots is compensated for by the presence of relatively common and dominant species in the plot (i.e. compensatory dynamics; González & Loreau 2009; Russildi *et al.* 2016).

Overall, our findings support the idea that rapid climatic changes in the region will have strong negative effects on

biodiversity in this species-rich SDTF. Predictive models about the potential impact of climate change in the region indicate that precipitation will decrease 22% by 2100 (Magrin *et al.* 2014), and we find that drier sites show impoverished plant assemblages that become more sensitive to chronic disturbances. Ribeiro *et al.* (2015, 2016) also demonstrate that chronic disturbances decrease tree species diversity and structure in a dry portion of Caatinga vegetation. The fact that rare species are the first to disappear in dry and disturbed sites, threatens future ecosystem function provisioning, as rare species are known to carry less-redundant combinations of functional traits that can be critical to ecosystem resilience (Moullot *et al.* 2013). Therefore, to avoid the potential desertification of this important biome (see Leal *et al.* 2005; Anderson-Teixeira *et al.* 2013) and maintain its unique biodiversity it is imperative to expand the coverage of protected areas, and limit livestock production and collection of forest products inside them. The protected areas must include a representative portion of the diverse existing Caatinga phytophysiognomies – with special emphasis on wet areas – to ensure the maintenance

of diversity, ecological stability and ecosystem functions. Moreover, outside these protected areas we should promote the introduction of management techniques allied to traditional knowledge [e.g. efficient cookstove, Lambe *et al.* (2015); agroforestry, Chhetri, Mugisha & White (2003)] to help rural populations to maintain their livelihood by decreasing the pressure of exploitation of natural resources.

Authors' contributions

K.F.R., V.A.R., I.R.L. and M.T. conceived the ideas and designed methodology; K.F.R. collected the data; K.F.R. and R.T.Q. analysed the data; K.F.R. and V.A.R. led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.8r8sj> (Rito *et al.* 2016)

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Species diversity, evenness factor, stem density and sample coverage of plant assemblages in 19 plots with different precipitation.

Table S2. Additive and multiplicative models assessing the effects of precipitation and chronic and acute anthropogenic disturbance predictors on plant species richness.

Table S3. Additive and multiplicative models assessing the effects of precipitation and chronic and acute anthropogenic disturbance predictors on the number of common species.

Table S4. Additive and multiplicative models assessing the effects of precipitation and chronic and acute anthropogenic disturbance

predictors on the number of dominant species.

Table S5. Additive and multiplicative models assessing the effects of precipitation and chronic and acute anthropogenic disturbance predictors on community evenness.

Table S6. Additive and multiplicative models assessing the effects of precipitation and chronic and acute anthropogenic disturbance predictors on stem density.

Table S7. Additive and multiplicative models assessing the effects of precipitation and chronic and acute anthropogenic disturbance predictors on plant above-ground biomass.

Table S8. Cook's distance values for each plot calculated from the best model predictions for the additive and interacting effect of precipitation and acute (VC) and chronic anthropogenic disturbances (CDI) on species diversity.

Table S9. Distribution of stem density per species along the precipitation gradient.

Table S10. Distribution of above-ground biomass per species along the precipitation gradient.

Fig. S1. Total stem density and above-ground biomass of plant assemblages in 19 plots distributed along the chronic and acute disturbance gradients.