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LETTER

Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest

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Abstract

The effects of human disturbance on biodiversity can be mediated by environmental conditions, such as water availability, climate and nutrients. In general, disturbed, dry or nutrient-depleted soils areas tend to have lower taxonomic diversity. However, little is known about how these environmental conditions affect functional composition and intraspecific variability in tropical dry forests. We studied a seasonally dry tropical forest (SDTF) under chronic anthropogenic disturbance (CAD) along rainfall and soil nutrient gradients to understand how these factors influence the taxonomic and functional composition. Specifically we evaluated two aspects of CAD, wood extraction and livestock pressure (goat and cattle grazing), along soil fertility and rainfall gradients on shrub and tree traits, considering species turnover and intraspecific variability. In addition, we also tested how the traits of eight populations of the most frequent species are affected by wood extraction, livestock pressure, rainfall and soil fertility. In general, although CAD and environmental gradients affected each trait of the most widespread species differently, the most abundant species also had a greater variation of traits. Considering species turnover, wood extraction is associated with species with a smaller leaf area and lower investment in leaf mass, probably due to the indirect effects of this disturbance type on the vegetation, i.e. the removal of branches and woody debris clears the vegetation, favouring species that minimize water loss. Livestock pressure, on the other hand, affected intraspecific variation: the herbivory caused by goats and cattle promoted individuals which invest more in wood density and leaf mass. In this case, the change of functional composition observed is a direct effect of the disturbance, such as the decrease of palatable plant abundance by goat and cattle herbivory. In synthesis, CAD, rainfall and soil fertility can affect trait distribution at community and species levels, which can have significant implications for the ecosystem functioning of SDTF under increasing levels of disturbance, climate change and soil nutrient depletion.

1. Introduction

Seasonally dry tropical forests (SDTF *sensu* Pennington *et al* 2009) have unique floras, characterized by small deciduous species, which are often succulent and thorny (Murphy and Lugo 1986, Banda-R *et al* 2016) with high wood densities (Chave *et al* 2009). The SDTF experience extremes of total rainfall, ranging from 240 mm–1500 mm per year, with extremely irregular inter- and intra-annual rainfall (Pennington *et al* 2009). Rainfall gradients are strongly related to the diversity of plant species (e.g. higher rainfall is associated to higher diversity; Moro *et al* 2014) and to different trait arrangements that allow species to avoid, resist or tolerate water stress (Borchert 1994, Hulshof *et al* 2013). The response of each species in dry forests to water stress can be as, or more important, than other factors, such as light (Markesteijn *et al* 2007). Water
availability (Borchert 1994, Hulshof et al 2013) and soil fertility (Buzzard et al 2016) are two major features of SDTF that can influence the functional composition of woody plant assemblages.

SDTF are also under chronic anthropogenic disturbance (CAD), defined as the continuous removal of small fractions of forest biomass through grazing, firewood and non-timber forest product extraction (definition modified from Singh 1998). CAD is one of the most widespread sources of habitat degradation across developing countries (Singh 1998) and has been shown to decrease taxonomic (Ribeiro et al 2015, Rito et al 2017a) and phylogenetic diversities (Ribeiro et al 2016). Considering the functional composition of plant assemblages, grazing, for instance, can influence life-form, decreasing plant height (Diaz et al 2007) and promoting plants with tough leaves (Diaz et al 2001). Selective logging, on the other hand, can promote trees with low wood density and high leaf area, i.e. more resource-acquisitive species (Carreño-Rocabado et al 2012). Therefore, different types of CAD can impose distinct shifts on the vegetation, including the functional profile of plant assemblages. Moreover, different types of CAD together with abiotic variables, such as light, soil nutrients, and rainfall, are able to operate synergistically to restructure plant assemblages (Albuquerque 1999, Carmona et al 2012, Ribeiro et al 2015, Ribeiro-Neto et al 2016, Rito et al 2017a).

Although most studies on community-level functional diversity have focused on species or trait turnover, trait intraspecific variability in the context of community organization has gained increasing attention (Albert et al 2011, Bolnick et al 2011, Leps et al 2011, Violle et al 2012, Funk et al 2017), particularly at landscape and local scales, where species turnover can be reduced (Siefert et al 2015). Traits can vary intraspecifically along environmental gradients, such as rainfall (Jung et al 2014), soil fertility (Le Bagousse-Pinguet et al 2014, Siefert et al 2014) and human disturbance (Volf et al 2016). In SDTF, some species can be favoured in high intensity disturbance areas (Rito et al 2017b) due to different tolerances of CAD (Villarreal-Barajas and Martorell 2009) and, thus, change the functional composition of plant assemblages (Sonni et al 2010, Carmona et al 2015, Carreño-Rocabado et al 2015). Although it is known that spatial variation in traits can be strongly related to environmental variables in SDTF (e.g. Rito et al 2017b), the relative importance of the influences of species turnover and intraspecific variability along environmental gradients for functional composition and community organization is still poorly understood.

The Brazilian Caatinga, one of the largest and most diverse SDTF (Portillo-Quintero and Sánchez-Azofeifa 2010, Silva et al, in press), has an average annual loss of native vegetation of about 0.3% per year (Beuchle et al 2015), with more than 48% of the native vegetation already cleared by 2009 (MMA/IBAMA 2011). The remaining vegetation continues to be exploited by industry, big and small farmers, irrigation projects, for firewood, timber, and fodder for goats and cattle, causing habitat degradation and the impoverishment of plant assemblages at the local spatial scale (Lapola et al 2014, Ribeiro et al 2015, Rito et al 2017a). At landscape scale, such disturbances have caused taxonomic homogenization of plant assemblages and the proliferation of disturbance-tolerant species (Ribeiro-Neto et al 2016). In addition to CAD, the Caatinga flora is also very sensitive to climate change (Collevatti et al 2013) and soil nutrient depletion (Menezes et al 2012). Thus, studying how functional composition varies along environmental gradients of rainfall and soil fertility, as well as along different types of CAD, is a compelling approach to understand how functional composition will vary under increased intensity of climate change, desertification and CAD.

Here, we study an area of Caatinga (i.e. SDTF) exposed to different levels of wood extraction, livestock pressure, rainfall and soil fertility. Under this scenario, we posed the question: how does chronic anthropogenic disturbance, rainfall and soil fertility influence the functional composition of trees and shrubs in an area of Caatinga? To answer this question, we evaluated species turnover and intraspecific variability along these gradients, considering traits related to water-use strategy, competition, colonization and large-herbivore defense.

2. Methods

2.1. Site description and data sampling

The study area is located in the Catimbau National Park (hereafter, Catimbau), in the municipalities of Buique, Tupanatinga, and Ibirimirim, in the state of Pernambuco, Brazil (8°25′17″− 8°36′35″S; 37°11′00″− 37°33′32″W; figure 1). This is one of the few protected areas of Caatinga, with an area of c. 60 000 ha. There is a high variation in rainfall (ranging from 480–1100 mm year$^{-1}$) and the mean annual temperature is 23°C; being classified as tropical semi-arid (Koeppen’s classification Bsh). Approximately 70% of the park has sandy soils and the Catimbau’s vegetation is mainly composed of shrubs and trees (Rito et al 2017a). There are approximately 300 families living inside the Catimbau (Arnan et al submitted) due to slow implementation of park regulations. Their livelihoods are based on goat farming and subsistence agriculture (Santos 2015).

We sampled 19 plots (20×50 m) at least 2 km distant from each other along a gradient of rainfall and chronic human disturbance (figure 1). In each plot, all shrubs and trees with diameter at soil height $\geq$ 3 cm and with a height $\geq$ 1 m were sampled. Among these individuals, 10–20% of them were randomly sampled (following Paine et al 2015) for trait measurements. We considered the following traits: 1. maximum height (Hmax); 2. number of branches (BR); 3. stem
Figure 1. Location of the study area in (a) Brazil and (b) the Catimbau National Park (rectangle) in the Pernambuco state. The study was conducted along the gradients (c) wood extraction (ranging from zero to 96.06), (d) livestock pressure (ranging from zero to 59.94), (e) soil fertility (ranging from 5.003–5.121) and (f) rainfall (ranging from 538 mm–931 mm) in the Catimbau National Park. The 19 0.1 ha plots are represented by a circle, in which larger circles represent higher intensity of the gradient.

specific density (SSD); 4. specific leaf area (SLA); 5. leaf dry matter content (LDMC); 6. leaf area (LA); 7. leaf thickness (Lth); and 8. seed size (SS). All measurements followed Pérez-Harguindeguy et al (2013) and the details of their measurement and biological significance are in supplemental material 1, available at stacks.iop.org/ERL/13/025005/mmedia.

As measures of disturbance for each plot, we considered the wood extraction index (WEI), and the livestock pressure index (LPI), i.e. the herbivory caused mainly by goat and cattle. In four 2 × 2 m subplots within each plot we counted all goat dung pellets and the biomass of dead woody litter. The biomass of wood litter was first computed following the equation of the volume of a conical frustum and, then, used a mean value of the wood density in the study area (0.634 g cm$^{-3}$), to transform the volume values to biomass values. The biomass of woody litter was divided by the aboveground biomass (following the equation in Sampaio and Silva 2005) of woody living plants in the plot and, finally, computed the inversed value, since low proportion of wood debris biomass is related to more use of wood debris for firewood by human population. In entire plot all cattle dung were counted, the goat trail length was measured with an odometer, and the basal area of all cut stems were recorded. To compute the goat herbivory we used the first axis of a PCA calculated by goat trail length and their dung counts (the first coordinate explained 86% of the variance). The basal area of cut stems and the biomass of woody debris were used to calculate WEI, whereas goat herbivory and cattle dungs were used to calculate LPI according to the following formula:

$$I = \frac{\sum_{i=1}^{n} (y_i - y_{\text{min}})/(y_{\text{max}} - y_{\text{min}})}{n} \times 100$$

where $I$ is the overall pressure index (WEI or LPI), $y_i$ is the observed value for each disturbance metric in each plot $i$, $y_{\text{min}}$ is the minimum observed value for the disturbance metric considering all plots, $y_{\text{max}}$ is the maximum observed value for the disturbance metric considering all plots, and $n$ is the number of individual disturbance metrics considered in the index.

LPI and WEI vary from 0 (no livestock or wood extraction pressure in the plot, respectively) to 100 (maximum livestock pressure or wood extraction in the plot, respectively). For detailed information about the calculation of the WEI and LPI and discussion on these indices, see Arnan et al (submitted).

We considered soil fertility (SF) and total rainfall in a year (RF) as environmental variables. For SF, we considered 10 samples of 10 × 10 cm$^2$ of superficial soil (up to 30 cm deep)(summing nearly 3000 cm$^3$ of soil and analyzed their micronutrients, water content, organic matter and acidity (following Embrapa 1997 protocol) to calculate the soil evaluation factor, a measure of soil fertility (Lu et al 2002):

$$SF = [\text{Ca} + \text{Mg} + \text{K} - \log(1 + A1)] \times \text{OM} + 5$$
where SF = soil fertility, Ca = exchangeable calcium (cmolc dm$^{-3}$), Mg = exchangeable magnesium (cmolc dm$^{-3}$), K = exchangeable potassium (cmolc dm$^{-3}$), Al = exchangeable aluminium (cmolc dm$^{-3}$), and OM = organic matter (g kg$^{-1}$). Whereas Ca, Mg, and K are considered nutrients, Al is toxic to plant growth and OM is related to other soil fertility factors, e.g. nutrient availability, soil structure, air infiltration and water infiltration and retention (Lu et al 2002). The values of SF are independent among the plots and can also be compared with other areas.

For RF, we used the data available in the Worldclim 2 database, in which we considered the mean annual total rainfall from 1970–2000 (Fick and Hijmans 2017). The rainfall for each plot was calculated by interpolation of the data from climatic stations near to the studied area. The spatial resolution was 1 km$^2$ (Fick and Hijmans 2017) and the data were gathered using the ‘raster’ package (Hijmans 2016) in R version 3.4 (R Core Team 2017). Mean annual rainfall is correlated with other climatic variables, such as mean annual temperature, precipitation in the driest month and temperature seasonality (supplemental material 2).

2.2. Data analysis
To test the environmental preference of the species, we performed a redundancy analysis (RDA) between the taxonomic composition of the plots and the predictor variables WEI, LPI, SF and RF. Due to the high number of rare species, we used the Hellinger transformation in the community matrix (Legendre and Gallangher 2001) and tested the significance of the RDA with analysis of variance with 999 permutations (Legendre and Legendre 2012). To test if abundant species, which are also widespread (correlation of Spearman between abundance and number of plots in which the species occur: $r = 0.84$; $P < 0.001$), have greater trait variation, we performed a Pearson correlation (Zar 2012) between the abundance of the species and the coefficient of variation for each trait. Species abundance, stem specific density and leaf thickness, area, dry matter content and specific leaf area were ln-transformed to achieve normality of data (Zar 2012). To understand how plant traits change along the WEI, LPI, SF and RF gradients, we chose the species that occurred in more than 50% of the plots and performed linear models (Crawley 2013) in which the response variable was the mean value of the trait in each plot. Generalized linear models with Poisson distribution corrected for overdispersion were also used, in which the response variable was the species abundance and the predictor variables were WEI, LPI, SF and RF (Crawley 2013). We considered Pityrocarpa moniliformis (Benth.) Luckow and R W Jobson, Poincianella microphylla (Mart. ex G Don) I. P Queiroz, Senegalia sp., Piptadenia stipulacea (Benth.) Ducke, Pelogyne pauciflora Benth., of the Fabaceae family; Cridosolus pubescens Pohl, and Jatropha mutabilis (Pohl) Baill. of the Euphorbiaceae family; and Commiphora leptophloeos (Mart.) J.B.Gillett of the Burseraceae family. Seed size was not considered in both analyses because this trait was not gathered in every plot (supplemental material 1).

The trait variation among sites can be related to the species composition with different traits, which is calculated by the community weighted mean (CWM; Garnier et al 2004). Therefore, CWM is based on fixed trait values of the species, i.e. the average of a trait considering the whole gradient or all sampling units, thus it does not account for the intraspecific variation of the trait (Lep$^*$ et al 2011). For this reason, we considered an approach that decomposes the fixed average (i.e. species composition or turnover) and intraspecific trait average into sums of squares of one ANOVA for each component of species turnover, intraspecific variability effect and their covariation: SS$^*$ = SS$^*$fixed + SS$^*$intraspecific + SS$^*$cov. SS$^*$fixed considers the mean trait value over all plots, whereas SS$^*$intraspecific considers the average trait value for each specific plot, thus including inter- and intraspecific effects (Lep$^*$ et al 2011). Thus, the intraspecific plot average is the difference between specific average and fixed plot-average trait values. SS$^*$cov, on the other hand, is the covariation between SS$^*$fixed and SS$^*$intraspecific: positive covariation indicates that inter- and intraspecific components vary in the same direction, whereas negative covariation indicates that both components vary in opposite directions, e.g. as the intraspecific component increases, the intraspecific component decreases along a gradient and vice-versa (Lep$^*$ et al 2011). Each component of each trait was related to LPI, WEI, SEF and RF using linear models performed in ‘trait,flex.anova’ function in R provided by Lep$^*$ et al (2011). All analyses were performed in R version 3.4 (R Core Team 2017).

3. Results
Taxonomic composition was significantly related to the environmental and disturbance gradients ($F_{1,14} = 1.55$; $P = 0.003$), particularly RF ($F_{1,14} = 1.73$; $P = 0.03$) and WEI ($F_{1,14} = 2.62$; $P = 0.002$) (figure 2). J. mutabilis, C. leptophloeos and P. microphylla occurred preferentially in drier areas, whereas P. moniliformis, occurred in areas with lower WEI (figures 2 and 3). The other most frequent species (Senegalia sp. P. stipulacea, P. pauciflora; C. pubescens and C. leptophloeos) were weakly correlated with the extreme conditions posed by both gradients (figures 2 and 3). On the other hand, species abundance correlated positively with intraspecific trait variation as follows: maximum height ($r = 0.30$; $P = 0.01$, figure 4(a)), number of branches ($r = 0.31$; $P = 0.01$, figure 4(b)), stem specific density ($r = 0.40$; $P = 0.001$, figure 4(c)); leaf thickness ($r = 0.30$; $P = 0.01$, figure 4(d)); leaf dry matter content ($r = 0.25$; $P = 0.04$, figure 4(f)) and specific leaf area ($r = 0.36$; $P = 0.002$, figure 4(g)). With the exception of leaf area, which was not correlated to intraspecific trait variation ($r = 0.13$; $P = 0.28$; figure 4(e)).
The most frequent species responded to CAD and environmental gradients, but the response was species-specific (figure 3, supplemental material 3). Whereas livestock pressure promotes shorter *P. moniliformis*, with more branches and investment in leaf mass, this disturbance type was related to the thin leaves of *Senegalia* sp., but promoted *C. leptophloeo* individuals with larger leaves (figure 3, supplemental material 3). Wood extraction promoted taller trees of *P. stipulacea*, but was related to few branches of *P. moniliformis* and *P. microphylla*. Wood extraction also promoted higher wood densities of *P. microphylla*, but influenced *J. mutabilis* and *P. stipulacea*, leading to lower investment in leaf mass (figure 3, supplemental material 3). Soil fertility influenced leaf thickness in *Senegalia* spp. and the number of branches in *P. moniliformis*. In wetter areas, *P. microphylla* had higher leaf area (figure 3, supplemental material 3). *C. pubescens* and *P. pauciflora* were not influenced by any of the four variables considered (figure 3, supplemental material 3). *P. moniliformis* was more abundant in areas with lower wood extraction levels, whereas *P. microphylla* and *C. leptophloeo* was more abundant in drier areas (figure 3, supplemental material 3).

Only wood extraction and soil fertility were related to species composition (figures 5(a)–(c)). Higher WEI favored species with smaller leaf area and higher investment in leaf mass (i.e. higher specific leaf area) (figures 6(a)–(b)), whereas higher SF was related to species with low specific leaf area (figure 6(c)). On the other hand, relative to intraspecific variability, in areas with higher LPI, the individuals with higher stem specific density, leaf dry matter content, but lower specific leaf area were favored (figures 5(b), figures 6(d)–(f)).

Finally, the covariation between turnover and intraspecific variability for the LPI, WEI, RF and SF was negative for 19 of 32 analyses (59.37%, figures 5 and 6, supplemental material 4). All above predictor variables had negative covariation for maximum height and seed size, indicating that, whilst turnover increases, the intraspecific variability decreases (figure 4, supplemental material 4), which could be considered a sort of compensation in the effect of turnover and intraspecific trait variability. For most traits, with the exception of the number of branches, the total intraspecific variability is similar or larger than species turnover (figure 5).

4. Discussion

Our results indicate that CAD (wood extraction and livestock pressure) and environmental variables (soil fertility and rainfall) jointly affect plant taxonomic composition and trait distribution. However, the influence of CAD on the distribution of plant traits depends on the ecological level (species or community), the focal trait and the type of disturbance. At species level, many traits respond to gradients, but the response or sensitivity of some traits are idiosyncratic. Moreover, the most abundant species exhibit the highest scores of trait variability. At community level, while wood extraction has greater influence on species turnover, livestock pressure has greater influence on intraspecific variability. Apparently, wood extraction promotes species with traits associated with resistance to water loss (i.e. species with smaller leaf area and higher investment in leaf mass), while goats and cattle negatively affect the presence of individuals with softer tissues. Finally, intra- and interspecific trait variation are negatively correlated in many situations, such as maximum height and seed size, suggesting that both mechanisms are important and complement each other in terms of species assembly along the whole gradient. In other
words, the increase in one trait due to species turnover can be compensated by the decrease of the same trait due to intraspecific trait variability. This potential compensation mechanism could represent a sort of buffer by which functional composition is maintained despite the changes in the structure of the community.

These findings demonstrate that in parallel to changes in rainfall and soil fertility (commonly recognized as important factors in plant assembly) CAD can also affect plant trait distribution and thus operate as a driving force relative to population distribution and community structure and organization. Although acute disturbance can affect plant diversity, in the studied area CAD can play a major role on plant community assembly than acute disturbance (Rito et al. 2017a). Furthermore, trait variation (both intra- and interspecific) can offer a baseline mechanism for several community-level changes associated with CAD, such as taxonomic (Singh 1998, Sagar et al. 2003, Ribeiro et al. 2015, Ribeiro-Neto et al. 2016, Rito et al. 2017a) and phylogenetic impoverishment exhibited by plant assemblages in highly disturbed sites (Ribeiro et al. 2016). Our findings also highlight the role played by trait intraspecific variation as an assembly force.

At global scale, intraspecific variability contributes substantially to trait variation, but less than species turnover (Siefert et al. 2015). Therefore, intraspecific variability is expected to be more easily detected at regional and local scales (Siefert et al. 2015). Many studies show the relative importance of intraspecific variability and species turnover in community organization (Albert et al. 2011, Bolnick et al. 2011, Kichenin et al. 2013, Leps et al. 2011, Violle et al. 2012, Funk et al. 2017), however, we show the local impact of this driving force documenting its response to concomitant environmental gradients and species-specific
responses. In this sense, our results are complementary to previous studies, which show that the density of each species can have a particular response to different types of CAD (Martorell and Peters 2009, Rito et al 2017b) and that some species are tolerant of CAD (Diaz et al 2001, Cingolani et al 2005, Villarreal-Barajas and Martorell 2009). For instance, the abundance, height, number of branches and leaf dry matter content of \( P. \) moniliformis is very sensitive to gradients and CAD, while \( P. \) pauciflora, does not exhibit a functional response to any gradients. Therefore, the complex response of species due to the different types of CAD can blur the overall functional composition of a community along environmental gradients, with potential implications for ecosystem functioning, such as primary productivity (Maestre et al 2016).

Although the different gradients can result in this complex functional response of plant species at species level, at community level wood extraction is the main factor influencing species assemblage. Humans extract wood for fuel and construction generally focusing on the most abundant and frequent woody plant species near by their residences (Soldati et al 2017), regardless of their functional group (Specht et al 2015). Therefore, it is reasonable to assume that wood removal reduces tree and shrub density, clearing the vegetation and exposing the soil, with a consequent increase in light incidence and water loss in these portions of vegetation. In fact, as WEI considered not only the number of cut stems, but also the biomass of the wood debris, higher values of this index can indicate less litter and, thus, more exposed soil. These areas of low plant density and exposed soil can promote more acquisitive species, i.e. those species with rapid acquisition of resources (Diaz et al 2004), as observed in moist tropical forests (Carreño-Rocabado et al 2012, 2015). In SDTF, on the other hand, drought can be more important than light for plant strategies (Markesteijn et al 2007). In this sense, avoidance of water loss can also be an important strategy and, thus, species with tougher and smaller leaves are favored (Ackerly et al 2002, Sterck et al 2011). As a consequence, species that are less tolerant to disturbance, i.e. species that lose water more easily, and are more dependent on their neighbors to germinate, grow or reproduce (Villarreal-Barajas and Martorell 2009), can have higher mortality rates and experience decreased abundance in the community.

Whereas wood extraction has indirect effects on functional composition, grazing can have direct effects on populations of woody species. Grazing can promote shorter woody and herbaceous species (Cingolani et al 2005, Diaz et al 2007) with tougher leaves (Diaz et al 2001), resulting in species that tolerate grazing, or are avoided by grazers (Diaz et al 2001, Cingolani et al 2005). Cattle and goat are generally selective about which resources they consume and probably eat more edible (Albuquerque 1999, Diaz et al 2007) and nutrient-rich (Nunes et al 2016) saplings and seedlings, i.e. plants with lower stem specific density and softer leaves. On the other hand, goats, the most common

Figure 4. Correlation analyses between the abundance and the coefficient of variation of the trait of the species (a) \( \text{Hmax} \)—maximum height; (b) \( \text{NB} \)—number of branches; (c) \( \text{SSD} \)—specific stem density; (d) \( \text{Lth} \)—leaf thickness; (e) \( \text{LA} \)—leaf area; (f) \( \text{LDMC} \)—leaf dry matter content; and (g) \( \text{SLA} \)—specific leaf area. \( \text{SSD}, \text{Lth}, \text{LA}, \text{LDMC}, \) and \( \text{SLA} \) were ln-transformed to achieve normality of data.
Figure 5. Percentage of the contribution of variability of traits to species composition turnover (grey bars) and intraspecific trait variability (white bars). The vertical lines are the total variation; the space between them and the bars are the covariation: if the line is above the bar, the covariation is positive; otherwise, the covariation is negative. Significant relationships between traits and variables are indicated by * (P < 0.05) and are located inside grey bars for turnover of species and inside white bars for intraspecific variability. SS = seed size (cm); Lth = leaf thickness (mm); LA = leaf area (cm$^2$); LDMC = leaf dry matter content (%); SLA = specific leaf area (cm$^2$ g$^{-1}$); SSD = stem specific density (g cm$^{-3}$), NB = number of branches; Hmax = maximum height (m).

Figure 6. Representation of the significant relationships between environmental variables and traits concerning species turnover (a)–(c) and intraspecific variation (d)–(f) that are shown in figure 5. Regression lines are represented by continuous black lines. Dashed lines are the regression lines of the most frequent species (i.e. occurring in more than 50% of the plots). LA = leaf area (cm$^2$); SLA = specific leaf area (cm$^2$ g$^{-1}$), SSD = stem specific density (g cm$^{-3}$); LDMC = leaf dry matter content (%).
livestock in Caatinga (Lapola et al. 2014), are considered generalist herbivores, being less selective during harsher dry seasons (Pfister and Malechek 1986). Under this intense pressure from herbivory, almost all plant species are consumed and, thus, the livestock pressure should be more intense at population level. Despite the known effects of overgrazing on functional species composition (Díaz et al. 2001, 2007, Cingolani et al. 2005) and diversity (Carmona et al. 2012), our results show that the effects of grazing are higher on intraspecific variability than on species turnover. Some species seem to be particularly affected, such as, P. moniliformis a widespread species, and one of the most abundant in the studied area, in which overgrazing favors individuals with high leaf dry matter content.

The relatively high negative covariation between species turnover and intraspecific variability may indicate a compensatory effect in the studied area (Leps et al. 2011). This compensation effect of species turnover and intraspecific variability can lead to the absence of a response in the mean trait value of the community (Leps et al. 2011, Kichenin et al. 2013), may be context-dependent and be caused by only some species (Kichenin et al. 2013), probably the most abundant ones. In human disturbed areas, different ecological factors can act on a particular set of traits among the species in a community (Ackerly et al. 2002, Cingolani et al. 2007, Maire et al. 2012). These ‘winning traits’ (Smart et al. 2006, Wiegmans and Waller 2006, Marinsek et al. 2015) characterize species that are tolerant to disturbance (Cingolani et al. 2005, Maire et al. 2012), leading to increased abundance (Cingolani et al. 2007). Nevertheless the species that occupy all environmental gradients do not always have a set of ‘winning traits’ (Pitmann et al. 2001), but, instead, may simply exhibit greater trait variation than rarer species. This variation, whether due to phenotypic plasticity or to heritable variation (Sultan 2000), may indicate that these dominant species are also generalists at landscape level (Sanaphre-Villanueva et al. 2017), and can cope with greater range of environmental constraints.

It is important to note the limited importance of the environmental variables soil fertility and rainfall at community and species levels. In fact, while soil fertility had a significant relationship with species turnover regarding specific leaf area, number of branches of P. moniliformis and leaf thickness of Senegalia sp., rainfall only affected the leaf area of P. microphylla. Although previous studies have shown the importance of soil fertility (e.g. Ordoñez et al. 2009, Hodgson et al. 2011, Jager et al. 2015) and rainfall (e.g., Wigley et al. 2016, Grossiord et al. 2017) on species trait variation and functional composition, the relatively low importance of environmental gradients in Catimbau must not be overlooked. For instance, our results indicate that more acquisitive species are favored in areas with low soil fertility, which may lead to increased distributions and abundance of these species in areas with soil nutrient depletion or even desertified areas (Reynolds et al. 2007). Climate change, on the other hand, is predicted to result in decreases in rainfall and more intense droughts in the Caatinga (Collevati et al. 2013), which could change species composition and demographic processes (Allen et al. 2017). Therefore, severe environmental variations, especially when combined with CAD, can change the function of SDTF in irreversible ways (Maestre et al. 2016).

5. Conclusions

In synthesis, changes in CAD, rainfall and soil fertility can affect trait distribution by selectively filtering trait values at community and species levels in SDTF whereby potential changes in light intensity, water availability, herbivory by mammals, nutrients and direct species exploitation are able to alter the spatial distribution of particular traits and increase species turnover and intraspecific variability. Thus, trait responses can operate as deterministic assembly forces along the whole gradient through a combination of intraspecific and interspecific variation. However, trait-sensitivity can be species-specific, adding complexity to community reorganization in response to local human disturbances and climate change. This is particularly important for SDTF as they have experienced increasing levels of chronic disturbance and are exposed to local (Collevati et al. 2013) and global (Blackie et al. 2014) climate change. As a consequence, this increase in disturbance may not only reduce vegetation regeneration (Villarreal-Barajas and Martorell 2009, Marinho et al. 2016), but also change the functioning of SDTF, with pervasive consequences for ecosystem processes and services, such as carbon storage (Schulz et al. 2016) and decomposition rate (Chillo et al. 2017).

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