Research Letters

Divergent herb communities in drier and chronically disturbed areas of the Brazilian Caatinga

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HIGHLIGHTS

- Caatinga dry forests are becoming increasingly drier and chronically disturbed.
- Herb communities negatively respond to rainfall reduction and increase disturbance.
- Responses may be mediated by the local density of woody plants.
- Multiple successional pathways should emerge with the new environmental conditions.
- Management and conservation actions are urgent to protect Caatinga herb diversity.

GRAPHICAL ABSTRACT
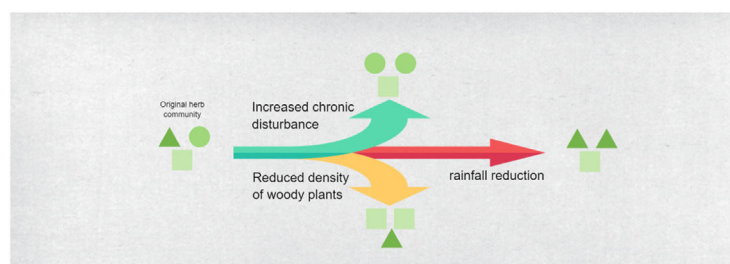
ABSTRACT

Although the herbaceous plants concentrate the diversity of vascular plants in the largest dry forest of South America, the Brazilian Caatinga, their responses to environmental modifications are poorly known. We assessed the taxonomic, phylogenetic and functional responses of herb communities to independent gradients of annual rainfall (510–940 mm), chronic disturbance (0–100%), and local density of woody plants in 19 forest sites of the Catimbau National Park, Northeast Brazil. We expected that drier and more chronically disturbed stands with greater density of woody plants would support less-dense and impoverished herb communities. We recorded 6787 individuals belonging to 57 species and 53 genera, predominantly dicots. Rainfall reduction decreased herb density, benefited a small set of particular genera, increased phylogenetic clustering within terminal clades and favored species pollinated by birds and butterflies. Increased chronic disturbance did not affect herb density and richness, but benefited another set of herb genera, reduced phylogenetic clustering and favored dicot herbs pollinated by bees. The density of woody plants also affected different aspects of taxonomic, phylogenetic and functional dimensions. By shaping different components of herb diversity, rainfall reduction and increased chronic disturbance are likely to act synergistically and drive the Caatinga towards multiple successional pathways.

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Introduction

Global warming are changing rainfall regime around the world, affecting species distribution, ecological interactions, and ecosystem services (Gilman et al., 2010). It is well-known that some regions are experiencing an increase in rainfall along with extreme storms and hurricanes, while others are facing marked reductions in rainfall and prolonged drought events (Dai, 2013). The seasonally dry tropical forests, such as the semi-arid Brazilian Caatinga, are among the ecosystems that will become increasingly drier. By 2100, the Caatinga is forecast to heat up between 3.5°C to 4.5 °C and rainfall is estimated to decrease between 40% and 50% (PBMC, 2013). The consequences for biodiversity are poorly known (Parmesan, 2006; Santos et al., 2014; Silva et al., 2019), but the general expectation is that species-rich biological communities, such as herb communities, will loss diversity in taxonomic, phylogenetic and functional terms.

Climate-driven biological impoverishment may be exacerbated by chronic anthropogenic disturbances, which imposes additional pressure on the remaining biota (Antongiovanni et al., 2020). Unlike acute disturbances such as deforestation and urbanization, chronic disturbances consist in the continuous removal of small amounts of biomass (Singh, 1998). Examples include fuelwood extraction, harvesting of non-timber forest products, free-range livestock farming and hunting. The increase in chronic disturbances has been associated with species loss (Ribeiro et al., 2015), proliferation of native and exotic disturbance-adapted species (Rito et al., 2017a), phylogenetic and functional impoverishment of woody plant communities (Ribeiro et al., 2016, 2019), and changes in plant-animal interactions (Leal et al., 2014). Nonetheless, the potential synergism between increased disturbance and reduced rainfall has been rarely assessed (Rito et al., 2017b). Understanding this synergism is critical in regions where rural people are strongly dependent on forest products, including savannas, moist and dry forests.

The Brazilian Caatinga is recognized as the world's second richest seasonally dry tropical forest in terms of woody plant species (DRYFLOR, 2016). Recent reviews demonstrate that herb species richness surpasses that of woody plants (Moro et al., 2015; Queiroz et al., 2015), reinforcing the need for a better understand of how herb diversity responds to environmental changes (Araújo et al., 2005; Silva et al., 2009). Besides soil coverage and protection, herbs provide floral resources for pollinators, fruits for seed dispersers, and food for a myriad of herbivores, including livestock (Queiroz et al., 2015). They rapidly respond to rainfall by germinating, growing and reproducing in a few weeks, but shrubs and trees may inhibit their development (Cicuzza et al., 2013). If reduced rainfall and increased disturbance disfavor the woody stratum (Rito et al., 2017b), it is likely that herbs thrive in drier and more disturbed areas. However, experimental exclusions of goats in Caatinga rangelands have resulted in a small but significant increase in herb species diversity and above-ground biomass (Menezes et al., 2021). Also, observational studies have indicated that leaf-chewing insects increases herbivory pressure on herb foliage in drier areas (Andrade et al., 2020). Together, these studies suggest that rainfall reduction and increase in chronic disturbance may operate synergistically to promote the erosion of herb diversity in the Caatinga.

In this study we assessed the taxonomic, functional and phylogenetic responses of herb communities to gradients of rainfall, chronic disturbance and local density of woody plants in the Catimbau National Park, Northeast Brazil. We expected that drier and more disturbed forest stands would support less-dense and impoverished herb communities as a result of the proliferation of a few disturbance-adapted species (e.g. Euphorbiaceae) in detriment of many disturbance-sensitive species (Ribeiro et al., 2015, 2016, 2019). Because the proliferating species tend to belong to a few related clades and perform similar functions in the ecosystem (Rito et al., 2017a), we expected that communities in drier and more disturbed areas diverged taxonomically, functionally and became more phylogenetically clustered than communities in wetter and conserved areas. Because trees and shrubs may constrain herb establishment below their crowns, we also expected that herb communities were less-dense and impoverished in stands with higher density of woody plants.

Material and methods

Study area

The study was carried out in the Catimbau National Park, a protected area covering about 62,000 ha of the Caatinga dry forest (Fig. 1). The climate is tropical semi-arid, with an average annual temperature of 23 °C and average annual rainfall ranging from 486 mm to 975 mm. The rainy season usually takes place between March and June, when the herbs grow and spread throughout the park, but some zones also receive rainfall earlier (January and February). Although the Catimbau National Park has been created in 2002 through a Federal Decree (without number) signed by president Fernando Henrique Cardoso in December 13 of that year, there are dozens of small landholdings within its borders, particularly small farms devoted to subsistence agriculture and livestock production (mostly goats) (Specht et al., 2019). Farmers depend on forest resources for food, energy and water security, such as firewood, fodder, and timber (Arnan et al., 2018; Specht et al., 2019). Consequently, this region has been converted into a vegetation mosaic consisting of old- and second-growth stands (i.e., regenerating forest stands), crops, and pastures (Souza et al., 2019). Goats, sheep, and other cattle roam freely across the park, feeding on the remaining vegetation (Alves et al., 2020). The woody stratum is dominated by Fabaceae, Euphorbiaceae, and Cactaceae families (Rito et al., 2017b) and cover a gradient of plant density and aboveground biomass (Souza et al., 2019). The herbaceous stratum is poorly known (Andrade et al., 2020; Menezes et al., 2021).

Herb community sampling

We surveyed herb species in 19 0.1-ha permanent plots (20 m × 50 m) that were established ≥ 2 km from each other across the environmental gradients. These permanent plots were devoted to the study of the woody flora on previous studies (see Rito et al., 2017b for further details). In each plot we systematically established one subplot every 10 m along the imaginary line that split the plot longitudinally into two symmetric parts, totaling five subplots per plot and 95 subplots in the entire study. Because herb communities are transitory in the Caatinga, we conducted the surveys in three consecutive seasons – July 2015, January 2016 and April 2016 – to ensure high levels of sample completeness (0.92–1.00; see Appendix S1 for details). In each subplot, we counted all herbaceous plants (i.e. no sign of woody tissue) and collected for further species identification. Plants were identified at species level using analytical keys, specialized literature, consulting specialists, based on our own field experience (Queiroz et al., 2015; Andrade et al., 2020; Menezes et al., 2021), and through comparisons with material previously identified in master and PhD projects of our team. For the purposes of the analyses, we summed up the data from the three seasons and the five subplots into a single replicate and extracted key community descriptors at the plot level, such as herb density, species richness, and species composition. These metrics were used to describe the taxonomic responses of communities to the environmental gradients.
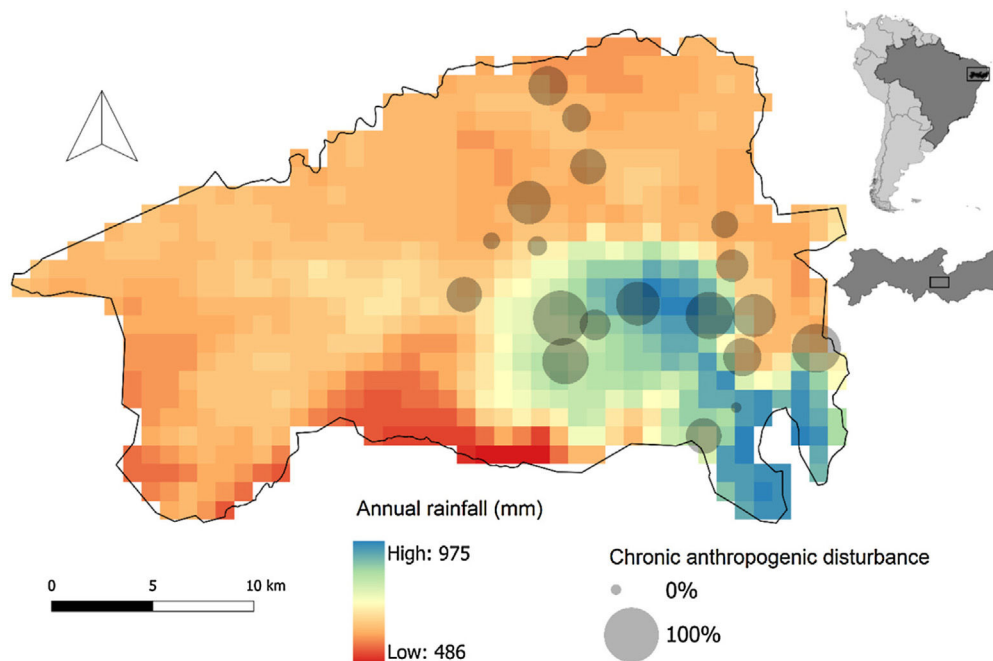
Fig. 1. Location of the study area in the Catimbau National Park, Pernambuco State, northeast Brazil. Circles indicate 20 × 50 m plots where herb communities were sampled. The size of the circle is proportional to its level of chronic anthropogenic disturbance. Pixel color indicates the annual rainfall.

Phylogenetic metrics

To identify the phylogenetic responses of herb communities to the environmental gradients, we took into account components of phylogenetic richness, divergence and structure of the communities (*sensu* Tucker et al., 2017). After constructing a time-calibrated molecular phylogenetic tree (Fig. S1; see details of phylogeny construction in Appendix S2 and Table S1), we used the *com-struct* function of Phylocom 4.2 (Webb et al., 2011) to calculate complementary phylogenetic metrics based on abundance and presence/absence: mean phylogenetic distance (MPD), mean nearest taxon distance (MNTD), net relatedness index (NRI) and nearest taxon index (NTI). MPD estimates the mean distance between all pairs of species or individuals (if weighted by abundance) while MNTD estimates the average distance to the nearest relative of all species or individuals (Webb et al., 2011). Both are measures of phylogenetic divergence and are expressed here in millions of years (Tucker et al., 2017). NRI and NTI are standardized measures of MPD and MNTD, respectively, based on 999 random communities. Positive values of NRI and NTI indicate that taxa are more related to each other than expected by chance (i.e. phylogenetic clustering), while negative values indicate the opposite (i.e. phylogenetic dispersion). We also calculated three metrics of phylogenetic richness and divergence based on Hill's numbers, $^{\circ}D(T)$, $^{1}D(T)$ and $^{2}D(T)$, which express the mean effective number of lineages for rare, common and dominant taxa (Chao et al., 2010; see details in Appendix S3).

Functional profile of herb communities

To examine the functional responses of herb communities to the environmental gradients, we classified all herb species according to four key functional attributes: (1) life forms, following the Raunkiaer spectrum — chamaephytes, geophytes, and therophytes (Raunkiaer, 1934); (2) pollination syndrome — autophily, anemophily, melittophily, psychophily, phalaenophily, chiropterophily, and ornitophily (Quirino and Machado, 2014); (3) seed dispersal syndrome — autochory, anemochory and zoochory

(Freitas et al., 2013; Gomes and Quirino, 2016); and (4) palatability — presence of secondary compounds, spines, or stinging hairs that protect against goats and other herbivores (obtained in the field and from the literature on toxic plants; Campos et al., 2016). We also classified the species in dicots and monocots. From each plot, we calculated the proportion of species or individuals in each trait category and modelled it against the explanatory variables.

Explanatory variables

Herb communities were assumed to result from three main forces: chronic anthropogenic disturbance, mean annual rainfall, and local density of woody plants. To estimate the chronic disturbance of each plot, we adopted direct (in the field) and indirect (interviews and geographic data) measurements of anthropogenic disturbances in forest stands, such as length of goat tracks, litter volume, number of tree stumps, number of residences and distance to the nearest road (see details in Arnan et al., 2018). We first checked for correlations between disturbance-related variables so we could select those that were not highly correlated ($r < 0.7$). We then integrated the selected variables using principal component analysis (PCA), with the significant PCA axes capturing most of the variability in the disturbance metrics. The mean was weighted by the variance explained by each PCA axis and varied between 0 (least disturbed) and 1 (most disturbed). The final values were multiplied by 100 and presented as percentages. Mean annual rainfall 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 and Lewin-Koh, 2015). Mean annual rainfall in the plots ranged from 510 to 940 mm. We used data on the density of woody plants from Rito et al. (2017b).

Data analyses

We used linear models to test the effect of annual rainfall, chronic disturbance, and density of woody plants on herb den-
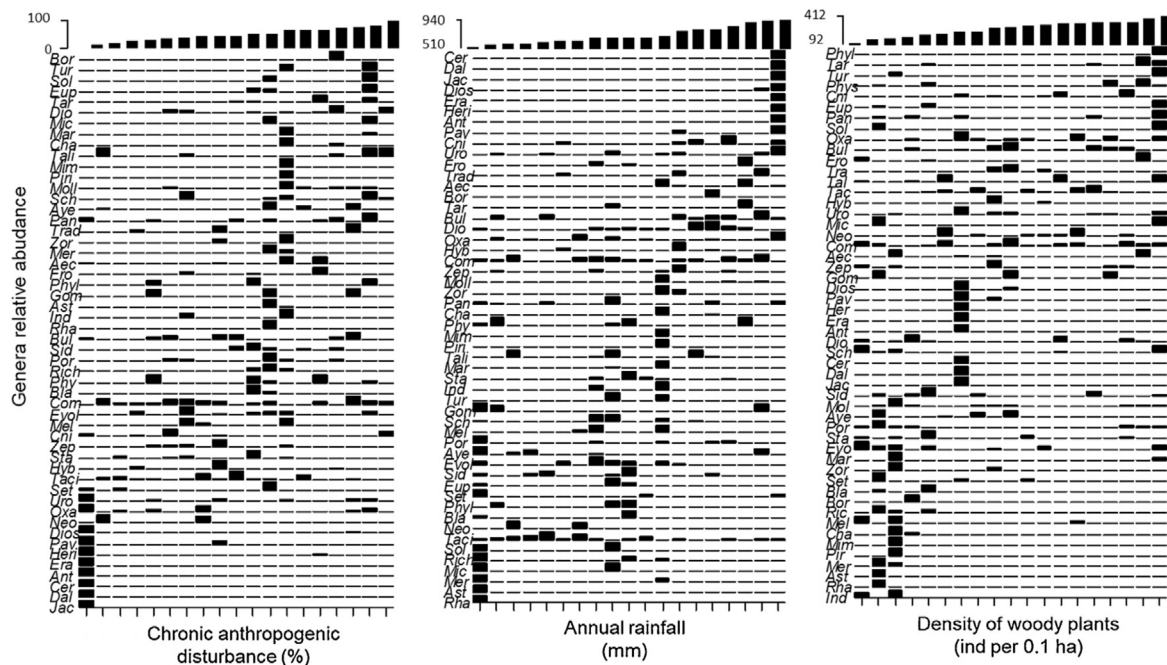
Fig. 2. Direct ordering of herb genera and their relative abundance as a function of the chronic anthropogenic disturbance, annual rainfall and density of woody plants across 19 stands of the Caatinga dry forest, northeast Brazil. Aec—*Aechynomene*; Ant—*Anthephora*; Ast—*Astraea*; Aye—*Ayenia*; Bla—*Blainvillea*; Bor—*Borreria*; Bul—*Bulbostylis*; Cer—*Ceratosanthes*; Cha—*Chamaecrista*; Cni—*Cnidoscolus*; Com—*Commelina*; Dal—*Dalechampia*; Dio—*Diodella*; Dios—*Dioscorea*; Era—*Eragrostis*; Eup—*Euphorbia*; Evol—*Evolvulus*; Fro—*Froelichia*; Gom—*Gomphrena*; Heri—*Herissantia*; Hyb—*Hybanthus*; Ind—*Indigofera*; Jac—*Jacquemontia*; Mar—*Marsypianthes*; Mel—*Melocactus*; Mer—*Merremia*; Mic—*Microtea*; Mim—*Mimosa*; Moll—*Mollugo*; Neo—*Neoglaziovia*; Oxa—*Oxalis*; Pan—*Panicum*; Pav—*Pavonia*; Phyl—*Phyllanthus*; Phy—*Physostemon*; Piri—*Piriqueta*; Por—*Portulaca*; Rha—*Rhaphiodon*; Rich—*Richardia*; Sch—*Schwenckia*; Set—*Setaria*; Sid—*Sida*; Sol—*Solanum*; Sta—*Staelia*; Taci—*Tacinga*; Tali—*Talinum*; Tar—*Tarenaya*; Trad—*Tradescantia*; Tur—*Turnera*; Uro—*Urochloa*; Zep—*Zephiranthes*; Zor—*Zornia*.

sity, richness, and taxonomic, phylogenetic and functional metrics. Before constructing the models, we performed linear correlations between the explanatory variables to check for multicollinearity. None of the correlations were significant, with *r* ranging from 0.11 to 0.18. Herb density was log-transformed due to the substantial variation across the plots (54–2291 plants per 5 m^2). Shapiro-Wilk tests were used to check whether model residuals were normally distributed. We used direct ordering to examine how species composition responded to the explanatory variables. Analyses were performed in the *R* 3.2.1 (R Core Team, 2020) and *JMP* 8.0 programs (Proust, 2009).

Results

Taxonomic responses

A total of 6787 individuals belonging to 57 species, 53 genera, and 24 families were recorded across the 19 forest stands (Table S2). Euphorbiaceae, Fabaceae, Malvaceae, Rubiaceae, and Poaceae were the most species-rich families (4–5 species each). The most abundant species were *Eragrostis pilosa* (24% of all herbs recorded), *Mollugo verticillata* (18%), *Panicum* sp., *Urochloa mollis* and *Bulbostylis* sp. (6% each), *Diodela teres* and *Herissantia crispa* (4% each). A small number of species were common and occurred in more than 60% of the plots (e.g. *Commelina erecta*, *M. verticillata*, *U. mollis*, *Portulaca oleraceae* and *Tacinga inamoena*). Most species occurred in five or less plots.

Species composition clearly varied across the environmental gradients. In the wettest and most conserved extremes of the gradient, the genera *Ceratosanthes*, *Dalechampia*, *Jacquemontia* and *Dioscorea*, all with climbing habit, plus *Eragrostis*, *Herissantia*, *Antefora* and *Pavonia*, dominated the communities (Fig. 2). In the driest stands, *Rhaphiodon*, *Astraea*, *Merremia*, *Microtea*, *Richardia*, *Solanum*, *Tacinga* and *Neoglaziovia* were more com-

mon, while in the most disturbed areas *Borreria*, *Turnera*, *Solanum*, *Euphorbia* and *Tarenaya* predominated (Fig. 2). This suggests that rainfall reduction and increased disturbance are driving communities towards different successional pathways. The genera *Rhaphiodon*, *Astraea*, *Merremia*, *Richardia* and *Borreria*, common in drier or disturbed areas, also dominated the plots with lower density of woody plots, along with *Melocactus*, *Chamaecrista*, *Mimosa*, *Piriqueta*, *Blainvilea* and *Indigofera*. Only *Physostemom* occurred exclusively in areas with higher density of woody plants.

Overall, forest stands supported relatively species-rich communities (5–26 species per 5 m^2), with herb density varying from 54 to 2291 individuals per 5 m^2. Herb density responded positively to rainfall as expected, but species richness did not (Fig. 3, Table S3). Chronic disturbance did not significantly affect herb density or species richness. Density of woody plants negatively affected species richness, but surprisingly did not influence herb density (Fig. 3, Table S3).

Phylogenetic responses

The level of relatedness close to the tips of the phylogeny (NTI) increased in the drier areas, but decreased in the more disturbed areas (Fig. 3, Table S3). Consistent with the taxonomic responses, these contrasting trends suggest that rainfall reduction and increased chronic disturbance are driving communities towards different phylogenetic profiles. Nonetheless, phylogenetic richness [$^0D(T)$] and divergence [MPD, MNTD, $^1D(T)$, $^2D(T)$] were not significantly affected by rainfall and disturbance (Fig. 3, Table S3).

The reduction in the density of woody plants increased the effective number of lineages [$^0D(T)$], the level of relatedness close to tips (NTI) and across the entire phylogeny (NRI), and the phylogenetic divergence in the terminal branches (MNTD) (Fig. 3, Table
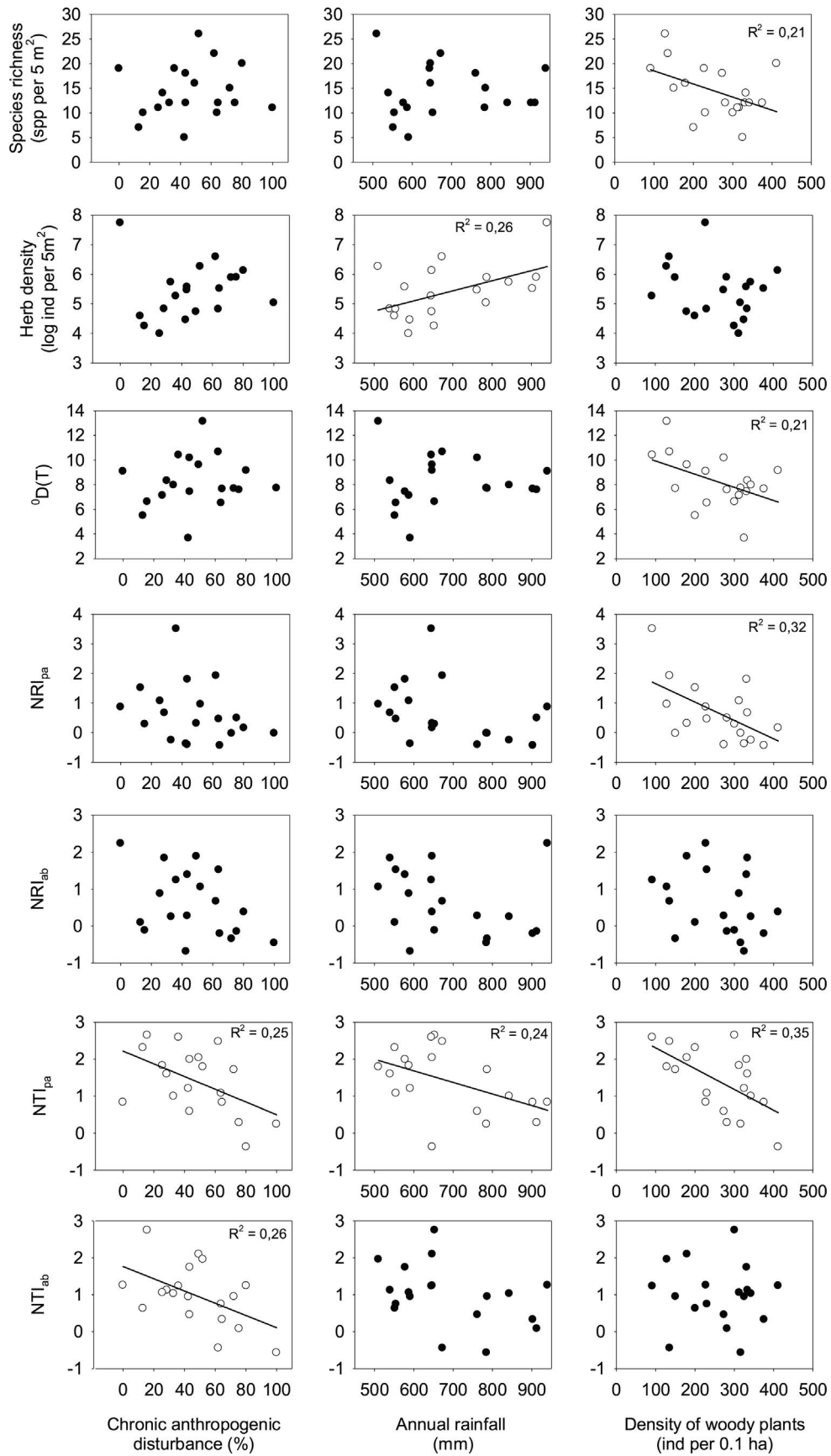
Fig. 3. Relationships among chronic anthropogenic disturbance, annual rainfall and density of woody plants with species richness, herb density, and phylogenetic metrics of herb communities across 19 stands of the Caatinga dry forest, northeast Brazil. *ab* and *pa* refers to abundance-based and presence/absence metrics, respectively. Statistics are shown in Table S3.
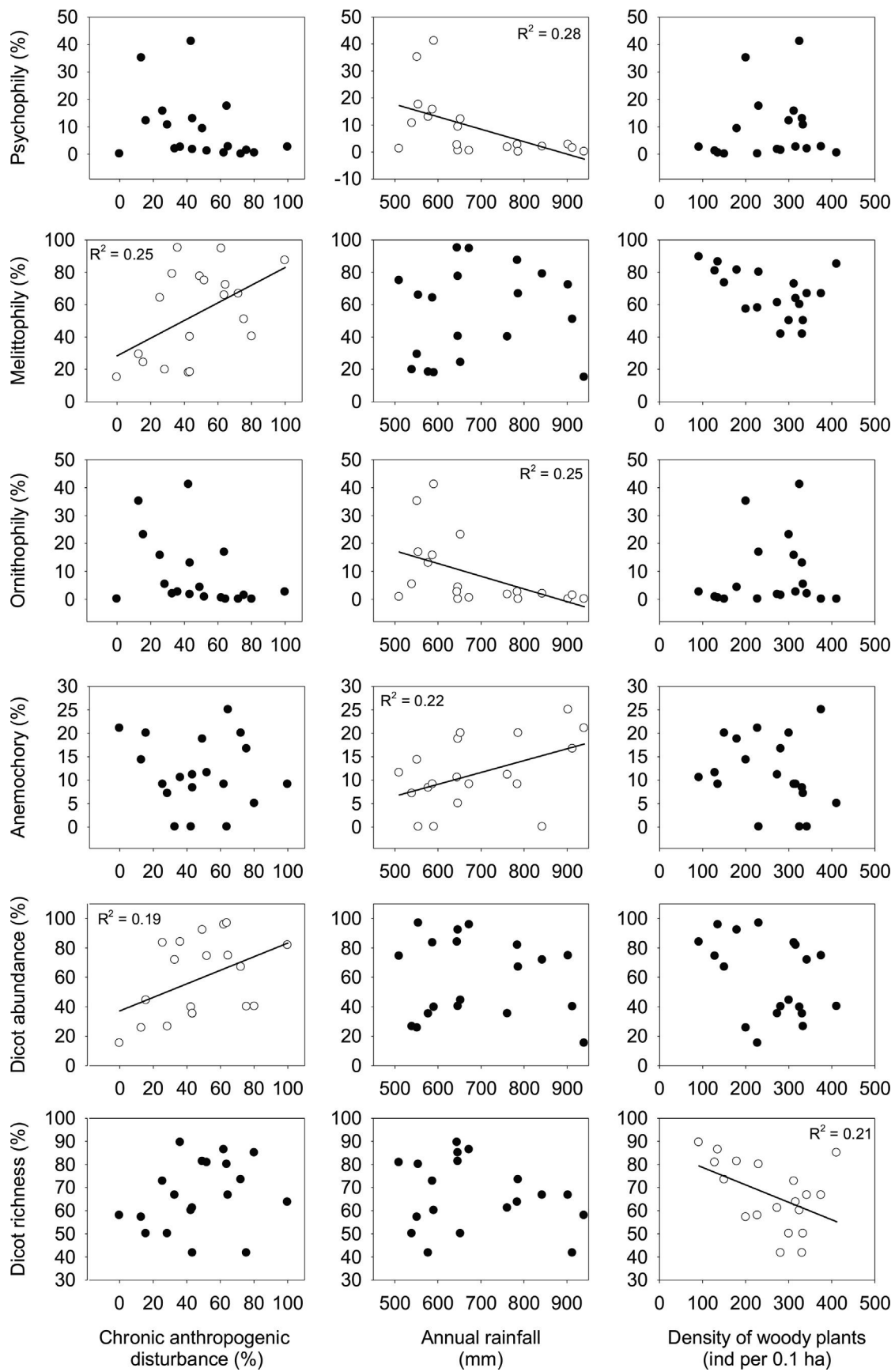
Fig. 4. Relationships among chronic anthropogenic disturbance, annual rainfall and density of woody plants with functional metrics of herb communities across 19 stands of the Caatinga dry forest, northeast Brazil. Statistics are shown in Table S5.

S3). In summary, drier, less disturbed and less dense forest stands supported more phylogenetically clustered communities.

Functional responses

Herb communities were dominated by dicots (82.4% of species and 49.4% of individuals), therophytes (80.7% of species and 90.5% of individuals), species pollinated by bees (71.9% of species and 48.6% of individuals) and dispersed via autochory (61.4% of species and 47.9% of individuals). Grasses played a minor role in terms of number of species (8.8%), but were representative in terms of number of individuals (46.9%) (Table S4). The majority of species and individuals exhibited traits associated with high palatability to livestock (59.6% of species and 60.7% of individuals) (Table S4).

With the exception of life form and palatability, explanatory variables affected different functional attributes of herb communities (Table S5). Dicot abundance was positively related to chronic disturbance (Fig. 4, Table S5), while dicot species richness was negatively correlated with the density of woody plants (Fig. 4, Table S5). Chronic disturbance also affected positively the abundance of individuals pollinated by bees, while rainfall correlated negatively with the abundance of individuals pollinated by butterflies and birds, and positively with plants dispersed by wind (Fig. 4, Table S5).

Discussion

Our findings support the hypothesis that the reduction in rainfall and the increase in chronic disturbance erode different dimensions of plant diversity in the Brazilian Caatinga (Ribeiro et al., 2015, 2016, 2019; Rito et al., 2017b). Rainfall and chronic disturbance do not affect species richness, but favor floristic divergence by increasing a set of genera in drier areas and another set of genera in more disturbed areas. Rainfall and chronic disturbance also affect the phylogenetic and functional dimensions of communities differentially, affecting the level of relatedness among species and the functional profile of communities in contrasting ways. Our analyses also indicate indirect effects of rainfall and disturbance via local changes in the density of woody plants, which may affect all dimensions of herb diversity. Altogether, these findings suggest a profound reorganization of herb communities in face of human-driven environmental changes.

The outcome of this process will be biased herb communities with quite unpredictable composition, as each human driver pushes the herb flora towards a given successional pathways. If any, predictability in our study region will be restricted to a few genera such as *Rhaphiodon*, *Astraea*, *Merremia*, *Richardia* and *Borreria*, which converged the herbaceous flora of drier and more disturbed areas. Actually, multiple successional pathways are expected in response to the human-driven environmental changes in air temperature, rainfall and woody stratum (Arroyo-Rodríguez et al., 2017). Trajectories will depend not only on the local drivers that influence plant life cycle (i.e., recruitment, growth, seed germination, seed dispersal, fruit production), but also on the landscape and regional contexts in which the herb community is inserted (Arroyo-Rodríguez et al., 2017). But whatever the trajectory, the herb communities are not likely to gain taxonomic, phylogenetic, and functional diversity in face of the new conditions. In fact, rainfall reduction and increased chronic disturbance operate synergistically to degrade different aspects of herb diversity.

The mechanisms underlying the structure of herb communities along the environmental gradients are likely to involve disruptions in herb life cycle and their ecological interactions with woody plants and animals. Firstly, our analyses indicate that rainfall reduction resulted in lower herb density, probably due to water shortage for germination, growth and reproduction (Cicuzza et al., 2013). However, rainfall reduction did not result in lower species richness. This could be happened because recruits in wetter areas belonged to species already established in the plot, allowing communities in wetter areas to be denser, but not richer in species than those in drier areas. Secondly, the inhibitory effect of woody stratum on herbs appears to vary across species. Apparently, as more trees and shrubs are removed from the forest stand, representatives of *Rhaphiodon*, *Astraea*, *Merremia*, *Richardia*, *Borreria*, and other disturbance-adapted genera replace those more disturbance-sensitive ones (e.g. *Physostemom*), but herb density does not change. This interaction between woody plants and herbs is poorly known in the Caatinga and merits further in-depth investigation (Queiroz et al., 2015). Finally, the functional responses of communities in terms of pollination and dispersal syndromes also suggest that ecological interactions are underlying the reorganization of herb communities, as supported by other studies performed in the Catimbau National Park (Leal et al., 2014; Câmara et al., 2019; Oliveira et al., 2019; Andrade et al., 2020).

In summary, our results demonstrate that (1) the Caatinga herb communities may take multiple successional pathways in response to human-driven environmental changes; (2) the pathways may change not only basic components of community structure, such as herb density and species composition, but also hidden aspects of functional and phylogenetic dimensions; (3) animals that interact positively or negatively with herbs might be affected, particularly birds and insects, potentially scaling up the phenomenon to the ecosystem level. If the projected reductions in rainfall are confirmed (PBMC, 2013) and public policies are not implemented to minimize local pressure on natural resources (Antongiovanni et al., 2020), we believe that a significant amount of the plant diversity of Caatinga dry forests may be vanished irreversibly (Queiroz et al., 2017).

As argued elsewhere (Ribeiro et al., 2015), we recommend four actions for practitioners, decision-makers, stakeholders and politicians: (i) developing research and rural programs able to support better practices of land use, sustainable exploitation of forest resources, and agricultural production, such as the sustainable agricultural landscape model described in Araújo et al. (2021); (ii) improving governance, law enforcement, and environmental education to shift extractivism towards sustainable standards, reducing chronic disturbances at local and regional levels (Antongiovanni et al., 2020); (iii) expanding the coverage and effective implementation of strictly protected areas to minimize changes in the woody stratum and protect the biodiversity that interact with herbs; (iv) and acting against any practice that results in global warming to avoid rainfall reduction in the region. The implementation of these recommendations should take place locally, in private or public lands, with small groups of people, but the outcomes will be collectivized if the conservation strategies are planned for the entire Caatinga.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Acknowledgments

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pecon.2021.12.002.

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