

Rainfall reduction increases insect herbivory in tropical herb communities

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Abstract

Questions: Climate change is dramatically altering rainfall patterns and species distribution around the world. However, little is known about how rainfall reduction may affect plant–herbivore interactions that are crucial to the of input energy and nutrients into terrestrial ecosystems. Following Coley's growth rate hypothesis, we assessed whether rainfall reduction in a seasonally dry tropical forest decreases community-level herbivory owing to water shortage in drier areas.

Location: Catimbau National Park, Northeast Brazil.

Methods: We sampled 16 herb communities along a rainfall gradient (564–917 mm). Using digital photographs, we monitored for 3 weeks the frequency, magnitude and type (feeding guild) of insect damage on young, fully expanded, short-lived leaves (lifespan <1 month). We related herbivory levels to local rainfall and examined potential confounding effects of herb abundance, richness and floristic composition on such relationships.

Results: We monitored 290 leaves from 202 plants belonging to 28 species. About one-third of the leaves and six species escaped from herbivory. Leaf-chewing insects were the most frequent herbivores, attacking 17 species, 44% ± 15% of the leaves and removing the same amount of foliar tissue as all the other insects combined removed (sap-sucking, rasping, leaf-mining and 'unknown'). Contrary to expectations, foliar damage accumulated more in drier areas following the increase in the frequency of leaf-chewing damage. In addition, frequency and magnitude of herbivory did not vary with herb abundance and richness and were weakly influenced by floristic composition.

Conclusions: Our findings suggest that rainfall underlies community-level herbivory by mechanisms not related to plant availability, identity and diversity. Based on recent evidence that aridity favours leaf-chewing proliferation in the study region, we hypothesize that rainfall reduction may weaken the top-down control of herbivores, increasing folivory pressure on herbs. If prolonged droughts become more frequent in the coming decades, plant–herbivore interactions may be altered permanently.

KEYWORDS

aridity, Caatinga, climate change, dry forest, environmental gradient, folivory, plant-insect interaction, precipitation

1 | INTRODUCTION

The effects of global warming and climate change are no longer debatable: the question now is how plants and animals will adapt to these (if they do so) and how this will impact on our ecosystems (Bonan & Doney, 2018; Rogelj et al., 2018). In South America, the emissions of greenhouse gases are expected to raise mean air temperatures from +1.7°C to +6.7°C during this century (Magrin et al., 2014), drastically affecting the rainfall regime (Weltzin et al., 2006). This warming is predicted to be more severe in regions with arid and semi-arid climate (Feng, Porporato, & Rodríguez-Iturbe, 2013) such as north-east Brazil, which in turn should face a 22% decrease in annual average rainfall and an increase from 2% to 6% in dry season spell (Magrin et al., 2014). This region is home to over 30 million people, most of whom depend upon forest resources for food and energy, and covers about 1 million km² with unique seasonally dry tropical forests (Silva et al., 2017; Specht et al., 2019). Understanding how species will interact to each other under the new drier conditions is therefore critical for the region.

Plant-insect interactions are the basis of terrestrial food chains (Scherber, Heimann, Köhler, Mitschunas, & Weisser, 2010; Schmitz, 2008) and herbivory is amongst the most important ecological interactions because it represents the first entry of energy and matter into consumer trophic levels (Coley & Barone, 1996). To be established, herbivory requires not only the host (palatable) plant and the insect, but also suitable conditions for both. Unsuitable environmental conditions such as shade in tropical rainforests and aridity in dry forests may disrupt, strengthen or weaken the interaction by modifying the establishment and performance of plants (Moro et al., 2015) and insects (Ayres & Lombardero, 2000). Rainfall reduction is likely to reduce soil moisture and, consequently, plant ability to tolerate or resist to herbivore attack; physical, chemical, and nutritional foliar characteristics may change in response to drought or warming (Santos & Benítez-Malvido, 2012; Zhang et al., 2018). Similarly, rainfall reduction may reduce air humidity and rise air temperature, modifying insect growth, dispersal and feeding intensity on their host plants (Weltzin et al., 2006; Wilf, Labandeira, Johnson, Coley, & Cutter, 2001). Thus, the level of foliar damage (i.e. the frequency and magnitude of herbivore attack) will be ultimately driven by the environment (Santos & Benítez-Malvido, 2012).

One of the most acceptable hypotheses to explain patterns of insect herbivory in tropical forests is Coley's Growth Rate or Resource Availability hypothesis (Coley, Bryant, & Chapin, 1985). It assumes that fast-growing species have short-lived leaves because energy acquisition in nutrient-rich environments is maximized by rapid leaf turnover, whereas slow-growing species have long-lived leaves because slow turnover is advantageous in a nutrient-poor environment where (re)growth is constrained (Stamp, 2003). Among its

predictions, is that in low-resource environments (e.g. dry or shaded habitats), resource limitation favours slow-growing plant species that bear conservative traits and allocate more resources to avoid being attacked (Coley et al., 1985; McBranch et al., 2016; Wigley et al., 2016). Conversely, high-resource environments (e.g. wet and sunny habitats) favour plants with more acquisitive characteristics that allow them to tolerate and compensate for herbivore damage (Coley et al., 1985; Endara & Coley, 2011). These responses are expected to scale up from populations to the whole community, making herbivore damage less frequent and intense in low-resource (drier) habitats (Coley et al., 1985; Loughnan & Williams, 2019; Rodríguez-Castañeda, 2013).

The herbivorous insects also respond to environmental conditions (Weissflog, Markesteijn, Lewis, Comita, & Engelbrecht, 2018) depending on their feeding habits (Anstett, Naujokaitis-Lewis, & Johnson, 2014; Huberty & Denno, 2004). In wetter environments, damage by free-living insects such as leaf-chewing and sap-sucking may be more prominent owing to increased insect survivorship in such areas (Mazía, Chaneton, Dellacanonica, Dipaolo, & Kitzberger, 2012). In contrast, drier environments can improve the performance of leaf-mining (Mazía et al., 2012) and galling insects (Lara & Fernandes, 1996; Price et al., 1998), increasing their foliar damage. In a multi-trophic perspective, it is also possible to observe changes in the interaction between herbivorous insects and their natural enemies. As shown by Connahs, Aiello, Van Bael, and Rodríguez-Castañeda (2011), parasite and parasitoid species that are limited by water scarcity may reduce predation and parasitism in drier seasons, relaxing the top-down control of insect herbivore populations they prey on. Similarly, insectivory by birds, bats and other vertebrates may be weakened in response to anthropogenic modifications that make the environment drier and warmer, increasing the frequency of herbivory (Greenberg et al., 2000; see also Roslin et al. (2017) for global patterns of arthropod, bird and mammal predation along latitude and elevation gradient).

In the present study, we assessed whether rainfall reduction in the Caatinga decreases community-level insect herbivory owing to water shortage in drier areas (*sensu* Coley's hypothesis). We took advantage of the natural variation in annual rainfall observed in one of the largest protected areas of north-east Brazil (480–1,100 mm), the Catimbau National Park (see also Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017). We focused on the herb stratum, which is known to concentrate the plant species diversity of the Caatinga (Moro et al., 2015), and used non-destructive methods (digital photographs) to monitor the frequency and magnitude of foliar damage by leaf-chewing, sap-sucking, rasping, leaf-mining and galling insects along the rainfall gradient. We expected that wetter areas would present more foliar damage such as leaf-chewing, rasping, and sap-sucking by free-living insects, while endogenous insects

such as leaf-mining and galling insects would damage more leaf tissue in drier areas (Mazía et al., 2012). We also examined potential confounding effects of herb abundance, richness and floristic composition on herbivory patterns across the rainfall gradient.

2 | METHODS

2.1 | Study area

The study was performed in the 640-km² Catimbau National Park, north-east Brazil (8°24'00" and 8°36'35"S, 37°0'30" and 37°1'40"W). The climate is predominantly semi-arid (Koeppen's classification Bsh), with an average annual temperature of approximately 23°C. Rainfall decreases sharply from east to west, from 1,100 mm to 480 mm annually, and the rainy season usually occurs from March to June (Rito et al., 2017). The soil is predominantly quartz-type regosol with coarse granulation. The vegetation varies from herbaceous, shrub to arboreal with deciduous species. Herbaceous is the most representative plant growth form, with 33% (202 species) of the total Catimbau flora (Rito et al., 2017). Fabaceae and Euphorbiaceae are the most common botanical families in the woody strata (Rito et al., 2017). The herbaceous stratum is mainly composed of Poaceae, Asteraceae, Cyperaceae, Bromeliaceae, and Fabaceae (Athiê-Souza et al., 2019) and the most common species are *Commelina erecta* (Commelinaceae), *Mollugo verticillata* (Molluginaceae) and *Urochloa mollis* (Poaceae) (Vieira, 2017). Most of them have very short life spans (<2 months), germinating, growing and reproducing within the short rainy season (Vieira, 2017). The insect community is dominated by representatives from Coleoptera, Hemiptera, Orthoptera, Hymenoptera, Lepidoptera and Phasmatodea (Santos-Neto, 2016). These orders are very diverse with representatives in different trophic levels, including many herbivores (Rafael et al., 2012).

2.2 | Plant sampling and herbivory monitoring

We started our fieldwork in June 2017 at the end of the rainy season. This year was the first following a long drought period between 2012 and 2016, which possibly collapsed herb and insect populations across the entire Caatinga. At our study sites, the first rains started in March and April 2017. Therefore, we waited some weeks to allow herbs to fully expand their leaves and insects to recover their populations. We then proceeded with our survey by sampling herb communities in 16 plots of 20 m × 20 m (400 m²). Plots were at least 1 km away from each other and encompassed an annual rainfall gradient that varied from 564 to 917 mm (Figure 1). Annual average temperature is quite constant among the plots, usually reaching 21°C in July (coldest month) and 25°C in December (warmest month). Plots were protected against herbivorous mammals with barbed wire fences, including livestock (mainly goats) raised extensively within the park (Specht et al., 2019). Rainfall data was extracted from WordClim global climate data repository at 1 km²

scale (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) (www.worldclim.org), which calculated averages for the 1960–1990 period. In each plot, we systematically established five equidistant subplots of 0.25 m² (0.5 m × 0.5 m) and randomly marked representatives of the most abundant herb species to be monitored (N = 202 across the 80 subplots). Species were selected from a previous study on the herb communities of the Catimbau National Park (Vieira, 2017). Subplots were needed to capture the patchy distribution of many herb species within the plots, but all statistical analyses were performed at the plot level (N = 16) by collapsing subplot data, thus avoiding pseudoreplication.

To estimate the frequency and magnitude of foliar damage (i.e. proportion of leaves attacked and percentage of leaf area damaged, respectively), in the first week (time 0) we randomly sampled one to six young, healthy, fully expanded leaves (N = 297 leaves) from each plant and monitored them weekly for the next three weeks. The number of leaves varied between plants, species, subplots and plots because many leaves did not match our conservative criteria at time 0. To monitor the injuries by leaf-chewing, rasping, sap-sucking, leaf-mining and unknown insects, if any, we used a 10-megapixel digital camera (Nikon Coolpix P80) and a white background panel. We took digital photographs with maximum focal length of 84.2 mm and a scale of 2 cm × 2 cm. The images were then processed and analysed with the ImageJ software (Rasband 1997–2006). We considered as damage any injury present in leaf blade caused by herbivorous insects, following Filip, Dirzo, Maass, and Sarukhan (1995).

Because herbivore attack by different feeding guilds may be infrequent but very intense (low frequency and high magnitude) and vice versa (high frequency and low magnitude), we examined herbivory levels in several complementary ways. We used herbivory frequency to describe the prevalence of folivory on Caatinga herbs. Frequency reached 1 when all leaves were attacked and was 0 when all remained intact by the end of the monitoring. Second, we estimated herbivory magnitude as daily rates (% day⁻¹) to allow comparisons with other studies and across plant species (Coley & Barone, 1996). Weekly rates were used to support our repeated measures analyses on damage evolution, given that our sample size was not large enough to perform analyses by day; this would imply 21 levels within the factor time and require dozens of plots. Finally, we used the damage accumulated over the three weeks to compare herbivory levels among feeding guilds across the rainfall gradient. In that case, time was controlled instead of being considered a source of variation. It is important to note that the leaf lifetime varied across species: 86 leaves dropped before monitoring ended, so those cases, herbivory level was assumed to be the same recorded in the last week.

2.3 | Feeding guilds

To quantify the relative damage caused by leaf-chewing, rasping, sap-sucking, leaf-mining and unknown insects, we classified the injuries into six main types of damage following Loranger et al. (2014) and Andrade, Batista, Pereira, Fernandes, and Santos (2019): (a)

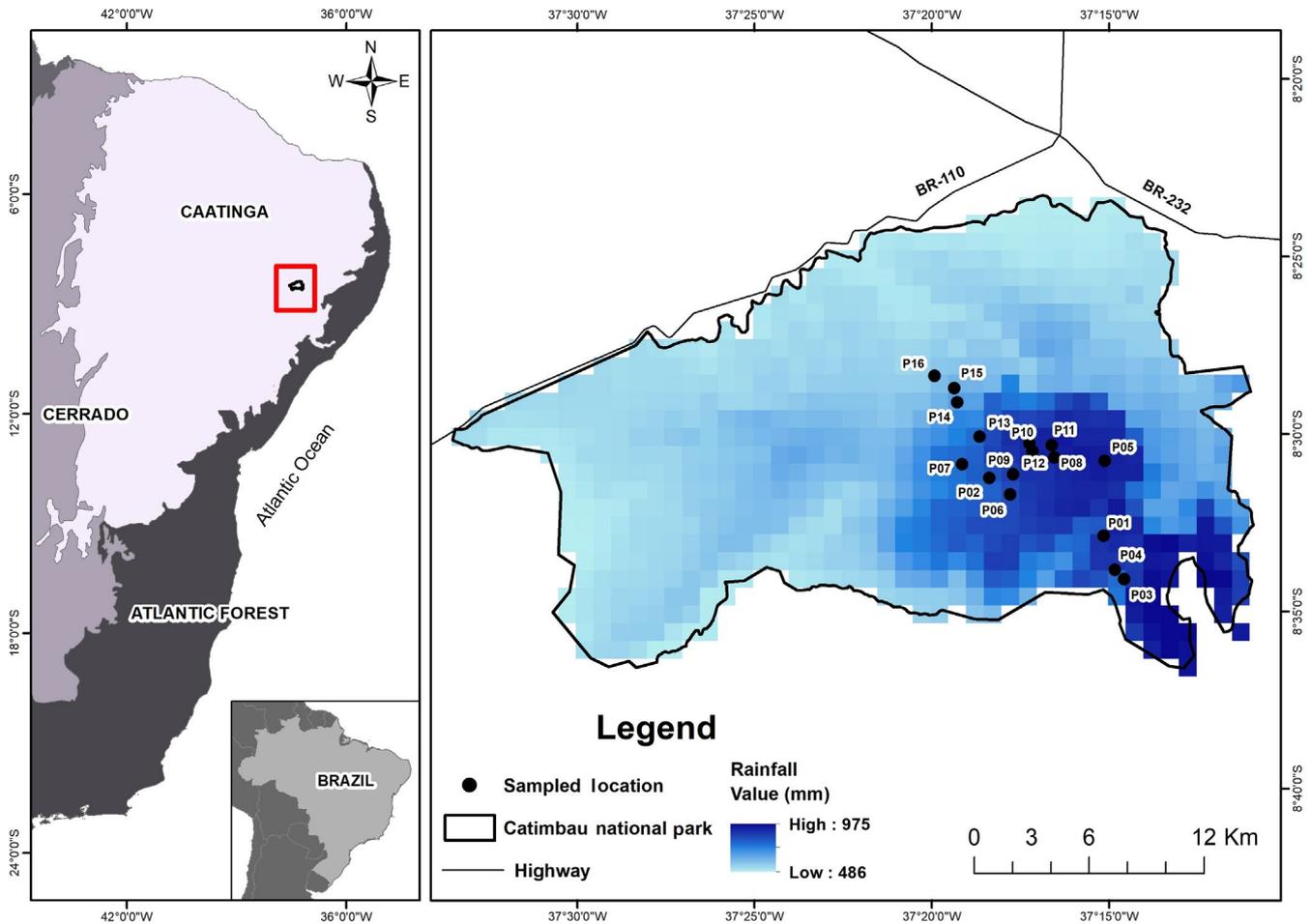


FIGURE 1 Location of the study region in Northeast Brazil, Catimbau National Park, indicated by the small red square on the left and enlarged on the right. Different shades of blue describe the rainfall gradient in which the 16 herb communities were monitored [Colour figure can be viewed at wileyonlinelibrary.com]

leaf-chewing damage – any completely missing area of the leaf blade with regular (e.g. leaf-cutting ants) or irregular shape (e.g. caterpillars, beetles) in the border or in centre of the leaves; (b) sap-sucking damage – regular or irregular shape scars, as well as small holes in the leaf blade (e.g. Hemiptera, Thysanoptera); (c) rasping damage – a kind of damage that only part of the leaf blade is removed from the abaxial or adaxial blade surface but leaving the ribs, and no hole is formed (e.g. young caterpillars); (d) leaf-mining damage – the removal of the leaf mesophyll conserving abaxial and adaxial surfaces causing a serpentine or blotched dead areas in the leaves (e.g. larval stages of Coleoptera, Diptera, Hymenoptera and Lepidoptera); (e) galling damage – protuberances on the abaxial and/or adaxial surfaces, smooth or covered by trichomes (e.g. Diptera, Coleoptera, Hymenoptera, Hemiptera, Thysanoptera and Lepidoptera); and (f) unknown damage – caused by insects that did not fit the categories above.

2.4 | Herb density, richness and composition

Working with the most abundant species of each plot ensured a reliable description of the herbivory at the community level, but

resulted in strong differences in plant composition that could underlie herbivory patterns along the gradient. We solved this problem statistically by assessing a posteriori the effect of plant composition on herbivory levels (see Section 2.5). To that end, we first counted and identified all herb plants recorded in the subplots following the botanical nomenclature of APG III (Angiosperm Phylogeny Group, 2009). We identified the species by consulting experts and comparing the records with previously identified material from our research team (Vieira, 2017). Specimens that we were not able to identify at the family level were treated as morphospecies. These variables were finally used to decouple the effects of herb density, richness and species composition from the effect of rainfall on herbivory.

2.5 | Statistical analyses

To test whether herbivory levels decreased with rainfall as time advances, we used generalized linear mixed model (GLMM) (Bolker et al., 2009). We set rainfall, time (weeks) and their interaction as fixed effects and plot identity (ID) as random effect. The response variable (damage accumulated per week) was arcsine square-root

transformed to satisfy model assumptions (Crawley, 2007). We performed the GLMM in JMP 7 (SAS Institute Inc.) using the restricted maximum likelihood method to separate the variance of fixed effects from that of the random effects (Bolker et al., 2009).

We also performed GLMMs to assess if wetter areas presented more foliar damage by free-living insects and less damage by endogenous insects. In these cases, we set rainfall, feeding guild and their interaction as fixed effect and plot identity (ID) as random effect. Because damage by leaf-chewing insects was much more frequent than the other feeding guilds (see Section 3), we collapsed damage by the other feeding guilds into a single category and compared it against leaf-chewing insects. The response variables of these GLMMs (herbivory at the end of the sampling period) were also arcsine square-root transformed to satisfy model assumptions.

To explore the effects of herb density and richness on herbivory levels, we modelled the cumulative damage as a function of herb density and richness per plot using multiple linear regression. Finally, to assess how herb species composition affected herbivory levels, we performed Mantel tests in PRIMER 6.0 Software (Clarke & Gorley, 2006). We constructed a species similarity matrix based on Bray–Curtis abundance-based index to describe the variation in species composition across the plots. Then we constructed similar matrices based on the Euclidian distance of cumulative frequency and cumulative magnitude of damage, which were then correlated to the species similarity matrix.

3 | RESULTS

We recorded 28 herb species belonging to 21 genera and 17 families (Table 1). Approximately 36% of the leaves remained intact throughout the monitoring period. Surprisingly, no leaf was damaged by galling insects, even in the driest plots. Only six species escaped herbivore attack.

While some species had all their leaves damaged (frequency of 1.0) or showed daily rates of herbivory as high as 2.7% per day (Figure 2), herbivores removed <12% of the herb community tissue by the end of the monitoring (Figure 3). Leaf-chewing insects were the most frequent herbivores, attacking 17 species, $44\% \pm 15\%$ (mean \pm SD) of the leaves and removing the same amount of foliar tissue damaged by the other insects combined (sap-sucking, rasping, leaf-mining, and unknown together).

Contrary to expectations, herb communities in drier areas accumulated significantly more foliar damage than communities in wetter areas (Table 2; see also the red and green lines above blue ones in Figure 3). This pattern followed the increase in the frequency of leaf-chewing damage in the drier areas, which was twice that of all other guilds together (Table 3; Figure 4). However, the magnitude of the damage by leaf-chewing insects did not vary consistently with rainfall (Table 3; Figure 4).

With regard to the effects of herb density and richness on herbivory levels, both frequency and magnitude of foliar damage varied

TABLE 1 Herb species and morphospecies recorded along a rainfall gradient in the Catimbau National Park, north-east Brazil.

Species	Family	Total abundance
<i>Richardia</i> sp.	Rubiaceae	103
<i>Herissantia</i> sp.	Malvaceae	89
<i>Portulaca mucronata</i>	Portulacaceae	51
<i>Commelina</i> sp.	Commelinaceae	45
<i>Galactia</i> sp.	Fabaceae	23
<i>Urochloa mollis</i>	Poaceae	19
<i>Sida</i> sp.	Malvaceae	19
<i>Talinum paniculatum</i>	Talinaceae	18
Morphospecies M21	–	10
<i>Zornia grandiflora</i>	Fabaceae	8
<i>Chamaecrista rotundifolia</i>	Fabaceae	7
<i>Pavonia</i> sp.	Malvaceae	7
<i>Alternanthera brasiliana</i>	Amaranthaceae	5
<i>Ayenia erecta</i>	Malvaceae	4
<i>Aeschynomene viscidula</i>	Fabaceae	3
<i>Bidens pilosa</i>	Asteraceae	2
Morphospecies M20	–	2
<i>Marsypienthes chamaedrys</i>	Lamiaceae	1
<i>Boehavia coccinea</i>	Nyctaginaceae	1
<i>Jacquemontia</i> sp.	Convolvulaceae	1
<i>Kallstroemia grandiflora</i>	Zygophyllaceae	1
Morphospecies M11	–	1
Morphospecies M14	–	1
<i>Pombalia</i> sp.	Violaceae	1
<i>Schwendia americana</i>	Solanaceae	1
<i>Tarenaya spinosa</i>	Cleomaceae	1
<i>Tragos bertonianum</i>	Poaceae	1

Note: Total abundance refers to the total number of individuals observed in 80 subplots of 0.25 m². Their herbivory levels are described in Figure 2.

irrespective of these variables (Appendix S1). This pattern was also supported by rare and abundant plant species that presented similar herbivory levels (Figure 2), as well as by herb species with similar density but contrasting damage levels, for example *Urochloa mollis* (Poaceae) and *Talinum paniculatum* (Talinaceae). Furthermore, floristic composition did not affect the frequency of foliar damage ($\rho = -0.002$; $p = 0.43$) and weakly influenced herbivory magnitude ($\rho = 0.244$; $p = 0.042$), as indicated by the low ρ value.

4 | DISCUSSION

Our findings do not support Coley's Growth Rate hypothesis as a plausible explanation to describe community-level patterns of insect herbivory on native Caatinga herbs. To support it, the frequency and

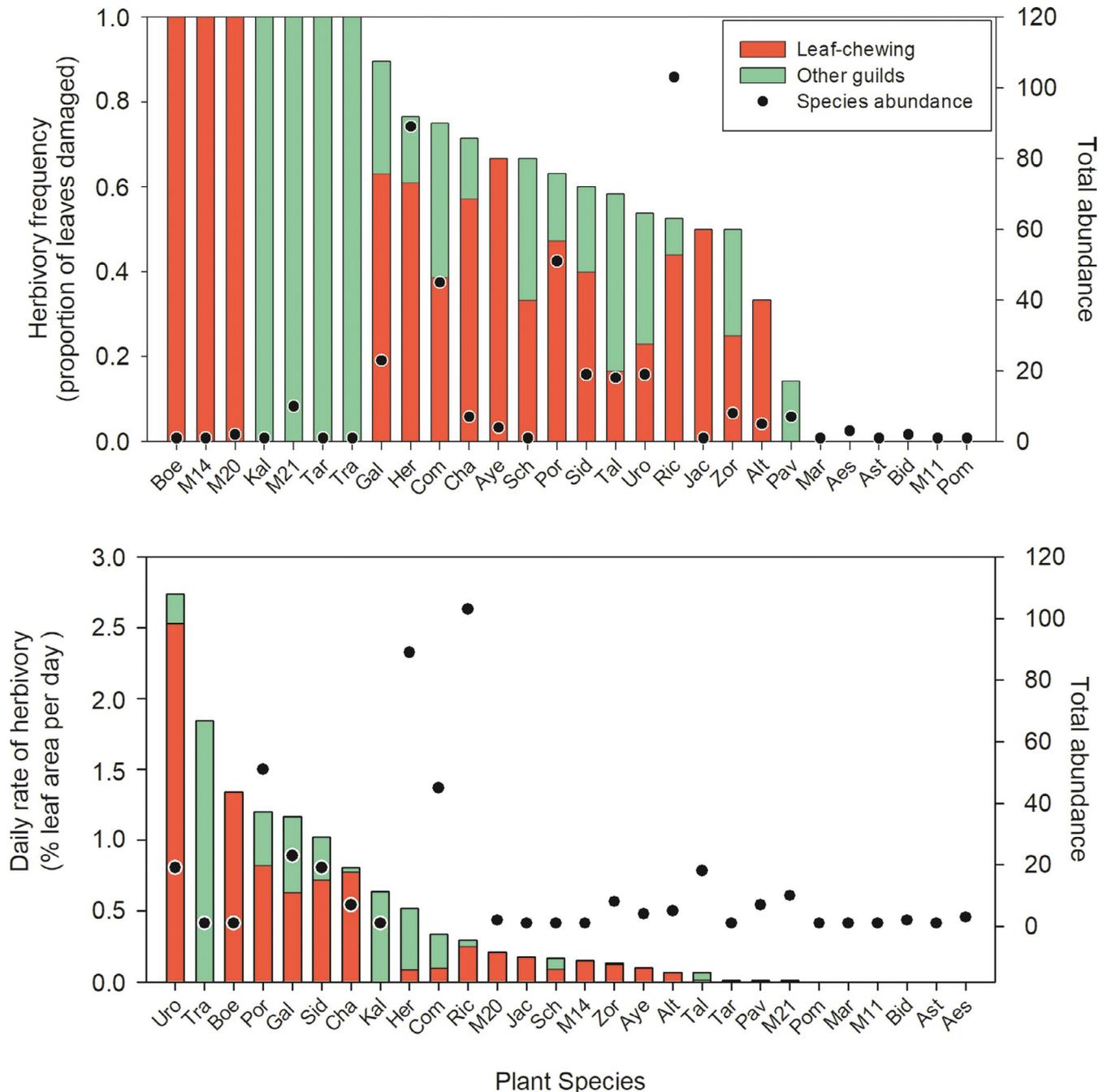
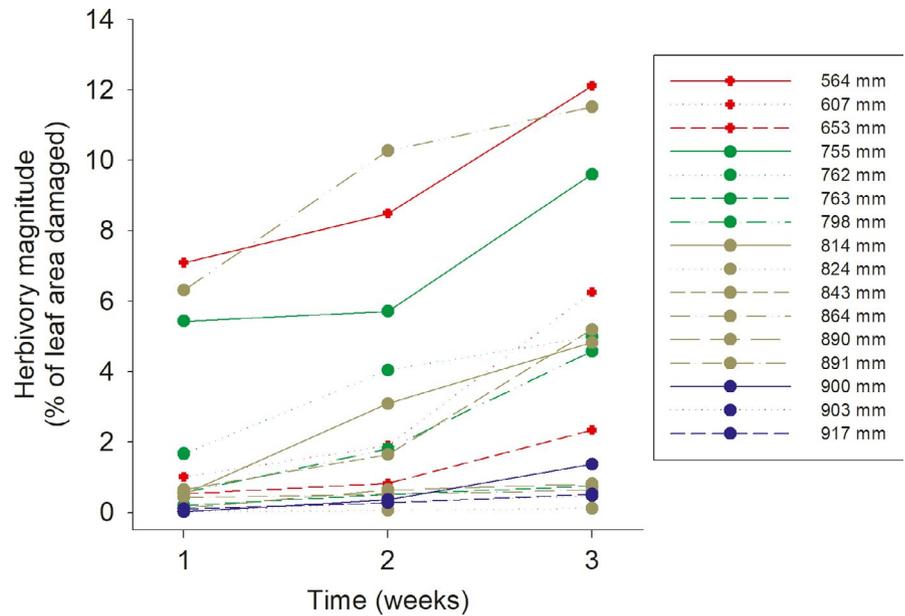


FIGURE 2 Herbivory frequency and magnitude (daily rate of damage) by herb species in the Catimbau National Park, north-east Brazil. 'Other guilds' refer to the damage caused by sap-sucking, rasping, leaf-mining and unknown insect herbivores combined. Total abundance indicates the abundance of each herb species recorded in 80 subplots of 0.25 m². Gal, *Galactia* sp. (Fabaceae); Por, *Portulaca mucronata* (Portulacaceae); Uro, *Urochloa mollis* (Poaceae); Her, *Herissantia* sp. (Malvaceae); Ric, *Richardia* sp. (Rubiaceae); Com, *Commelina* sp. (Commelinaceae); Sid, *Sida* sp. (Malvaceae); Cha, *Chamaecrista rotundifolia* (Fabaceae); Boe, *Boehavia coccinea* (Nyctaginaceae); Tra, *Tragos bertonianum* (Poaceae); Kal, *Kallstroemia grandiflora* (Zygophyllaceae); Zor, *Zornia grandiflora* (Fabaceae); Tal, *Talinum paniculatum* (Talinaceae); M20, Morph-specie 20; Aye, *Ayenia erecta* (Malvaceae); Jac, *Jacquemontia* sp. (Convolvulaceae); M14, Morphospecies 14; Alt, *Alternanthera brasiliana* (Amaranthaceae); Sch, *Schwendia americana* (Solanaceae); Mar, *Marsypienthes chamaedrys* (Lamiaceae); Aes, *Aeschynomene viscidula* (Fabaceae); Ast, *Astrea lobata* (Euphorbiaceae); Bid, *Bidens pilosa* (Asteraceae); M11, Morphospecies 11; M21, Morphospecies 21; Pav, *Pavonia* sp. (Malvaceae); Pom, *Pombalia* sp. (Violaceae); and Tar, *Tarenaya spinosa* (Cleomaceae) [Colour figure can be viewed at wileyonlinelibrary.com]

magnitude of herbivory should have been smaller in drier areas where the limiting resource water is scarce and plants should be better defended. However, we observed not only a similar high frequency of herbivory across the entire rainfall gradient, but also a significantly

greater magnitude of herbivory in the drier areas (the opposite). The explanation seems to be related to weak plant responses to rainfall at the Catimbau National Park and strong response of leaf-chewing insects to aridity, which we detail below.

FIGURE 3 Mean herbivory magnitude accumulated over 3 weeks on 16 herb communities in the Catimbau National Park, Northeast Brazil. Each line represents a community with its respective annual rainfall. Note that wetter sites (blue) accumulated less foliar damage. Statistics are shown in Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]



That plants from dry sites bear several conservative foliar characteristics (McBranch et al., 2016; Wigley et al., 2016) that contribute to defence against herbivore attack has been exhaustively discussed (Endara & Coley, 2011; Loughnan & Williams, 2019). Although there is no doubt that water is the main resource affecting the biological dynamics at the Caatinga (Silva et al., 2017), apparently the rainfall range of our gradient (564 to 917 mm annually) has been not enough to sort out defensive strategies against insect herbivores across the plots (Endara & Coley, 2011; Scherber et al., 2010). Consequently, herbs in drier plots may be as well defended as they are in wetter plots, violating the premise of Coley’s hypothesis of more defence in poor environments. Although we have not measured any kind of defence, this statement is supported by Sfair and colleagues’ study at the Catimbau National Park (Sfair, de Bello, de França, Baldauf, & Tabarelli, 2018), who found no relationship between environmental gradients and conservative or acquisitive plant traits (but see Moreira et al. (2018) and Cao, Li, and Chen (2018) for examples of significant environmental effects on leaf traits).

The weak effect of plant characteristics as a driver of herbivore damage also appeared in the analyses of the effects of herb density, richness and floristic composition on herbivory levels. Plant abundance is known to affect damage by leaving the host plants

more visible to insects [plant appearance hypothesis sensu Feeny (1976)]. Plant species richness may buffer foliar attack by providing alternative hosts to herbivores, thus avoiding the typical out-breaks seen in monocultures (Scherber et al., 2010; Weissflog et al., 2018). Even with host density and richness being equal, herbivory levels might be also influenced by plant composition membership, which will determine palatability and herbivory at the community level (Ruiz-Guerra, Guevara, Mariano, & Dirzo, 2010). However, our findings indicate that plots with greater herb density or richness do not exhibit greater herbivory levels than those with smaller density and richness. In addition, they show that floristic composition is a poor predictor of differences in damage caused. Asynchrony in leaf flushing might also have influenced the results, but the first rains of the rainy season synchronize herb growth across the study region.

TABLE 2 Fixed effects of generalized linear mixed models fitted for repeated measures of magnitude of herbivory (weekly rate of damage) as a function of rainfall and time (3 weeks) in the Catimbau National Park, north-east Brazil.

	df	F-ratio	p-value	Model R ² (%)
Rainfall	1,14	4.802	0.045*	95.7
Time	2,28	47.591	<0.001*	
Rainfall*Time	2,28	2.404	0.108	

Note: Refer to Figure 3 for graphical representation. The random factor (Plot ID) accounted for 8.5% of the residual variance.

TABLE 3 Fixed effects of generalized linear mixed models fitted for herbivory frequency and magnitude (damage accumulated over 3 weeks) as a function of rainfall and feeding guild (leaf-chewing insects vs. other guilds) in the Catimbau National Park, north-east Brazil. Other guilds combine the damage by sap-sucking, rasping, leaf-mining and unknown insect herbivores (see Figure 4). The random factor (Plot ID) accounted for 5.1% and 3.3% of the residual variance of the frequency and magnitude models, respectively

	df	F-ratio	p-value	Model R ² (%)
Herbivory frequency				
Rainfall	1,14	7.192	0.017*	24.1
Feeding guild	1,14	20.094	<0.001*	
Rainfall*feeding guild	1,14	0.831	0.377	
Herbivory magnitude				
Rainfall	1,14	2.533	0.133	12.8
Feeding guild	1,14	0.001	0.972	
Rainfall*feeding guild	1,14	0.706	0.414	

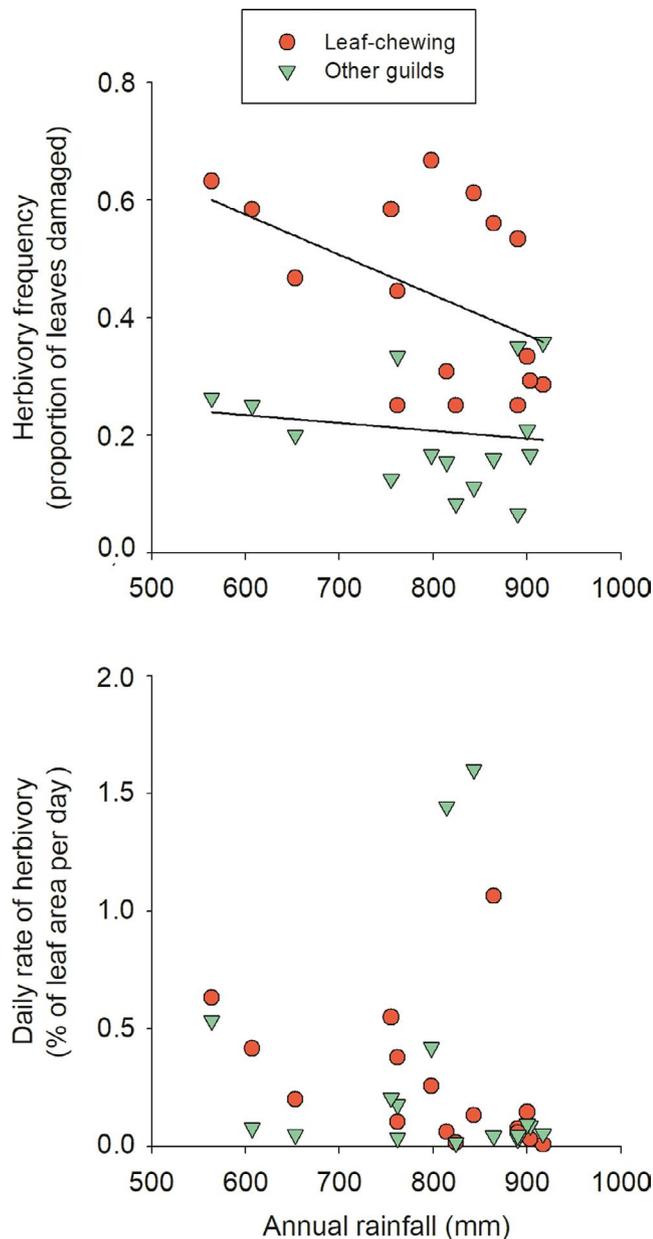


FIGURE 4 Herbivory frequency and magnitude on herb communities distributed across a rainfall gradient in the Catimbau National Park, north-east Brazil. Other guilds refer to sap-sucking, rasping, leaf-mining and unknown insect herbivores combined. Statistics are shown in Table 3 [Colour figure can be viewed at wileyonlinelibrary.com]

Jointly, these findings suggest that the interaction between herbs and herbivorous insects in the Caatinga is driven little by plant community characteristics.

We argue that herbivory patterns on herb communities are mainly ruled from top to bottom, with insects being the best predictor of damage levels. Although we have not been able to collect the herbivores and therefore describe insect dynamics at our plots, it is obvious that the interaction depends on insect abundance and feeding habits (Coley & Barone, 1996). Fortunately, a comprehensive assessment of herbivore insects has been conducted at the Catimbau

National Park (Santos-Neto, 2016). In the drier areas of Catimbau, there was an increase in abundance and richness of leaf-chewing insects such as Coleoptera, Orthoptera, and Lepidoptera (Santos-Neto, 2016), which clearly matches the increased frequency of damage we documented for this feeding guild in the drier areas. Our interpretation is that the leaf-chewing insects do not remove more tissue per leaf in the drier areas, but attack more leaves (i.e. increase their damage frequency) in the areas where they are more abundant.

The mechanisms underlying the leaf-chewing proliferation under drier conditions are not completely understood, as insect response to water availability is controversial in the literature (Huberty & Denno, 2004; Rodríguez-Castañeda, 2013). On one hand, dominance by leaf-chewing insects in wetter environments and by leaf-mining in xeric ones (Mazía et al., 2012), reduced grasshopper performance with increasing humidity (Barton, Beckerman, & Schmitz, 2009) and increase in damage by leaf-chewing insects from rain to dry forest has been documented (Brenes-Arguedas, Coley, & Kursar, 2009). On the other hand, in dry forests the rates of wasp parasitism, which control the populations of free-living insects, decrease sharply in dry season (Connahs et al., 2011) and predation on herbivorous insects decreases gradually with reducing rainfall (Rodríguez-Castañeda, 2013). Insectivory by birds, bats and other vertebrates, which are critical to control insect herbivore populations (Greenberg et al., 2000), might also be weaker in the drier areas. This phenomenon of reduced vertebrate predation and parasitism on insect herbivores has been described in forest remnants as ecological meltdown (sensu Terborgh et al., 2001), resulting in increased herbivory levels because of the relaxation of top-down control of herbivore populations.

Thus, we hypothesize that rainfall reduction in Catimbau National Park may weaken the top-down control of leaf-chewing herbivores, increasing folivory pressure on herbs. Such an increased impact of herbivores in drier environments has also been documented elsewhere. For example, Barton et al. (2009) observed that reduced water availability strengthened the herbivorous effect on the overall plant total biomass. In another study, leaf-cutting ants preferentially attacked plants from habitats with water limitation (Ribeiro-Neto, Pinho, Meyer, Wirth, & Leal, 2012), and at our study area, leaf-cutting ants pressure on woody plants (leaf consumption and herbivory rate) is higher in the dry season (Siqueira et al., 2018). The challenge arises in predicting the outcome of increased herbivory on the long-term persistence of herbs and the insects themselves. If prolonged droughts become more frequent in the coming decades (Magrin et al., 2014), plant-herbivore interactions may be altered permanently. Possible synergies with chronic anthropogenic disturbances may also impose additional threats (Rito et al., 2017). Further studies should investigate how rainfall drives insect development, dispersal and feeding strategies in the increasingly drier Caatinga. They should also deepen our understanding of the relative contribution of bottom-up and top-down drivers of insect herbivory, as both may be influenced by climatic factors.

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DATA AVAILABILITY STATEMENT

Raw data were generated at Long-Term Ecological Research (*Programa Ecológico de Longa Duração*) PELD Catimbau. Derived data supporting the findings of this study are available from the corresponding author (BAS) on request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Effect of herb density and species richness on herbivory frequency and magnitude (damage accumulated over 3 weeks) in the Catimbau National Park, Northeast Brazil

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