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TATIANE GOMES CALAÇA MENEZES

EFFECTS OF INTRODUCED HERBIVORES ON THE STRUCTURE AND DYNAMICS OF A SEASONALLY DRY FOREST

Recife

2018

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como requisito parcial para a obtenção do título de doutora em Biologia Vegetal, na linha de pesquisa Ecologia de Populações e Comunidades.

Área de Concentração: Ecologia Vegetal.

Orientador: Prof. Dr. Felipe Pimentel Lopes de Melo

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Aprovada em: 16/02/2018

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RESUMO

Grandes herbívoros estão entre os principais agentes de mudança nos ecossistemas terrestres, capazes de alterar desde biodiversidade, condições do solo, estrutura da vegetação, regimes de fogo até propriedades ecossistêmicas como produtividade primária e ciclagem de nutrientes. A pecuária extensiva é uma das principais atividades econômicas em ecossistemas tropicais secos, principalmente relacionadas às comunidades locais dependentes dos recursos naturais para sua subsistência. Efeitos destes herbívoros em ecossistemas naturais são amplamente conhecidos por modificar a organização de assembleias de plantas e o funcionamento dos ecossistemas, mas seus efeitos em florestas secas ainda são pouco explorados. Esta tese teve como objetivo entender os efeitos de herbívoros introduzidos na estrutura, composição e dinâmica de comunidades herbáceas em uma floresta sazonalmente seca, especialmente como a intensidade e direção dos efeitos se relacionam com a dinâmica temporal de chuvas. Primeiro, eu acessei os principais fatores capazes de moldar os efeitos de grandes herbívoros nos ecossistemas globais ao longo do gradiente organismo-ecossistema através de uma síntese dos recentes avanços sobre os efeitos de herbívoros na biodiversidade e funcionamento dos ecossistemas e proponho uma estrutura para analisar os impactos de grandes herbívoros, com foco em conservação e manejo de ecossistemas. Depois, eu avaliei a dinâmica temporal de efeitos de herbívoros introduzidos nas comunidades herbáceas em áreas de exclusão e áreas controle utilizadas pelos herbívoros (cabras). Os resultados mostram fortes efeitos dos herbívoros na biomassa acima do solo, riqueza e diversidade de herbáceas, mas pouco impacto sobre a frequência de grupos funcionais. Entretanto, a direção e intensidade destes efeitos foram mediadas pela sazonalidade das chuvas. Finalmente, eu acessei como comunidades herbáceas respondem funcionalmente à exclusão de herbívoros. Mesmo comunidades com similar composição taxonômica exibiram diferentes perfis funcionais. Herbívoros domésticos diminuíram a riqueza funcional, mas aumentaram a dispersão funcional. Caprinos não modificaram como as plantas utilizam os recursos (Área Específica Foliar, Conteúdo de Massa Seca), mas alteraram atributos relacionados ao desempenho das plantas (Áltura Máxima, Arquitetura), o que pode afetar a reprodução e renovação das comunidades de herbáceas. Os resultados encontrados reforçam que herbívoros introduzidos em ecossistemas secos podem promover efeitos negativos aditivos, o que pode conduzir estes ecossistemas a estados cada vez menos produtivos, e dessa forma, ameaçando a manutenção de biodiversidade e serviços ecossistêmicos. Futuros esforços de pesquisa devem ser direcionados a entender como a vegetação de florestas secas responde a diferentes regimes de pastejo e à variação na intensidade da sazonalidade, a fim de, acessar a viabilidade da criação de herbívoros domésticos em tais ecossistemas vulneráveis.

Palavras-chave: Herbívoros exóticos. Florestas secas. Caatinga. Perturbações antrópicas crônicas. Diversidade funcional. Dinâmica temporal. Conservação da biodiversidade.

ABSTRACT

Large herbivores are recognized among major drivers shaping terrestrial ecosystems. A broad range of ecosystem functioning aspects may be modified by effects of large herbivores such as primary productivity, nutrient cycling, vegetation structure, soil properties, fire regimes and biodiversity. Livestock breeding is one of the main human-related activities in tropical dry ecosystems, usually related to local communities highly dependent on natural resources for their livelihood. Herbivory by such introduced herbivores is a strong force able to modulating ecosystems dynamic and plant community assemblies, but their impacts on dry forests are still under-explored. This thesis aimed to understand effects of introduced herbivores on structure, composition and dynamics of herbaceous plant communities in dry seasonally forests, addressing which factors mediate the magnitude and sign of effects over time. A paired experimental approach was used to assessing effects of herbivores exclusion on natural vegetation of dry forest using both taxonomic and functional approach. Firstly, I reviewed main drivers shaping effects of large herbivores on global ecosystems on organism-ecosystem gradient through a synthesis of accumulated and recent advances on this topic and proposed a framework for looking at herbivores impacts with focus on biodiversity conservation and ecosystem management. Secondly, I performed an analysis of temporal dynamics and structure changes on herbaceous communities after experimental exclusion of introduced herbivores (goats). Strong negative effects of herbivores on aboveground biomass (AGB), species richness and diversity of herbs but low impact frequencies of functional groups were reported. However, the sign and magnitude of effects were mediated by seasonality. Finally, I focused on how functional traits of herbaceous layer responded to herbivore exclusion**.** Even though communities presented similar taxonomic composition, differences in functional diversity after herbivores exclusion were observed. Introduced herbivores did not modify plant abilities to use resources (SLA, LDMC), but impose strong effects on traits related to plant performance (H_{max}), which can prevent herbaceous plants from completing their life cycles and maintaining the renewal of their populations. Our findings reinforce that in dry ecosystems, herbivory may promote negative feedbacks in productivity which may lead to less productive states, therefore threatening biodiversity maintenance and ecosystem services provision. Research efforts should be directed to assessment of vegetation responses in different grazing regimes and productivity variation within dry forests in order to access extensive livestock breeding viability in such vulnerable ecosystems.

Keywords: Livestock. Dry forest. Caatinga. Chronic disturbances. Functional diversity. Temporal dynamics. Biodiversity conservation.

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1 INTRODUÇÃO

Human-related modifications on natural ecosystems

Natural ecosystems across the world are under a high level of intensification in land use and land conversion into human-dominated landscapes. These new arrangements impose two kinds of disturbances to natural communities of organisms, which are able to influence biodiversity and ecosystem' functions. The first one is an acute disturbance which consists in the removal of substantial amount of biomass and can result in habitat loss and fragmentation. In contrast, the second type of disturbance consists in a continuous and frequent removal of small portions of biomass due to several activities such as extensive livestock breeding, firewood extraction, gathering of non-timber forest products and introduction of exotic species (Singh 1998).

Although the latter kind of disturbance doesn't cause the complete removal of biological communities and successional resetting, chronic disturbances can modify the structure, composition and dynamics of communities as well as the interactions between organisms and thus, dramatically alter successional trajectories, ecosystem dynamics and communities' assembly rules (Leal et al. 2014, Ribeiro et al. 2015, Rito et al. 2017). The environmental degradation caused by chronic human disturbance is often discontinuous and non-linear. Global regions where the socio-ecological context is marked by poverty in rural populations are normally more susceptible to effects of chronic disturbances (Singh 1998, Martorell & Peters 2005) as local populations have their income sources more closely related to natural resources provided by forests (Djoudi et al. 2015).

This scenario is observed in many regions and ecosystems of developing countries, like in the Caatinga dry forest in the northeast of Brazil. The Caatinga ecosystem consists of a broad mosaic of seasonally dry tropical forest and shrub vegetation (Veloso, Sampaio & Pareyn 2002) and supports over 28 million people, being one of the most populated semiarid regions in the world (Silva et al. 2018). Local human populations use the natural resources in an exploitative way, thus, affecting a serie of aspects in plant community assembly and ecosystem processes (Leal et al. 2014, Ribeiro et al. 2015, Schulz et al. 2016).

Large herbivores on natural ecosystems

Large herbivores are recognized among the major drivers shaping terrestrial ecosystems. A broad range of aspects of ecosystem functioning may be modified by effects of large herbivores such as primary productivity, nutrient cycling, vegetation structure, soil properties, fire regimes and biodiversity. Understanding the role of these herbivores on plant community assembly and the ecosystem dynamics under herbivory pressure is essential not only for species conservation, but also for the importance of these animals as keystone in many ecosystems.

An intense defaunation have been observed in most part of earth ecosystems as a consequence of both overexploitation and human-related habitat loss. We have experience on of most strong series of extinctions in the recent geological history, which has leading to a discontinuance of many species interactions and ecosystem processes. The absence of native large herbivores has lead ecologists and conservationists to implement practices of rewilding as substitutes to role before played by native herbivores that became extinct due to human activities on natural ecosystems. Positive and negative effects have been discussed and an important concern is the introduction of exotic animals on natural ecosystem and its consequences (Nuñez et al. 2010).

Likewise another shift in natural ecosystems is the replacement of native herbivores by livestock breeding as one of major economic activities. Despite of key role of livestock in some grassland ecosystems where they shape plant structure and ecosystem functioning, the introduction of exotic species may be a significant threat to biodiversity. Wild herbivores populations are kept in an ecosystem balance due to their dependence of natural resources and interactions as predation and competition. Instead, livestock and introduced herbivores can be released of such herd size controls leading to overgrazing and, consequently, strong impacts on plant community structure and ecosystem functioning (Eldridge et al. 2016).

Effects of herbivory: from populations to ecosystems

Understanding the interactions between vertebrate herbivores and plants is highly challenging, as herbivores make foraging decisions based on a range of spatial and temporal scales and plants also respond on a similarly varied scales, ranging from one leaf to the entire community (Hester et al. 2006). Herbivore effects on plants are not only direct, via consumption of plant parts, but also indirect, by altering species interactions. Grazing and trampling are the main ways by which vertebrate herbivores impose damages to plants.

The identity of herbivores plays an important role in determining which aspects will be affected by the foraging behavior and diet. Basically, herbivores vary in the intensity of feed preferences and three main feeding types are recognized, based on degree of selectivity (Hoffman1989): 1) Graze and roughage eaters (GR), which have adaptations to forage on resources rich in plant cell wall (e.g. fibrous food). Some species in this group are cattle, sheep and water buffalo. 2) Concentrate selectors (CS), which thrive on natural "high-quality" diets, since are equipped with a digestive system far less suited to optimise plant fibre digestion, concentrating in easily digestible forage rich in accessible plant cell contents (solubles). Some examples are roe deer and moose. 3) Intermediate types (IM), which are morphophysiologically intermediate between the above mentioned types. They have a marked degree of forage selectivity; choose a mixed diet as opportunistic foraging and avoiding fibre as long and as much as possible. They adapted food intake to changes in metabolism. To this group belongs domestic goat, red deer and impalla.

However, this division is not categorical and needs to be considered as a continuum across herbivores species. For example, cattle and sheep feed basically on grasses, even so it can be utilized browse material to a considerable extent. But in the case of goats, the frequency of browsing is higher and the use of grasses becomes less frequent (Mitchell & Kirby 1990). In general, such variations are also dependent on environmental conditions and preferred resources availability (Sharpe 2001).

Plants developed a set of mechanisms and strategies to deal with herbivory. Such mechanisms are related to strategies of escape, tolerance and resistance to herbivory. Escape strategies are used by those species that evade contact with herbivores, such as densification of individuals or phenotypic changes in the plant architecture to become less apparent/accessible (Janzen 1970, Connell 1971, Díaz *et al.* 2001, Charles-Dominique *et al.* 2017). Tolerance strategies are performed by those plants that have the ability to maintain their fitness through growth and reproduction after herbivore damage (Rosenthal & Kotanen 1994). Intrinsic physiological traits such as growth rate, storage capacity and growth plasticity promote tolerance in plant species showing a compensatory re-growth after herbivory (Rosenthal & Kotanen 1994). Resistance strategies are related to those species which have constitutive chemical or structural traits of plant tissues as defense against herbivores (Coley & Barone 1996, Boege & Marquis 2005).

A global review of the effects of vertebrate herbivores on plant communities highlighted that they are primarily a function of primary productivity and ecosystem evolutionary history, showing that changes in species composition increased with increasing productivity and with longer, more intense evolutionary histories of grazing (Milchunas & Lauenroth1993), but the effects on plant diversity are quite different. Effect sizes become stronger negative in less productive environments (Bakker et al. 2006, Young *et al.* 2013) with herbivores increasing plant diversity at higher productivity but decreasing diversity at low productivity. Although the effects of herbivores have been more dependent on environmental conditions than on intensity of herbivory, they affected more negatively grasslands than shrublands (Milchunas *et al.* 1988). This more subtle response to herbivory of shrublands can also be related to studies bias to areas of grasslands where grazers feeding are predominant and where long-term studies are concentrated (e.g. African savannas and European grasslands).

Introduced herbivores also have been shown to reduced ecosystem structure (by 35%), function (24%) and composition (10%). And these negative effects of grazing on plant biomass, plant cover, and soil function were more pronounced in drier environments (Eldridge et al. 2016). Interestingly, some works have shown that the sign of introduced herbivores impacts may change over productivity gradient, with positive effects of herbivory in high productive environments (e.g. Su *et al.* 2017). Increases in species richness, herbaceous productivity and decrease in species dominance were recorded in high productive grasslands and savannas (Lezama et al. 2013, Charles et al. 2017). But if these positive effects can be extrapolated to no grasses-dominated ecosystems is still unclear.

Functional changes mediated by herbivores

An effective method for assessing underlying mechanisms by which herbivores drive ecosystem functioning is using traits based measures. Plant functional traits are relevant attributes of species that are related to plant individual performance or that can have an impact on ecosystem functioning (Violle et al. 2007). Functional traits allow to address ecosystem functioning not only through presence or absence of ecological niches being occupied by species, but also through changes in the frequency of important traits or functional group (mass effect) that determine ecosystem functions (Le provost et al. 2017).

Functional diversity (FD) is now an established concept and is assumed to be directly related to ecosystems services provision and protection to communities from drastic climatic changes (Lavorel et al. 2011). Several metrics are used to quantify FD and each one gave an idea of different aspect of range and distribution of the species niches. The most common measures are: **1) Functional Richness (FRic)** – a measure of the volume occupied by distinct species in the multidimensional trait space; **2) Functional Evenness (FEve)** – a measure of regularity of traits distribution and how species abundances account for that along the multidimensional functional space; **3) Functional Dispersion (FDis) –** a measure of the mean distance in multidimensional trait space of individual species to the centroid of all species in the community; it can account for species abundances by shifting the position of the centroid toward the more abundant species and weighting distances of individual species by their relative abundances; **5) Community Weighted Mean (CWM) –** a measure of the mean value for each trait weighted by the species abundances (Mason et al. 2005; Villéger et al. 2008).

The relationship between functional traits and herbivory encompasses a broad range of aspects. Responses of plant functional groups are divided in three plant defense syndromes against herbivores: 1) poorly defended plants with phenological escape mechanisms; 2) plants with high nutrients and edible leaves with chemical and physical defenses, and 3) plants with poor edible leaves (Agrawal & Fishbein 2006). Such different strategies are widely distributed among growth forms, life-forms and ecosystems types. For instance, in seasonally dry ecosystems, the most common escape strategy among herbaceous species is the whole life cycle restricted to a short period of time in which resources are abundant and effects of herbivory are supposedly more dispersed. Such life-form is known as therophyte plants. In general, annual plants such as terophytes have shown to replace perennial species under effect of grazing (Díaz et al. 2007). Such effects were more pronounced in humid environments, but in dry systems this information is still insufficient.

Herbivores have been show to impose strong effects on functional diversity in varied ecosystems with contrasting effects. Both, increase and decrease in functional diversity have been found (Carmona et al. 2012, Peco et al. 2012, Hallet et al. 2017). Moderate grazing were associated with stability on productivity across rainfall gradient, but in wet conditions functional diversity rapid decline in grazed areas with communities converging to resource-acquisitive traits (Hallet et al. 2017). Functional responses can vary between functional groups of herbs with positive effects of grazing on annual and perennials plants, but increasing relative importance of the latter (Zheng et al. 2015). Interestedly, functional diversity can be uncoupled from taxonomic diversity becoming an important tool to complete address effects of herbivores in communities and ecosystem functions. Carmona et al. (2012) found reduction in taxonomic diversity but high temporal stability of functional diversity in the driest conditions under impact of livestock showing that environmental constraints (drought) may be more important than grazing in structuring communities in dry habitats.

Although high herbivore pressure may be a concern, its complete exclosure may have negative ecological effects. In grasslands ecosystems, total exclosure of ungulate herbivores results in a shift from functional patterns of over-dispersion to clustering, with increase local clustering of individuals, indicating that communities free of disturbance gradually become dominated by competitively superior species, leading to a low species diversity and biotic homogenization (Nishizawa et al. 2016). This highlights the potential role of herbivores in mediating competition among plants for multiple resources and to contribute to increase functional richness and evenness in grazed ecosystems (Niu et al. 2016).

Herbivory in seasonally dry environments

Drylands cover about 41.5% of the Earth’s land surface and contain some of the most threatened, yet less protected, ecosystems (Bastin *et al.* 2017). The unifying feature of seasonally dry environments is the strong seasonality and unpredictability on occurrence and spatial distribution of rainfall so that organisms are submitted to marked water deficits during considerable time periods throughout the year (Monney et al. 1995). These dry environments are subject to multiple, often simultaneous, pressures (Miles *et al.* 2006) and the seasonal aspect of these areas lead to some important differences in the dynamics of communities and ecosystem processes.

Overall, seasonally dry ecosystems are characterized by the occurrence of phenomena such as sudden increase and slow reduction of resources availability (Monney et al. 1995). This dynamics is caused by pulses of water availability resulting from the main wet season as well as isolated rains during the dry season or frequent drought during the wet season (Monney et al. 1995). A classical hypothesis claims that due to intense environmental variability, some systems can display dynamic non-equilibrium properties, in which biotic relationships are expected to be weak while abiotic limitations and resource constraints impose large stochastic effects with release from density-dependent processes (Wiens 1984). Impacts of herbivores on these systems should be absent or attenuated due to population density-control by mortality due to frequent episodes of drought and primary production largely dependent on precipitation conditions (Illius & O’Connor 1999). This lack of balance predicts that populations are exposed to a dynamics described as a model of lottery or gap, in which colonization and extinction rates are probabilistic. Therefore, climatic events, such as prolonged droughts, increase the importance of density-independent processes in assembly rules (Illius & O’Connor 1999). Thereby, herbivore populations are expected related to the carrying capacity of the ecosystem during growing season, resulting in a weak or absent regulation of animal or plant populations via density-dependent processes (Illius & O’Connor 1999).

In contrast, large herbivores may cope with such seasonality in resources availability and uncoupled this density-independent mortality showing a strategy as generalist feeding with variables items consumed according their natural availability. Variations in feed include resources highly profitable such as fruits, flowers and green foliage during growing season to barks and litter during dry season. Others strategies showed by herbivores is migration to others ecosystems or areas of key resources used during dry season as riparian areas (Illius & O’Connor 1999). Additionally, introduced human-related herbivores (livestock) also can be favored by absence of natural specific plant defenses and by feeding supplementation that release herbivore herds of drought mortality. Such cases can concentrate high levels of accumulated effects of herbivores, especially in dry years. Among such effects have been observed a negative feedback between reduction in biomass and reduction in resources for plant growth, thus imposing catastrophic impacts on vegetation and soil (Rietkerk & van de Koppel 1997).

Herbivores on Brazilian Seasonally Dry Forests

Caatinga ecosystem is the largest continuous area of seasonally dry tropical forest of South America and is contained integrally within Brazilian territory. This vegetation incorporates a set of varied physiognomies from open shrublands with cactus and bromeliads to forest formations of spinescent trees. Currently, the fauna of native large herbivores in Caatinga corresponds to two deer species (*Mazama americana* “veado mateiro” and *M. gouazoupira* “veado-catingueiro”) and one species of wild pig (Pecari tajacu “caititu”) (Oliveira et al. 2001). However, overexploitations of wildlife in the Caatinga lead to extinction of these animals in most areas of Caatinga, being now restrict to few conservation reserves.

Overall, herbivores of Caatinga are actually livestock species introduced raised extensively by local populations on areas of native vegetation. Cattle, sheep and goats were introduced during colonization of this region for at least 350 years. Large herds of cattle are restricted to mesic areas of ecosystems that sustain high primary productivity. But, the dominant herbivores in this ecosystem are goats which concentrate 93% of national production of 9.6 million animals (IBGE 2016). Goats are mixed-feeder herbivores and present a high adaptability to most varied environments. Such incredible performance and survival capacity are explained by their high adaptability features, such as low body weight and low metabolic rates, which make them able to reduce energy needs by up to 65% in response to reduction in food and water availability (Silanikove 1997). These ruminants are considered opportunistic feeders and select diets that tend to maximize their intake rate instead of species-specific preferences and this rate is primarily affected by the biomass density of the grazing stratum (Illius *et al.* 1999). To predict the quantity of vegetation consumed by goats in natural conditions is very difficult since their feeding behavior varies highly across seasons, vegetation structure and animal condition. A recent study comparing different methods of estimation of dry matter intake (DMI) for goats using data from 7 studies performed in several regions of Brazil recorded a high variation in goats DMI with 521±327 (mean ± S.D.) g/day (Teixeira *et al.* 2011).

Goats have lignocelluloses degrading abilities, with a clear preference for the defoliator behavior. Another notable ability is to adjust anatomical traits in accordance with available resources and forage quality, for example, larger salivary glands, which allow a higher capacity of serous salivary secretion and a larger surface area of absorbed mucosa than that found in grazer-herbivores (Hofmann 1989). Such ability to use fodder based on fibers with greater efficiency is due to combination of a higher fermentation rate and a longer time of rumen passage with a higher absorption surface area, allowing maximization of consumption and digestibility (Silanikove 1997). Additionally, goats also consume foliage rich in tannins counteracting negative effects on palatability and digestibility greater than sheep and cattle under comparable conditions (Silanikove 1997). This is particularly important in semi-arid areas such as Caatinga dry forest, where most trees and shrubs have high concentrations of defensive compounds. The physiological basis for such ability consists of a salivary defense mechanism and ruminal microbial degradation for phenolic compounds (Silanikove 1997).

In semi-arid environments, where food availability is limited in terms of both quality and quantity of resources, goats demonstrate a better adaptation compared to other herbivores (Silanikove 1997). This is achieved by their ability to adapt to different food sources according to its availability (Fig. 1), varying in frequency of grazing and browsing behaviours (Orihuela & Solano (1999). Although goats vary selectivity between grazing and browsing behavior in accordance with the height of grazing strata, plants browsed in previous years could be preferred compared to previously unbrowsed trees, thus these herbivores tend to over-consume some species more than available plant resources in the environment (Sharpe et al. 2007).

Long-term studies on island ecosystems with semi-arid climate have shown that after 4 years of goats exclosure no changes in species richness and diversity were found, but a species turnover was observed in response to the absence of goat herbivory, related to changes in soil properties (Fernández-Lugo *et al.* 2009). Primary productivity was indicated as a key factor that determines vegetation responses to grazing by goats. Removal of goats in areas of higher productivity resulted in just an apparent response in terms of species richness and functional composition, while stronger impacts were observed in drier and less productive areas (Fernández-Lugo *et al.* 2013b). In environments with no grazing and with higher productivity, grasses and shrubs became the most favored groups (Fernández-Lugo et al. 2013b).

The grazing pressure and exposure time to herbivory are also factors of taxonomic and functional differentiation in diversity. In heavy grazing areas, the frequency of annual grasses tended to be higher, while shrubs legumes tended to be more affected in light grazing areas becoming less abundant (Fernández-Lugo *et al.* 2013a). At low stocking rate (0.2 ind / ha) no effect on richness, above-ground biomass and organic matter were observed, independent of vegetation type - grasses, shrubs and open or closed forest (Arévalo *et al.* 2011). However, in seasonal dry forests, carrying capacity must be even less than 1.3 ind / ha (Araújo-Filho & Barbosa 1992).

Figure 1: Variety of food sources and vegetation strata used by goats to deal with seasonality of resource availability. Goat foraging in the Caatinga ranges from climbing to reach woody species, like shrubs and trees (a-b), to consumption of herbaceous plants (c) and dry litter (leaves, fruits, seeds) during the dry season (d).

Therefore, it can be seen that goats are complex herbivores, with no easy foraging decisions, that use a broad range of resources and have important characteristics that allow them to occupy habitats with wide environmental constraints, which makes it challenging to understand their effects on natural ecosystems. Recent studies in Caatinga dry forest have shown that goats exhibit a spatial preference to pasture in areas with low density-vegetation and close to human residences (Santos et al. - *in preparation*), and that they use a broad range of plant species (53 sp.) wherein 70% of all plant parts were used (flowers, fruits, young and mature leaves) (Leal et al. 2001). Heavy stocking rates of goats in this ecosystem have resulted in decreasing of plant species richness (Tavares et al. 2016) and caused a substantial release of soil organic carbon stocks (Schulz et al. 2016).

2 OBJETIVOS

Objectives of this study

Effects of vertebrate herbivores across ecosystems include a broad range of shifts in the taxonomic and functional profile of plant communities directly by reducing local abundance or completely eliminating species (direct effects, Fig. 2 - black arrow) or by interfering in the physiological, reproductive, dispersal and/or competitive capacity of plant species (indirect effects, Fig. 2 – white dotted arrow) (Marquis 2005). Through these mechanisms, herbivores can drive major changes in the structure, dynamics and composition of plant communities Fig. 2 – arrow 1), leading to ecosystem consequences such as shifts in primary productivity and biodiversity; moreover, they have the capacity of modifying nutrients cycling rates (Fig. 2 – arrow 2).

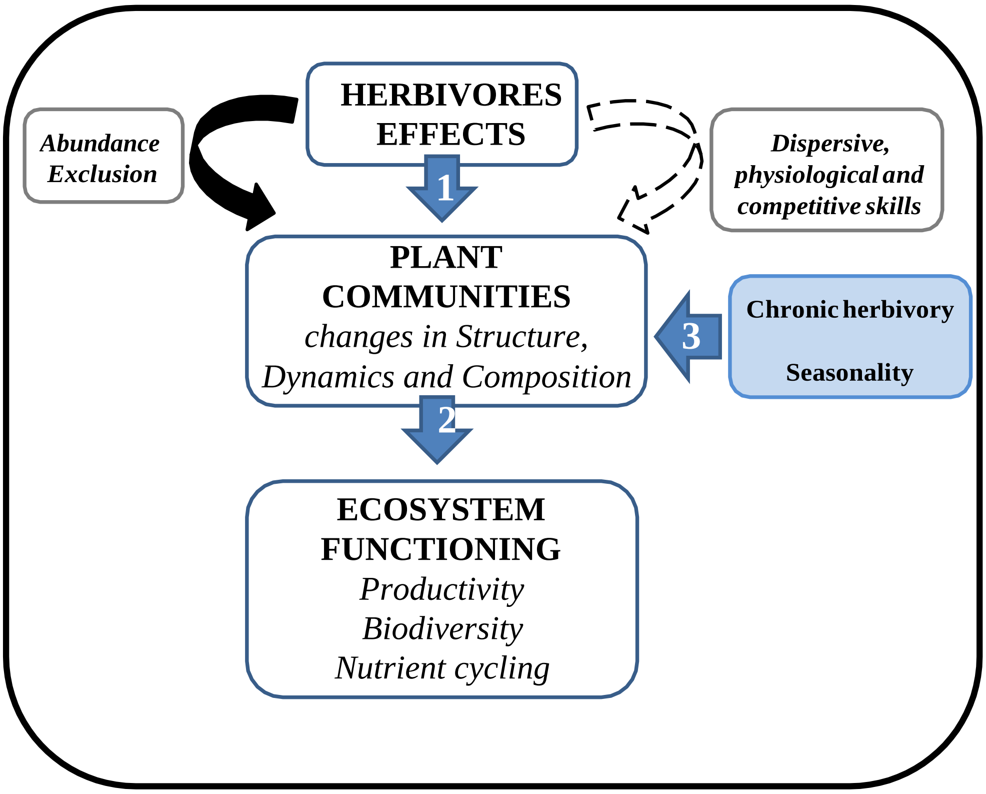

Figure 2: Conceptual framework of the present study. The framework represents how herbivores drive changes in plant communities (arrow 1) and influence ecosystems functions (arrow 2), via direct (reducing local abundance or completely eliminating species – black arrow) and indirect (influencing dispersal, physiological, reproductive and/or competitive capacity – white dashed arrow) mechanisms. In the present thesis I focus on the changes in structure,

dynamics and composition of herbaceous species and how these shifts can affect productivity, biodiversity and ecosystem functioning, taking into account for the effects of chronic herbivory and seasonality of the environment mediating such changes (arrow 3).

Nonetheless, the direction and intensity of herbivore impacts depends largely on a number of factors that may act individually or interact with each other. Seasonality on rainfall has been shown to be the major factor determining resources dynamics in dry ecosystems and mediating effects of chronic disturbances (Rito et al. 2017). Thus, chronic herbivory as one of the most frequent chronic disturbances in the Brazilian dry forest and seasonality are essential to understand effects of this herbivores on plant communities and ecosystem functioning (arrow 3).

The aim of this thesis is to understand the mechanisms, by which an introduced herbivore promote changes in plant communities and ecosystem functions and its consequences for provision of ecosystem services and forest management. Additionally, I expect to understand which factors mediate the sign and magnitude of effects in markedly seasonal environments. To achieve these goals, I used a paired experimental approach, performing exclosures of livestock (goats) in natural areas of Caatinga dry forest. This thesis is divided into three manuscripts:

In **Chapter 2**, I focus attention into synthesize the body of knowledge about the **drivers shaping effects of large herbivores on natural ecosystems**. Using recent advances in understand which factors can modulating such effects, I formulated a framework to understand effects of herbivores in diverse organizational levels from populations to ecosystems and which factors affect the impacts in each one of them.

In **Chapter 3**, I examined, experimentally, **effects of exclosure of introduced herbivores on herbaceous community dynamics and structure in a Seasonally Dry Tropical Forest,** accessing which factors (seasonality, time, functional groups and life-form) could mediate their effects on plant community structure and dynamics (species richness, diversity, biomass, plant density).

In **Chapter 4,** I investigated the **functional responses of herbaceous layer to herbivores exclosure,** focusing on how herbivory by goats can affect the performance of plant species and community functional diversity. In order to do that I used plant traits related to use of resources and performance to figure out the mechanisms by which introduced herbivores can modify ecosystem functioning.

Studying the effects of introduced herbivores in a natural and markedly seasonal ecosystem will contribute to our understanding of the recovery dynamics and resilience of seasonal tropical ecosystems to chronic disturbances and the role of seasonality in mediating these effects. Given that ongoing global changes in climate are foreseen to increase the seasonality of resources, especially in dry regions (Burkett et al. 2014), it is crucial to understand to what extent these forests can maintain high levels of biodiversity and critical ecosystem functions. Moreover, identifying drivers behind recovery and maintenance of productivity and biodiversity in a socio-ecologically vulnerable region can provide support to the development of sustainable management that provides income to local human populations and long-term sustainability and viability of ecosystem functioning.

3 RESULTADOS

3.1 ARTIGO 1: DRIVERS SHAPING LARGE HERBIVORES EFFECTS IN GLOBAL ECOSYSTEMS: CONCEPTUAL FRAMEWORK FOR BIODIVERSITY CONSERVATION AND ECOSYSTEM MANAGEMENT

as prepared for: **Ecological Applications**

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Abstract

Despite all accumulated knowledge regarding effects of large herbivores on natural and managed grasslands, savannas, meadows and temperate systems, global generalizations remain still missing. Even though exclosures experiments and paleo-ecological data have demonstrated key roles of large herbivores in structuring communities and ecosystem functioning, to determine the drivers mediating such effects is an open issue. In this review, I addressed main drivers influencing effects of herbivores on organism-community-ecosystem gradient and by which mechanisms herbivores modify plant assembly and ecosystem functioning. In addition to long-term recognized influence of herbivore type, plant functional group and grazing evolutionary history in mediating effects, it has been shown that sign and magnitude of effects are context-dependent, broadly varying with ecosystem productivity, seasonality and habitat structure. We propose a conceptual framework to describe drivers influencing effects of herbivores at each ecosystem level and how different outcomes can be found according to interaction among such mediating factors. A view on how such drivers are connected each other and produce different ecosystem trajectories can be a useful tool for biodiversity conservation and ecosystem management.

Keywords: herbivores, assembly rules, ecosystem functioning, seasonality, conservation, management.

Introduction

Long-term studies, exclosures experiments and paleo-ecological data have so long recognized large herbivores playing considerable role in shaping plant communities and ecosystem functioning (Milchunas et al. 1988, Huntly 1991, Malhi et al. 2016). However, as ecosystems vary broadly in properties and structures it remains difficult to make generalizations about effects of herbivores in global scale, and observed patterns rarely are homogeneous across vegetation types and climatic gradients (Díaz et al. 2007, Su et al. 2017). Additionally, there is a vast variety and complexity in plant-herbivore responses to herbivory and understand how herbivores affect communities and ecosystems is a hardy task.

Main evidences of herbivores shaping vegetation structure and ecosystems functioning come from exclosure experiments and manipulated systems in grasslands and temperate systems (Mitchell & Kirby 1990, Milchunas et al. 1993, Mason & Crone 2006), which do not encompass all variety in structure and complexity across terrestrial ecosystems. Large herbivores promote significant damages on individual plants and species, influencing their abilities to reproduction, dispersal and interact with others species (Mason & Crone 2006). By acting in the organism level, herbivores spread their effects through plant communities and ecosystem functioning (Huntly 1991). However, the context in which effects of herbivores is analyzed matter, as a large quantity of factors is able to influence and shape the intensity and course of impacts on plant communities and ecosystem functions.

A large body of evidence has been accumulated on the effects of herbivores on different levels of biological organization as species, community and ecosystem functions (Liu et al. 2015). However, interactions between factors result in ambiguous herbivore effects, making difficult to synthesize patterns and processes. Accordingly, an overall more intuitive framework showing major drivers to be considered when addressing effects of large herbivores on natural ecosystems and how they influence each other is a useful predictive tool to biodiversity conservation goals as well as ecosystem management. Herbivores affect populations and communities by both density-independent and density-dependent processes (Huntly 1991). In the first case, herbivores can modify physical environmental conditions, which may lead to changes in species ability to occupied ecological niches and, in latter case, herbivores influence populations and communities dynamics processes which can determine species turnover, extinctions, diversity and ecosystem functioning.

Conceptual framework for looking at factors mediating effects of large herbivores on global ecosystems

Herbivores can affect species, communities and ecosystems thought distinct mechanisms not mutually exclusive producing different outcomes and trajectories (Milchunas et al. 1993, Huntly 1991, Maron & Crone 2006) according to combination of various states of factors mediating effects in each organizational level. Plant-herbivore interactions on species level vary broadly according different feeding behavior, feed preferences of herbivores and plant life cycle (Maron & Crone 2006). Therefore imposing disproportionately effects on population growth rates of plants, herbivores affect plant demographic processes and disproportionate mortality or tissue loss rates for certain plant species (Huntly 1991) influencing community assembly by altering diversity, structure, dynamics and composition of plant communities (Maron & Crone 2006). Ultimately, herbivores drive important ecosystem functions such as productivity and nutrient cycling as result of plant community functional changes (Pinheiro et al. 2010, Tilman et al. 2012). But, the magnitude of such effects depend on ecosystem dynamics and structure (Young et al. 2013). Accordingly, multiple pathways can arise from these mechanisms through interactions between all driver states that mediate effects of large herbivores (Figure 3).

Herbivores disproportionately damaging more common species in a patch or community in a general way tend to increase plant diversity and biodiversity conservation value of herbivory; if disproportionately affected species are not rare plants (Huntly 1991). But for ecosystem management, the ultimate goals must be considered and depends on dynamics and structure features of each particular ecosystem associated with plant community attributes and herbivores diversity and feeding characteristics. To understand such complex interactions between driver states mediating effects of large herbivores is necessary to address how each organizational level is influenced by herbivory and their resulting different responses.

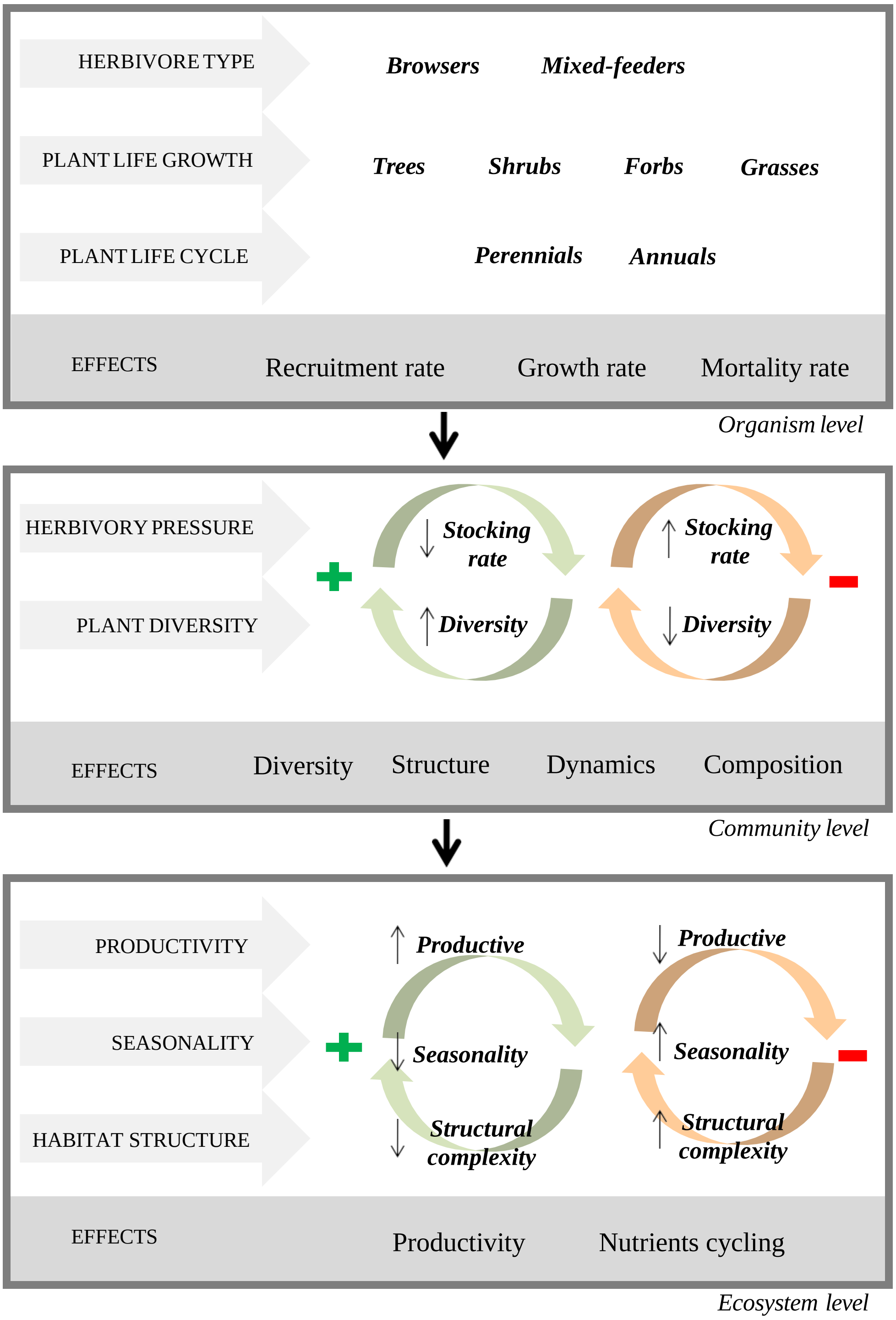

Figure 3: Conceptual framework highlighting main drivers mediating effects of large herbivores in each ecosystem organizational level (boxes). The drivers (grey arrows) impose effects in different properties (grey background) for each level. The possible states for each driver (bold italic) interact each other across organizational levels which can produce different outcomes from herbivore effects and communities trajectories. The combination of some states is more likely to produce positive (green arrows and symbol) and negative (red arrows and symbol) feedbacks on magnitudes of herbivore effects.

Organism level

Herbivores affect individual plants by either direct consumption of plant tissues leading to changes in plant abundance and/or exclusion of species or affecting their dispersive, competitive or physiological abilities (van der Waal et al. 2011). In both cases, large herbivores can drive rates of recruitment, growth and mortality of species that will affect population processes (Maron & Crone 2006). How herbivores will affect these properties for individual species depend on herbivore type and plant attributes such as plant growth-form and life cycle.

1. Herbivore type

Large herbivores affect species, communities and ecosystems in many ways. Feeding and foraging behaviors highly varied between herbivores types which implies in how herbivores will damage plant populations. Different herbivore species had different impacts on plant communities and impacts changed between plant diversity levels and herbivore diversities (Liu et al. 2015). Herbivore type implies in completely different foraging behaviors and feed preferences determining which plant groups will be disproportionally affected and which vegetation stratum will tend to undergo more changes in their dynamics and structural complexity. The level and intensity of plant selectivity by herbivores determines the damage distribution on plant community (Hoffman 1989). The more selective the herbivore is, the greater its impact altering diversity and its ability to impose shifts in habitat structure (Liu et al. 2015). Herbivore type determines not only diet range and selectivity, but also feeding behavior (patch grazing, homogeneous grazing or selective grazing), which implies on different changes in habitat heterogeneity and resources distribution (Adler et al. 2001).

Feed mode determines which type of impact on plant communities herbivores will impose. Browsers affect directly growth and survival rates of woody species via consumption, while grazers can increase recruitment of woody plants and survival through reduction of competition with herbaceous plants. But, effects of mixed-feeders are less understood and still poorly studied. Mixed-feeders adapt their diet to local resources availability and are likely to be diverse and successful in more seasonal environments. More generalist herbivores can maintain predation pressure even when prey abundance is low (Malhi et al. 2016), which can lead to strong damages on plant communities. Foraging selectivity patterns among herbivore species are influenced by a balance between food quantity and quality. Mixed-feeders herbivores supposedly should be more successful and print more damages where resource availability variation is high due their advantage of enlarge forage diet compared to more grazing or browsing selective herbivores (Hoffman 1989).

Much of our understanding of the impact of large herbivores on plant communities and vegetation types comes from savanna and grasslands ecosystems (Naeem et al. 2009), where usually populations and diversity of herbivores remain high. Thereby, damage distribution across plant functional groups and vegetation strata tend to be more widespread. However, where herbivores diversity is lower and/or herbivore types are disproportionately balanced, effects on plant functional groups and vegetation state transitions can be strongest (Holdo et al. 2009). The relative abundance of grazers and browsers can mediate transitions between structures from tree and grass-dominated vegetation (Devine et al. 2017). In this way, impact of large herbivores suppression in transitions between grass-woody dominated communities is likely to be strongest where herbivore diversity and ecosystem productivity is higher and resources availability and dynamics more predictable.

Considering herbivores types and their different effects, biodiversity conservation and management should focus on ecosystem dynamic balance considering temporal fluctuations on herbivores and plant populations and taking into account ecosystem productivity and seasonality which determine capacity and recovery rate of plant-herbivore biomass. Finally, introduced species are pointed out as one of three greatest threats to biodiversity globally, alongside climatic change and habitat loss (Nuñez et al. 2010). Native and introduced herbivores differ in their effects and capacity to impose negative effects on plant populations and community properties. So, more attention should be given for effects of introduced herbivores on this dynamic balance, as plant communities did not show the usual mechanisms of resistance, tolerance and recovery from herbivore damages that native plant-herbivore communities have to keep a balance on ecosystem functioning.

2. Plant life-growth

A wide range of plant life forms is found through all earth ecosystems, but the relative importance of each group strongly varied between ecosystems. Grasslands show basically a single stratum composed by a variation on forbs and grasses forms, while woodlands and forests are structured in more strata with strong variations on proportion of trees, shrubs and forbs according to environmental gradients. Analyzes on the effects of herbivores that intend to maintain organism diversity and maximize ecosystem services under different local environmental conditions must consider the variety of life history of plants for planning actions.

Besides herbivory decrease plant biomass or density, herbivores can change plant behavior by change their skills to use resources or space or forcing structural defenses on plants, often changing plant form or physiology (Huntly 1991). Transitions from three to shrub architecture and erect to prostate herbs are common effects of large herbivores in savannas and tree-dominated ecosystems (Díaz et al. 2007). Nevertheless, evaluations of herbivore effects on different plant life growth cannot be decoupled from herbivores type because feeding preferences determine the magnitude of impacts in different strata (Bullock et al. 2001). In addition, prevalence of specific plant life forms under effect of herbivores also should vary between ecosystems as a consequence of environmental gradients. Under grazing impact, woody species tend to be more successful in undermine grasses where ecosystem productivity is higher and seasonality is lower (Ward 2005), but these effects also depend on herbivores pressure (Weber & Jeltsch 2000).

3. Plant life cycle

Plant identity is closely related to trade-off between growing and defense. Fast-growing species are preferred to herbivores because they did not invest in defenses and hold high concentration of nutrients, while slow-growing species usually present high quantities of defensive compounds (Agrawal & Fishbein 2006). However, the plant life cycle is a crucial factor to understanding responses of plant communities to herbivore damages and to define the importance of such growth x defense trade-offs. Annuals and perennials have different strategies to cope with herbivory and relative importance of growth and defense strategies must be thought out to influence effects of herbivores in these groups. Tolerance strategies result from rapidly re-growing though a balance between high loss rates to herbivory and high growth rates, while resistance strategies come from species that deter herbivory by unpalatability (Huntly 1991). So, in low-productivity and more seasonal environments, in which plant growth is limited, resistance strategies is more likely, whereas in productive environments, re-growth is more likely response (Huntly 1991).

Most studies have recorded that perennial species are likely to be more negatively affected by herbivores than annuals species (Milchunas et al. 1993, Díaz et al. 2006), considered mostly escape strategists. However, considering that annuals plants are short-lived fugitive plants with a strong reliance on reproductive events to maintain regeneration of their populations, herbivory may have also strong negative impacts compared to long-lived perennials (Louda & Potvin 1995). In this sense, perennials species thought their long life cycle can buffered effects of herbivores maintaining a compensatory dynamics of regrowth and renew on their populations through years of more or less damage by herbivores (Hemrová et al. 2012).

A common response to herbivory is changing community composition to low-growing plants and prostrate growth forms as an avoidance mechanism (Díaz et al. 2007). Annuals and shrubs may often increase with grazing as perennials decrease (Milchunas et al. 1993). However, effects on life forms and growth forms are context dependent varying among different ecosystems, since relative frequencies of such groups broadly varied among global ecosystems. Therefore, conservation and management decisions should be guide by target ecosystem context considering how large herbivores can affect its natural balance between life cycle strategies.

Community level

Herbivores can alter all plant community properties by influencing structure and dynamics, diversity and taxonomic/functional composition. The intensity of herbivore impacts on plant species diversity and species composition seems to be a function of productivity-seasonality and evolutionary history of grazing. Changes in species composition increased with increasing productivity and with longer, more intense evolutionary histories of grazing (Milchunas et al. 1993).

Large herbivores influence plant diversity and composition by selecting palatable species and promoting changes in community composition by increasing the abundance of species that are resistant or tolerant to herbivory species. For increase plant diversity by herbivory, feed preferences must be associated to dominant plant species which decrease populations allowing species coexistence. Large herbivores shift plant communities in the direction of thorny or spines plants and/or chemically defended species. To understanding significant impacts of large herbivores at community level we should take into account both aspects, herbivore pressure and plant diversity.

1. Herbivore pressure

Herbivore pressure is one of most important factor to be considered to determine impacts on plant communities and variations on vegetation structure. The magnitude and sign of herbivores impact is directly related to the quantity of individuals living a certain ecosystem. Positive effects to plant diversity and productivity are related to intermediate densities of herbivores while both extremes are related to differentiated effects (Milchunas et al. 1988). Competitive exclusion in high productive ecosystems and environmental constraints in low productive ecosystems are between the used mechanisms to explain these relationships (Mortensen et al. 2018). At low grazing pressure, herbivores provide a greater diversity in vegetation structure and species composition in woodlands (Mitchell & Kirby 1990). In moderate to high grazing pressure there is usually strong effects on community composition in direction of low growing or shrub and prostrate plants (Chillo et al. 2017).

Recently, meta-analysis revealed that effects of herbivores on richness and diversity to increasing stocking rate are mostly negative and independent of rainfall, productivity or aridity (Herrero-Jáuregui & Oesterheld 2017). Also it has been demonstrated that compositional and structural changes were higher in high grazing intensity than moderate grazing in dry ecosystems in Africa (Hanke et al. 2014).

In seasonal environments, the intensity of herbivore pressure undergoes a seasonal variation according to resources availability. Herbivores can widespread damages across wide areas during growth season, imposing a more selective diet to more intake income sources (Kleynhans et al. 2010). During dry season, however, the strength of herbivore pressure tends to be stronger with proximity of water sources or key resources areas used during this unfavorable time (Illius & O'connor 1999).

2. Plant diversity

There is a growing body of evidence that biodiversity acts as a buffer against human-related disturbances increasing ecosystems resilience (Thébault & Loreau 2005) and protecting ecosystems from climate extremes (Isbell et al. 2015). The logic behind this is that species loss in richer communities is less likely to impose strong impacts on ecosystem functions since more species increase likelihood that many species will have closer ecological niches (Naeem et al.1998) and thus higher diversity allow higher functional redundancy among species.

More diverse communities also can improve associational resistance. Since herbivores tend to be attracted and stay in patches of high density of favored resources, more diverse stands dilute the amount of herbivory that other experiences by attracting herbivores to alternative food plants (Milchunas & Noy-Meir 2002, Barbosa et al. 2009). But effectiveness of associational resistance depends on herbivore foraging selectivity (Bergvall et al. 2017). Overall, plants gain protection with preferred neighbors when herbivore selectivity is higher, while plants gain protection with non-preferred neighbors when herbivore selectivity is low (Huang et al. 2016).

Ecosystem level

Negative effects of grazing in ecosystem functioning are generally more pronounced for plant cover, biomass and soil function in less productive and highly seasonal systems (Eldridge et al. 2016). Reductions on ecosystem functioning are related to decreases in diversity and disproportional contribution of different functional groups driven by herbivores (Tilman et al. 2012). Considering ecosystem level properties, effects of large herbivores are influenced by productivity, seasonality and habitat structure.

1. Productivity

Productivity among sites is one of most important driver of effects of large herbivores on plant diversity (Milchunas & Lauenroth 1993). Effects of large herbivores increasing plant diversity have been shown at higher productivity, and decreasing diversity occur low productivity (Bakker et al. 2006). In grasslands ecosystems with moderate to high-productivity, species diversity decrease pronounced with loss of herbivores and community composition change considerable (Burns et al. 2009).

Productivity gradient has so long been related to increase in diversity. Usually, unimodal pattern are found with the intermediate disturbance hypothesis used to explain high levels of diversity (Milchunas & Lauenroth 1993). Environmental constraints is attributed to explain low levels of diversity with low productivity and competitive exclusion is related to low diversity at high productivity. Thus, the unimodal pattern requires a regime of disturbances to keep diversity by prevent competitive exclusion of species (Huston 1994).

However, recently it has been show that the productivity–diversity relationship differs between temperate and tropical regions, where unimodal relationship dominates in temperate and boreal ecosystems, whereas positive relationship is more common in the tropics (Partel et al. 2007). In addition, the differential evolutionary history of the local species pools were used as probable cause for this because productive habitats are the rule in tropical regions throughout evolutionary history, while highly productive ecosystems in temperate zones are basically more recent, thus the scarcity of this habitat type reduced chance for speciation.

Productivity is basically a result of climatic conditions that combine high levels of resources for plants, but herbivores also can control productivity by manipulating bottom-up mechanisms that regulate plant growth such as reducing nutrient cycling. Findings indicating that herbivory strengthen climatic control of primary productivity have been found, suggesting that herbivores may increase sensitivity of dry systems to climate change, since strongest effects of herbivores limiting nitrogen levels for plants were found in dry habitats compared to mesic habitats (Frank et al. 2018). Introduced herbivores are also a concern issue because it has been demonstrated that coexistence of livestock grazing and plant diversity is only possible within more productive environments, because low to moderate productivity ecosystems showed strong negative effects under grazing, while indistinct or positive effects were found in high productivity (Eldridge et al. 2016).

2. Seasonality

Seasonal environments occupied large areas through different ecosystems, from savannas, deserts and dry tropical forests in low latitudes to seasonal temperate forests and tundra in high latitudes (Moen et al. 2006). Intense intra- and inter-annual variation in rainfall implies high unpredictability on availability of food resources which impose constraints to herbivores population dynamics (Hempson et al. 2015). Likewise, plant resources exert a bottom-up control related to water or nutrients constraits that determine tree-dominated or grass/forbs-dominated habitat. Thereby, as seasonal environments require life-history of plants and animals synchronized with such natural variation on resources (Snyder & Chesson 2004), herbivores can impose strong impacts and mortality in critical phases of plant life cycle such as reproduction and recruitment.

Seasonality promotes density-dependent controls over herbivore growth rates, keeping relatively low population densities of herbivores (Moen et al. 2006). Due to this, ecosystems with high seasonality should present strong constraints to herbivores resulting of density-independent mortality and less impacts during growing season (Illius & O’Connor 1999). However, human-related herbivores such as livestock can be protected from natural controls of populations through supplementation, releasing their populations from density-independent controls. Thereby, introduced herbivores have impacted seasonal environments in a strong way (Eldridge et al. 2016) with decreasing in structure, composition and function properties. It is a important concern related to seasonal environments that herbivory and drought can have addictive effects (Bansal et al. 2013) and thus is likely to direct negative feedbacks on productivity in ecosystems that already have lower productivity.

3. Habitat structure

Within semiarid grasslands, vegetation type was the main factor to explain grazing effects on community structure (plant cover, height, species richness) and ecosystem function (i.e. above ground biomass), where high differences were found in wet meadows while no effect were found in dry meadows showing that responses to herbivores are context dependent (Su et al. 2017).

Relationship of species richness and functional trait diversity on ecosystem functions may follow numerous response trajectories under effects of herbivores, but local diversity, productivity and intensity of disturbance are likely to be key factors in determining the trajectory (Mayfield 2010).

Structural heterogeneity

Vertebrate herbivores can alter habitat heterogeneity, influencing ecosystem processes and biodiversity (Adler 2001). Heterogeneity is closely related to biodiversity, so environments more diverse in habitats are likely to shelter more species since it is assumed that different ecological niches are available and can be occupied by species (Tews et al. 2004, Stein et al. 2014). Structurally more complex habitats may provide more niches and more diverse strategies to explore environmental resources showed by species (Palmer & Dixon 1990), which will determine community structure and dynamics.

Topography, soil conditions and other local environmental properties such as precipitation and temperature are important promoters of environmental heterogeneity which is also related to plant diversity (Ricklefs 1977). Effects of heterogeneity in vegetation and soil conditions on species richness may be due to increasing in available niches and resilience against disturbances by providing more habitat types for species (Stein et al. 2014). Therefore, habitat structure encompasses environmental heterogeneity that allows complexity on vegetation strata closely related to plant diversity. Herbivores can add complexity to environments creating structural layers by selective herbivory in palatable species and by differential selection of patches due to habitat preferences (McNaughton et al. 1989, Adler 2001). Nevertheless, the effect of environmental heterogeneity on diversity has been show to vary in according to ecosystem location along environmental gradients (Yang et al. 2015).

In light of these relationships between environmental heterogeneity and diversity we should expect that effects of herbivores determining plant assembly and ecosystem function depend of natural ecosystem structure, otherwise, structural heterogeneity. Large herbivores act promoting heterogeneity in structurally homogeneous ecosystems (Zhu et al. 2012; Pringle et al. 2016). In grasslands, for instance, herbivores are important producers of heterogeneity shaping vegetation structure in different strata by consumption of higher competitive species and allowing the coexistence of more species. However, in ecosystems where structural heterogeneity is already an evolutionary property, differential selection by herbivores can promote simplification of vegetation layers homogenizing habitat structure instead of creating heterogeneity (Fig. 4).

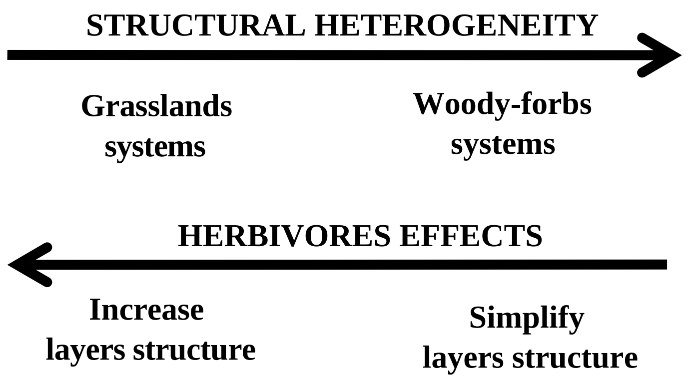

Figure 2: Effects of larges herbivores along structural heterogeneity gradients. Tropical systems are evolutionary more structurally heterogeneous and preferential herbivory in palatable species can lead to a simplification of structural layers of the ecosystem. In contrast, temperate and boreal systems are naturally more homogeneous, thus herbivory by vertebrates is an important mechanism to creating structural heterogeneity and habitat complexity allowing occurrence of more species.

In ecosystems where habitats are related to high structural complexity and herbivores present feeding behavior related to high habitat selection and/or disproportional plant selection on a specific functional group or growth-form, effects of herbivores are likely to impose negative feedbacks decreasing environmental heterogeneity. In contrast, in habitats with low structural complexity and where feeding behavior of herbivores is related to low habitat selection and/or plant selection on a specific functional group or growth-form, effects of herbivores are likely to impose positive feedbacks increasing environmental heterogeneity (modified from Adler et al. 2001). By considering the natural structural heterogeneity of each ecosystem, tools of management can be created aiming increase environmental complexity and conciliating conservation and ecosystem function.

Vegetation transitions

The effect of large herbivores driving vegetation transitions between grass and tree-dominated formations should not be generalizable for all systems and have been questioned (Eldridge et al. 2016). Transitions from ecosystems dominate by trees controlled by herbivores to ecosystems controlled by botton-up resources constraints (water and nutrients) after loss of megafauna seem to be less likely to occur in regions of low productivity or in regions with low megafauna density (Malhi et al. 2016). Examples of this are Pampas and Patagonia in which it is not registered transitions to forest formation after megafauna extinctions due to rainfall and nutrients constraints. Most part of assumptions of alternative vegetation states related to herbivores abundance before and after megafauna extinctions did not consider the variation in climatic conditions (Bakker et al. 2016), so did not consider abiotic factors governing impact of large herbivores on vegetation. So, is unlikely that absence of herbivores will stimulate a transition from open vegetation to closed canopy structure in semi-arid or arid climate and poor nutrient or low depth soil.

Another common transition related to large herbivores is shrub encroachment phenomenon already widely recorded in grasslands, open woodlands and savannas (Eldridge et al. 2013). Probable causes are overgrazing associated with climate, fire regime and competition between woody and grasses plants (Coetzee et al. 2008; Eldridge et al. 2011, Brandt et al. 2013). Effects of shrub encroachment and herbivory on ecosystem functions have been shown differentiated between ecosystems. While negative effects of shrub encroachment on ecosystem properties and processes such as nutrient cycling and soil stability were found in grasses-dominated ecosystems, in dry lands declining in ecosystem function were more related to herbivores overpressure than shrublands *per se* (Eldridge et al. 2011). Using low levels of grazing is likely to maximize the benefits from shrublands, such as the maintenance of biodiversity, water infiltration and C sequestration, while maintaining a productive herbaceous community (Eldridge et al. 2013).

Conclusions

Effects of herbivores on plant communities and ecosystem functioning follow multiple trajectories as result of combination of drivers acting in all organizational levels from individual plants to ecosystem. Although some aspects still remain poorly addressed, such as plant community trajectories under the effect of introduced herbivores in ecosystems where wild herbivores are lack, large herbivores have been demonstrated to be a strong driver shaping most diverse global ecosystems. Thereby, management tools must be elaborated according to each environmental context in order to take into account which properties of communities and ecosystem are being modified. Finally, it is necessary to balance research efforts in ecosystems where low information is available as wet and dry tropical forests. A disproportionate number of studies have been carried out in grasslands, savannas and temperate forests compared to other tropical systems, where introduced herbivores have been pointed out as a major source of disturbances causing serious impacts on biodiversity and ecosystem health. It is also a lack of controlled experiments on natural systems with temporal data to capture effects of seasonality on resources on strength of herbivore impacts.

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3.2 ARTIGO 2: SEASONALITY MEDIATES EFFECTS OF INTRODUCED HERBIVORES IN DRY FORESTS

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Summary

1. Livestock breeding is one of the main human-related activities in tropical dry ecosystems, usually related to local communities highly dependent on natural resources for their livelihood. Herbivory by such introduced herbivores is a strong force able to modulating ecosystems dynamic and plant community assemblies, but their impacts on dry forests are still under-explored.

2. We investigated responses of herbaceous communities to exclusion of introduced herbivores (goats) in seasonally dry forests in Brazil through temporal monitoring from 2015-2017. We addressed the following three questions: (1) How does herbivory by introduced herbivores affect herbaceous community structure (species richness, diversity, plant density and aboveground biomass - AGB)? (2) How does seasonality mediate effects on these metrics? (3) How do effects of herbivores vary among species life form and growth-form groups?

3. Exclusion of introduced herbivores increased species richness, diversity and AGB, but not plant density. Plant community responses increased over time and were bigger during wet season while during dry season no difference was recorded between areas with herbivores and exclosures.

4. Exclosures and areas used by herbivores remain similar in species composition over time. Excepted for legumes that increase in frequency in exclosures, herbivores did not affect other functional groups or plant life-forms, independently of seasonality and time after exclusion.

4. *Synthesis:* Our findings highlight strong effects of introduced herbivores on herbaceous communities and ecosystem productivity in dry forests with effects mediated by seasonality. Because seasonality is expected to increase due to ongoing climatic changes, our findings point out herbivory shaping plant communities in direction of less productive systems, which can lead to negative feedback in productivity and ecosystem functioning, since herbivores also modify frequencies of important functional groups in dry forests.

Key-words: Human-related disturbances, diversity, generalist herbivores, semiarid ecosystem, Caatinga.

Introduction

Herbivory by vertebrates is an important driver of structure and composition of plant communities in most diverse ecosystems (Huntly 1991, Kempel *et al.* 2015). A large body of evidence of herbivores effects on plant communities comes from modern exclosure experiments and paleo-ecological reconstructions of extinct megafauna impacts (Young et al. 2013, Bakker et al. 2016). However, rarely these studies consider the role of seasonality on climatic conditions mediating impacts of herbivores in natural ecosystems (Carmona et al. 2014).

Classical theories stand out that in seasonal environments, abiotic conditions outweigh biotic interactions and thus herbivory by vertebrates should play a less important role in biodiversity maintenance and ecosystem functioning (Milchunas & Lauenroth 1993). Such belief is attributed to high spatiotemporal variation in rainfall leading to recurring events of drought-related mortality keeping herbivores populations below ecosystem carrying capacity (Illius & O'Connor 1999). Thus, plant communities in seasonal ecosystems should be driven more by density-independent process related to stochasticity than density-dependent process (Ren *et al.* 2012). However, in case of human-related herbivores, management practices such as livestock supplementation during drought periods can release populations of herbivores from density controls and break down the dependence of natural resources by herbivores herds (Illius & O'connor 1999; Hempson *et al.* 2015). Therefore, increase in herbivores populations can impose strong damages on plant communities (Podwojewski *et al.* 2002; Díaz *et al.* 2007).

Responses of plant communities to herbivory vary broadly according to vegetation strata, life form and growth-form since plants exhibit a wide variation in ecological strategies to tolerate or avoid herbivory (Maron & Crone 2006). Depending on their life-forms, plants can be affected differently by herbivory (Díaz *et al.* 2007) since each strategy implies different periods of exposure to damages by herbivores. Chamaephytes are normally in constant exposure to herbivores while therophytes are exposed to herbivory only during short growing season usually matching with period of more resources availability for herbivores. Such contrasting groups might be differently affected by herbivores since different strategies are observed. While the vast majority of chamaephytes should be tolerance strategists, terophytes are basically avoidance strategists (Young et al. 2013). Therefore, annuals plants such as terophytes are less likely than perennials to decrease with increasing grazing pressure (Vesk et al. 2004).

Introduced species represent one of the three generalist threats to biodiversity globally alongside climatic change and habitat loss (Nunez et al. 2010). Some advantages can be attributed to exotic species on no-origin ecosystems such as release of native predators and absence of predator-specific defenses by native species (Parker et al. 2006). Taking this into account, introduced herbivores, mainly those of generalist feed behavior, are able to impose strongly impacts on plant assembly (Fernandez-Lugo et al. 2013). However, understanding how introduced herbivores affect plant communities in seasonal environments is still under-explored in tropical regions. An interesting model to study effects of herbivores on dry ecosystems is the Caatinga vegetation in the northeast of Brazil, which is the largest contiguous area of Seasonally Dry Tropical Forest (SDTF) in South America. Even though seasonally dry ecosystems are strong limited-resources to herbivores due to marked seasonality which determines high variation on resources availability throughout year, Caatinga ecosystem has been grazed by introduced human-related herbivores for at least 200 years. Although it is believed that strong climatic constraints control herbivores populations due to mortality by drought (Kempel et al. 2015), mismanagement of introduced herbivores is pointed out as a key driver of anthropogenic disturbances on drylands (Reynolds et al. 2007).

Incorporate impacts of herbivory in ecosystems with marked seasonality is essential to support predictions and develop rules for specific climate regimes underlying ongoing climate change (Díaz et al. 2007). In the Caatinga dry forest, goats (*Capra hircus*) are the major introduced herbivore and an interesting study model due to their particular adaptability to most varied climate conditions; as well as their ability to modify their foraging behavior, consumption and diet depending on seasonality and natural resources dynamics (Orihuela & Solano 1999; Skarpe *et al.* 2007). These mixed-feeding herbivores (exhibiting both browser and grazer behaviors simultaneously) and thus might impose large effects on plant community and community assembly. However, considering that Caatinga ecosystem has a marked seasonality is likely that this variation in climatic conditions might mediate herbivores effects. Here, we performed an experimental approach where exclosures were installed in areas used by goats to address variations on plant community structure and dynamics of Caatinga dry forest over time in order to understand the role of seasonality in mediate effects of herbivores. Specifically, we addressed the following three questions: (1) How does herbivory by introduced herbivores affect herbaceous community structure (species richness, diversity, plant density and AGB)? (2) How does seasonality mediate dynamics on these metrics? (3) How do effects of herbivores vary among life-form and growth-form groups of herbs?

Materials and methods

STUDY SYSTEM

The exclosure experiment was conducted in areas of Seasonally Dry Tropical Forests in the northeast of Brazil. Specifically, we performed the experiment at Catimbau National Park (8°24’00″ and 8°36’35″ S; 37°00’30″ and 37°10’40″ W), which has an extension of 623 km^2 composed by a mosaic of different vegetation physiognomies (from open areas dominated by Cactaceae and Bromeliaceae species, mixed forb-shrub areas to close areas dominated by shrub-tree plants) and a high variation on annual rainfall (i.e. 480–960 mm year). Even though the National Park was created in 2002, local communities continue living in its area using natural resources from Caatinga for their livelihood. Many of these communities have been raising goats extensively as main income source since long time, consequently, this study area had experienced herbivory by goats since at least 70 years. In 2015, sixteen paired blocks side-by-side composed by exclosure (fenced) areas and control (with goats’ use) areas. Since then, such areas have been quarterly monitored in order to investigate effects of goats through temporal variation on environmental conditions.

The regional climate is semi-arid with dry season during summer and wet season during winter with an annual mean temperature of 23 ºC. This region experienced strong seasonality within-year varying from 6 - 9 months with less than 100 mm rainfall (Sampaio 1995). There is also a high spatiotemporal variation in water availability due to high rainfall unpredictability in the occurrence of rains within- and between years. During our study period from 2015 to 2017, the first year was relatively dry (406.2 mm) and the second year was the wettest year (1258.3 mm), considering annual total rainfall. All blocks were located in areas with same soil type (sand soil), nutrient conditions and similar slope in order to control potential effects of terrain slope and soil features on communities.

Woody communities are dominated by Fabaceae (*Pityrocarpa moniliformis*, *Senegalia bahiensis, Piptadenia stipulacea* and *Poincianella microphylla)* and Euphorbiaceae species (*Croton argyrophyllus*, *Cnidosculus bahianus* and *Jatropha mutabilis).* Forbs communities are mostly represented by Malvaceae (*Herissantia*, *Sida*, *Pavonia*), Fabaceae (*Chamaecrista, Aeschnomne, Zornia*), Rubiaceae (*Richardia*, *Diodela),* Portulaceae (*Portulaca*, *Talinum)* and Asteraceae (*Ageratum, Bidens*). In contrast to other tropical areas under similar climatic conditions, Caatinga dry ecosystem is not related to fire dynamics, since grasses are not a dominant compound of vegetation structure.

DATA COLLECTION

In January of 2015, we installed 16 paired blocks of herbivores exclosures composed by a 20 x 20 m fenced plot (exclosures) and a control plot where goats remain with free access. The studied areas varied in grazing intensity (0.2 to 2.21 goats/ha) and woody vegetation density (0 to 100 %) in order to cover such natural spatial heterogeneity of Caatinga ecosystem. In order to detect seasonal effects of herbivores accordingly with the variation of rainfall occurrence, we survey temporally (3-month intervals) all plants from herbaceous strata in five fixed 1 x 1 m subplots per area (in each treatment). We recorded the individual number for each species. The aboveground biomass (AGB) of herbs was collected in five randomly distributed 1 x 1 m plots. Afterwards, samples were dried and weighted. All experimental blocks (exclosure and control) presented similar values for all community parameters (richness, abundance and aboveground biomass) at experiment start. Herbaceous plant species were classified regarding Raunkier's life-form (chamaephytes, therophytes, geophytes and hemicryptophytes) and functional groups based on growth form (grasses, wood forbs, forbs and legumes).

We classified all reported life forms according to the five main Raunkiaer categories: (1) phanerophytes, which have buds that are well above the ground during the dry season; (2) chamaephytes, which have buds close to the ground; (3) hemicryptophytes, which have buds at the ground level; (4) cryptophytes, which have buds below ground; and (5) therophytes, which are annual plants that complete their life-cycle, reproduce and die during a single rainy season (Raunkier 1934). We used Raunkiaer categories because they are based on life history features that are closely aligned with adaptation to the ecological conditions highlighted in our study.

STATISTICAL ANALYSIS

To test effects of herbivory by goats on vegetation structure and dynamics, we used Repeated Measures - ANOVA using treatment (exclosure vs control), time (eight repeated measures after exclosure) and season (dry and wet) as fixed factors and block (exclosure + control) as random factors. Differences in frequency among functional groups of herbs based on growth-form and species life-form also were tested using Repeated Measures ANOVA - for each group separately. All analyzes were performed in R, for each response variable related to herbaceous communities (AGB, species number, plant density and diversity) using the *nmle* package (Pinheiro et al. 2016). We applied NMDS ordination based on Bray-Curtis similarities to compare differences in community composition of herbs between exclosures and contr ol areas at experiment start when fences were installed and after 2 years of herbivores exclusion.

Results

We recorded 71 herbaceous species belonging to 27 botanical families (Appendix 1). Sixty-four species were found within exclosure plots whereas fifty-nine species were recorded in control plots. Fabaceae, Malvaceae, and Poaceae were richest families with 8 species each, followed by Rubiaceae (5), Asteraceae (5) and Portulacaceae (4).

Except for plant density, all communities' variables differed between treatments (control and exclosure) over time. Herbivores exclusion increased species richness and diversity (Fig. 1) compared to control plots browsed by goats. Aboveground biomass (AGB) was two-thirds larger within exclosures during wet season (Fig. 2), but no differences were found during dry season. Positive effects on AGB increased also over time (Tab. 1). Species composition of herbs in control and exclosure areas did not differ after 2 years of herbivores exclusion (Fig. 3). The frequency of Raunkier's life-form (Fig. 4A) and plant growth form (Fig. 4B) did not change over time, except for legumes, which increased in frequency in fenced areas (Tab. 2).

Discussion

Herbivores are an important group able to shape a range of aspects, from community to ecosystem level (Huntly 1991, Maron & Crone 2006). In dry environments, such role of large herbivores as driver modulating communities is questioned (Illius & O'Connor 1999) since seasonality on rainfall has been shown as major factor controlling productivity and community assembly even more important than human-related disturbances (Rito et al. 2017). Our findings highlight that introduced herbivores can impose strong effects on plant communities in seasonally dry ecosystems with seasonality modulating sign and magnitude of such effects.

Herbaceous communities presented an increase in diversity and AGB in exclosures compared to free access to goats (control) areas as expected. Goats reduced over 50% of AGB during growing season but not during dry season. Changes on magnitude of impacts through seasons are likely due to observed shifts in feed behavior according to resources availability from green vegetation during growing season to litter resources (dry leaves and barks) during dry season (*unpublished data*). Additionally, higher differences in AGB between exclosure and control plots during wet season, while no differences were found in dry season, indicate that perennial herbs, which is responsible by AGB during dry season, are resistant or tolerant to herbivory by goats, since no differences in frequency were found for most life-form or functional groups, except for legumes.

Such increase of legumes in exclosure areas indicates this functional group represent an important source of feed for goats. Legumes are an important group of plants in dry forests, which is responsible for most part of N-fixation in semiarid areas and maintenance of high levels of productivity during growing seasons (Raadad et al. 2005, Freitas et al. 2010). Thus, effects of goats on this target group can impose effects on ecosystem functions played by legumes as reducing nutrient supply, which can lead to consequent reduction in net primary productivity (Eldridge *et al.* 2016). The absence of herbivores effects on Raunkiaer's life-forms shows a contrasting trend compared to arid ecosystems that reported a replacement of perennial to annual species with herbivory (Freeman, Emlen 1995, Díaz et al. 2007). Interestingly, therophytes herbs (annuals plants) did not differ between treatments, suggesting that with such short-life cycles matching with temporal pattern of high resource availability to all herbivores is likely to result in a less effective seasonal damage by herbivory.

We found that exclosure of herbivores increase diversity of herbs, which counter to results obtained in other studies in temperate forests and grasslands (Fensham et al. 2014; Stahlweber & D'Antonio 2013; Faison et al. 2016, Lilleeng et al. 2016). The release of dominance control of plant species is used to explain lower diversity in exclosures areas in temperate areas (Lilleeng et al. 2016) and grasslands (Stahlweber & D'Antonio 2013). Likewise, Jacobs & Naiman (2008) showed that short-term exclosure of large herbivores in savanna ecosystems increased biomass but declined richness of herbs, due fast-growing grasses overtopped and shaded forbs. However, effects in semi-arid and arid systems are less clear shown inconsistent patterns (Hanke et al 2014, Eldridge et al. 2016). These contrasting results are likely to be related to high spatiotemporal variation on rainfall occurrence in seasonally dry forests resulting in high vegetation structural heterogeneity which may determine more complex plant-herbivore interactions, compared to structurally homogeneous and single vegetation stratum from grasslands and temperate forests (Vesk et al. 2004). In a highly heterogeneous dry forest as our study area, herbivores seem to act simplifying vegetation structure instead to create heterogeneity as observed in grassland and temperate systems. Evidence that effects of herbivores can be dependent-context has increased, showing that differences in response patterns were attributed to variations in vegetation structure, climatic conditions and foraging performance of livestock (Su et al. 2017).

Biodiversity has been showing to increases resistance of ecosystem productivity and stabilizes productivity-dependent ecosystem services (Isbell et al. 2015), where areas poorly in species tend to become more vulnerable to climatic extreme events as drought, already usual in seasonally dry forests. Our findings point out herbivory shaping plant communities in direction of less productive systems, which can lead to negative feedback in productivity and provision of ecosystem functions since herbivores altered ABG productivity and the frequency of important functional groups for nutrient cycling such as legumes (Carmona et al. 2014, Chillo et al. 2017). This point out concerns about the resilience of Caatinga dry forest under livestock breeding to ongoing climate changes, which foresee to reduce water availability becoming even less productive (Burkett *et al*. 2014). Research efforts should be targeted to understanding functional responses in different grazing regimes and productivity within dry forests in order to access the viability of extensive livestock breeding in such vulnerable ecosystems.

Our findings point out complexity of factors shaping community responses and essential role of seasonality in mediate, alongside time after exclosure and species growth form. Therefore, studies that intend to understand the consequences of herbivory in terms of successional processes and natural regeneration must consider these relationships and their consequences for ecosystem functioning. This has an interesting perspective since have been shown that biodiversity effects strengthened over time with a progressive increase in functioning in species-rich communities (Meyer *et al.* 2016), but these questions have been poorly addressed in seasonally dry ecosystems. In addition, it is important take into account that fast increase in diversity of herbaceous communities are a sign that the ecosystem can recover lost species, but to address underlying forces acting on ecosystem functioning must consider frequency shifts of diverse functional groups and their role on ecosystem functions.

Caatinga dry forest has a short evolutionary history of grazing by introduced livestock, so herbivory is less likely to have large positive effects on community and ecosystem functioning compared to other systems such as grasslands and African savannas. Recent researches have also given support to increasingly pronounce negative effects of livestock in semi-arid and arid systems compared to wet systems (Eldridge et al. 2016; Su et al. 2017).

Overall, our results evidence that introduced herbivores have strong effects on plant communities and ecosystem productivity declining extensively on average AGB, however, seasonality in rainfall has an important role mediating such effects. Our findings warn that management tools are important for keeping ecosystem functioning and maintenance of productivity. Managed techniques as seasonal herbivory and to sale animals during dry season can be a replacement to natural compensatory mortality and to prevent overpopulation of herbivores during wet season, supporting vegetation recovery and maintenance of ecosystem functioning.

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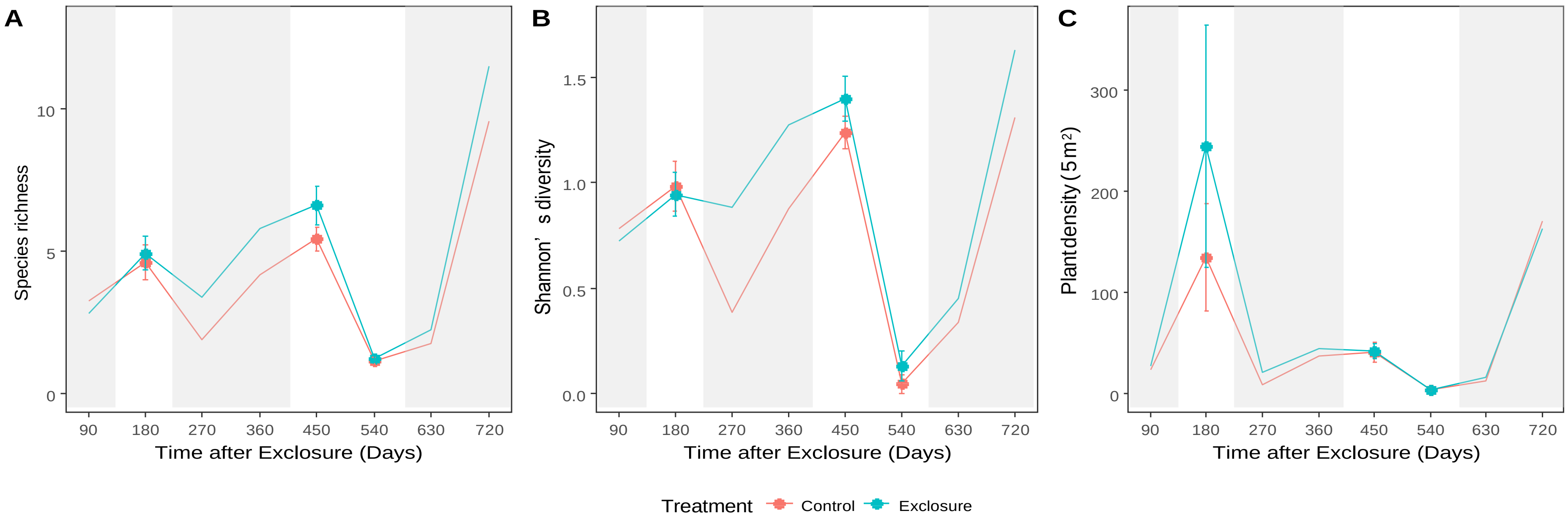


Figure 1. Effects of introduced herbivores (goats) in browsed areas (control) compared to free-goats areas (exclosures) in the Brazilian Caatinga dry forest. A) Number of herbaceous plant species, B) Diversity of herbs and C) Number of individuals. Shown are means ± SE and wet season (gray shadow).

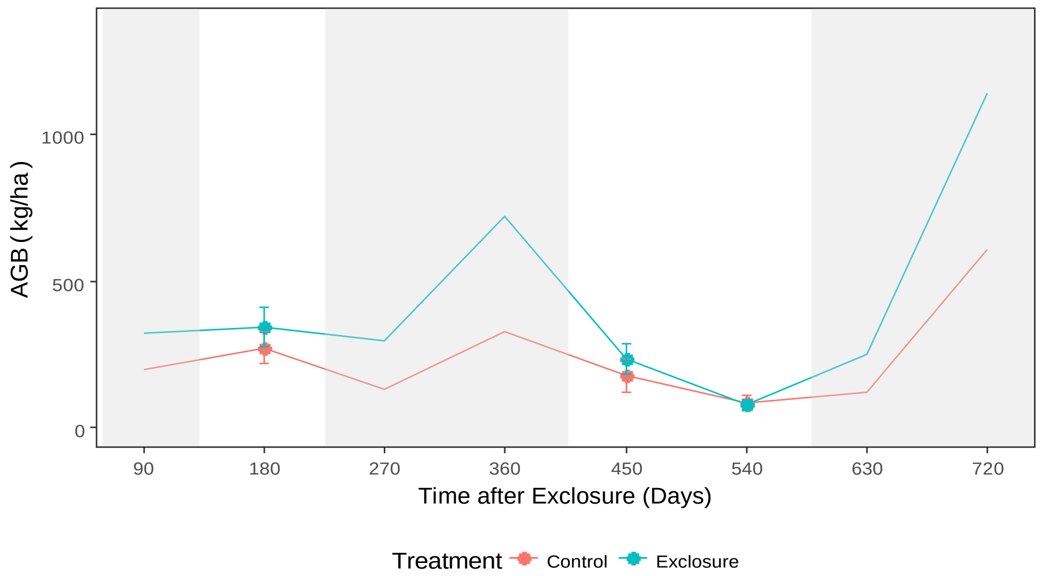
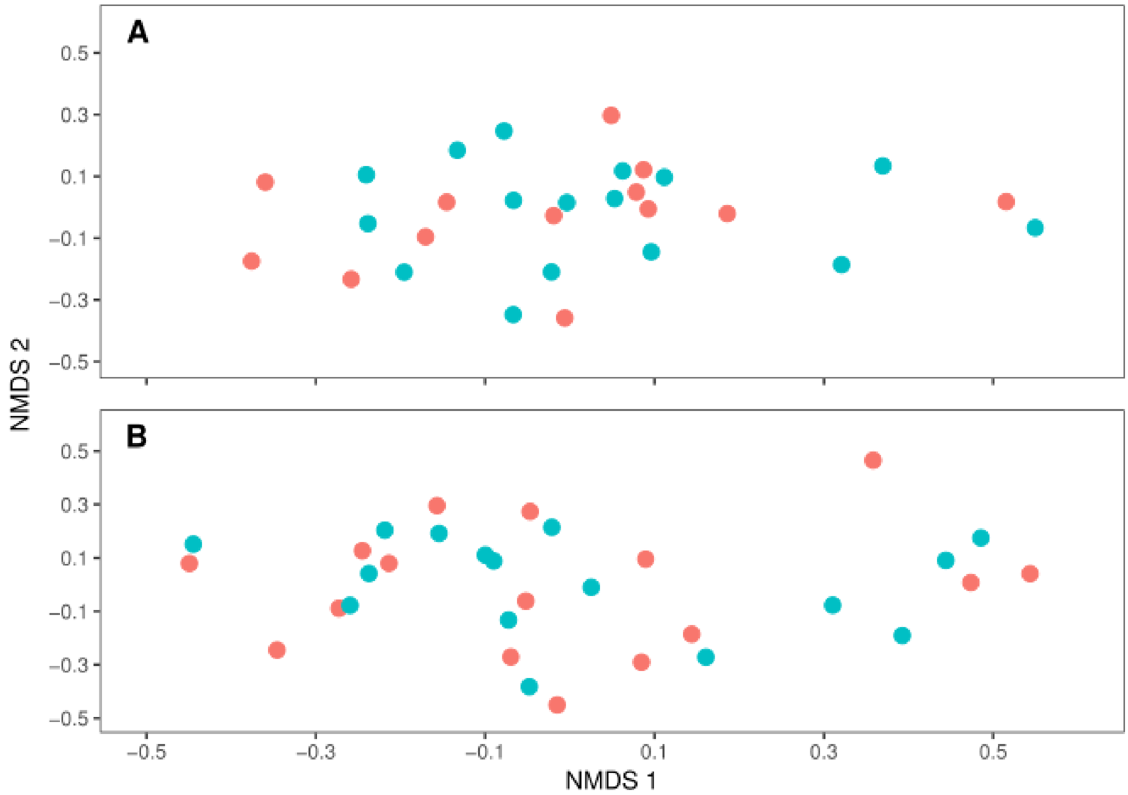


Figure 2. Above-ground biomass (AGB) of herbaceous strata in areas browsed by introduced herbivores (goats) compared to free-herbivory areas (exclosures) in the Brazilian Caatinga dry forest. Gray shadow corresponds to wet season. Shown are means ± SE and wet season (gray shadow).



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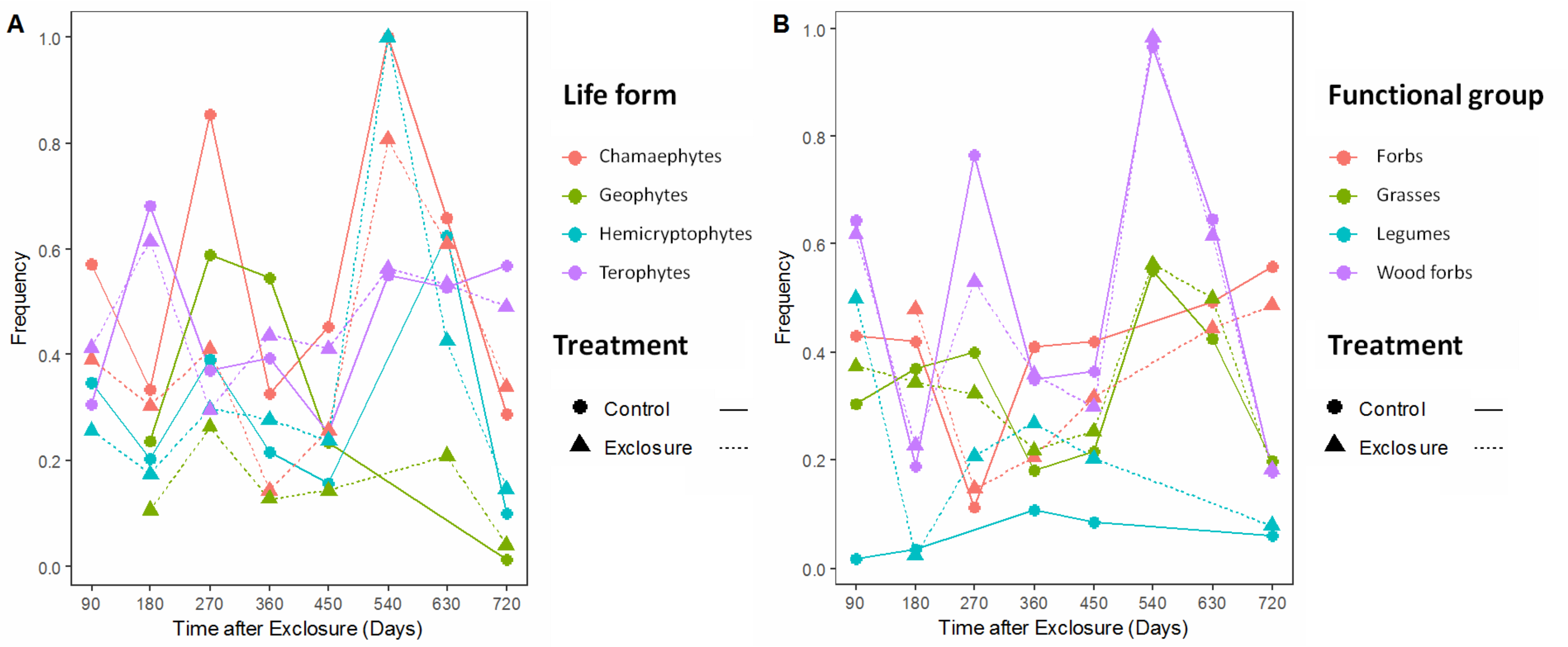

Figure 4. Differences over time in the frequency of functional groups of herbs (A) and Raunkier life-forms recorded between control areas browsed by introduced herbivores (goats) and exclosure areas free of herbivory by goats in the Brazilian Seasonally Dry Forest (Caatinga).

Table 1. Results of repeated measured ANOVAs - mixed models using goats herbivory treatment (exclosure x control) , time after exclosure of goats and season as fixed factors, d.f., F and *p* were the abbreviations of degree of freedom, F-test statistical and P values, respectively.

FACTORS		Species richness		Shannon's diversity		Plant density		AGB	
	d.f.	F	*p*	F	*p*	F	*p*	F	*p*
Herbivory	1	3,7	**0,05**	9,39	**< 0, 001**	0,41	0,63	23,99	**< 0, 001**
Time since exclosure	7	50,55	**< 0, 001**	35,4	**< 0, 001**	0,67	0,62	22,78	**< 0, 001**
Herbivory * Time	7	1,17	0,32	1,96	0,06	0,62	0,73	3,01	**< 0, 001**
Herbivory * Season	1	8,82	**0,01**	5,72	**0,03**	0,11	0,73	5,6	**< 0, 001**

Table 2. Effects of the exclosure of introduced herbivores (treatment control x treatment exclosure) and time after the exclosures of herbivores (goats) on each functional groups and life-forms of herbaceous plant communities. *ns:* non-significant.

Groups	**Treatment**	**Time**	**Treatment * Time**
Forbs	*F* = 0.171, ***ns***	*F* = 0.421, ***ns***	*F* = 0.013, ***ns***
Grasses	*F* = 1.232, ***ns***	*F* = 0.661, ***ns***	*F* = 0.000, ***ns***
Legumes	***F* = 4.599, *p* = 0.05**	*F* = 2.819, ***ns***	***F* = 6.592, *p* = 0.03**
Wood forbs	*F* = 0.655, ***ns***	*F* = 1.413, ***ns***	*F* = 0.834, ***ns***
Raunkier life-form			
Chamaephytes	*F* = 0.031, ***ns***	*F* = 0.862, ***ns***	*F* = 0.490, ***ns***
Geophytes	*F* = 0.599, ***ns***	*F* = 5.123, ***ns***	*F* = 5.048, ***ns***
Hemicriptophytes	*F* = 0.539, ***ns***	*F* = 1.958, ***ns***	*F* = 0.146, ***ns***
Terophytes	*F* = 1.609, ***ns***	*F* = 0.455, ***ns***	*F* = 0.051, ***ns***

3.3 ARTIGO 3: FUNCTIONAL CHANGES MEDIATED BY INTRODUCED HERBIVORES IN SEASONALLY DRY FORESTS

as prepared for: Functional Ecology

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Abstract

By shaping functional diversity of plant communities, livestock herbivory can affect important aspects of community assembly and ecosystem functioning. We investigated functional changes on herbaceous plants after exclosure of introduced herbivores. Using five functional traits related to resources use, plant performance and response against herbivory, we examined shifts in single traits of herbaceous plant community and multi-traits functional diversity indices between free access to herbivores (control) and fenced (exclosure) areas. The density distribution of 2 out for 5 functional traits differed between control and exclosures plots with herbivores decreasing maximum height and increasing branching of herbs. Herbivores decreased functional richness, but increased functional dispersion of herbaceous plants. Fenced areas became functional distinct from areas with herbivores but effect size was not explained neither herbivores pressure nor vegetation structure variables. Our findings showed that introduced herbivores did not modify the ability of herbaceous plants to use resources but impose strong effects on plants performance, which can prevent herbaceous plants from completing their life cycles and maintaining their population renewal.

Keywords: functional diversity, generalist herbivores, Caatinga, dry forests.

INTRODUCTION

Vertebrate herbivores are key species shaping community structure and ecosystem processes. Firstly, herbivores may reduce abundance or lead species to local extinction by consuming individual plants. Additionally, also can have strong effects on reproductive dynamics and competitive abilities of species by removing plant tissues without causing directly individual-plant dead (Aikens & Roach 2015; Adhiraki & Russel 2014). Through such mechanisms, herbivores may determine changes in both taxonomic diversity and functional diversity of plant communities. Because altering species frequency and/or species performance herbivores may influence plant-function relationship, thereby, imposing effects on the ecosystem functioning in important processes as primary productivity (White 2012), nutrient cycling (Tadey & Farji-Brener 2007) and succession delay (DiTomasso et al. 2014).

Although relationship between taxonomic diversity and functional diversity have been demonstrated (Devictor et al. 2010), uncoupled relations also were found (Carmona et al. 2012) showing that shifts in one component may not directly reflect in the other. This shows that even communities with similar taxonomic composition may exhibit significant functional changes in response to herbivory (Li et al. 2015). Thereby, selective pressures by herbivores may induce changes in plant performance and strategies for resource use, which in turn can lead species to changes in their occupied ecological niches (Bailey & Schweitzer 2010). These can be especially strong in ecosystems with introduced herbivores such as livestock animals since plant communities did not have specific defenses against exotic herbivores (Parker et al. 2006).

Selective herbivory on preferred and/or dominant species can shape functional community composition by altering trait average values at the community level (CWM) or modifying community functional diversity (FD). Previous studies support that herbivory can promote community functional diversity by removing biomass of abundant species and increase evenness, hence decreasing competition among neighbouring plants (Niu et al. 2016, Nishizawa et al. 2016). However, contrasting support also is given to community simplification by reduction on functional diversity and structure in overpressure or low-productive environments (Carmona et al. 2012, Chillo et al. 2016) where smaller plants, shorter-lived and with branching architecture are found in responses to herbivory by vertebrates (Jones et al. 2011, Díaz et al. 2007).

In grasslands with high productivity, plants usually a response to herbivory increasing specific leaf area but decreasing leaf dry matter content due to faster growth and regrowth under grazing pressure, consequently driving shifts in community strategies from conservative in ungrazed areas to resources exploitative under grazing (Niu et al 2016). In contrast, seasonally dry ecosystems where productivity tends to be low and species usually converge in strategies to cope with both herbivory and climatic constraints we could expect an opposite response in direction to conservative strategists. Considering that herbivores exclusion alter selective pressures over plant communities able to influence performance and plant strategies for resource use, the functional approach is an important tool to access mechanisms by which herbivores can be promoters of changes both species niches and ecosystem functioning. Here, we investigated functional effects of introduced livestock herbivores (goats) on herbaceous communities in seasonally dry forests. Using paired blocks composed of exclosure and free access to goats (control) areas, we addressed different issues related to functional aspects of plant communities.

(i) Whether herbivores exclusion induces community-wide shifts in functional traits related to use of resources and performance. Considering that herbivores can enhance selection of conservative attributes in dry environments, we expected that herbivores exclusion release species from conservative traits to more acquisitive strategies such as higher specific leaf area and maximum height.

(ii) Whether herbivores exclusion shifts functional diversity indices. Considering an environment with a short growing season, we expected herbivores exclosure to increase functional diversity.

(iii) Whether magnitude of herbivores effects is influenced by herbivores pressure or vegetation structure. We expected that effects of herbivores exclusion to be stronger with increase in herbivory pressure and decrease plant biomass (productivity).

MATERIAL AND METHODS

Study area

The study area was located in central region of Pernambuco state, Brazil. Corresponds to Catimbau National Park (8º23’17” to 8º36’35” S; 37º11’00” to 37º33’32”W) which has an area of 607 km^2 of seasonally dry tropical forests mosaic with different vegetation structures, locally known as Caatinga dry forest. Seasonality is a very marked characteristic of this area, where rains are concentrated in three/four months by year and severe droughts occur frequently (Sampaio 1995). Such natural conditions impose a high intra-annual and inter-annual variation and unpredictability in resources availability. Although it is a natural reserve, human communities still continue to live and develop activities as agriculture and livestock breeding inside the National Park. So, the area has been grazed extensively by goats for at least 70 years. Animal density within the National Park varies between 0.2 and 2.21 goats/ha. The climate, with annual rainfall varying from 550 - 950 mm and mean annual temperature of 23 º C, is characterized as semi-arid (Peel et al. 2007). The main plant communities in the study area are: shrublands dominated by *Croton* species and *Jatropha mutabilis* (Euphorbiaceae), interleaved with woodlands from open to close structure dominated by *Ptyrocarpa moniliformes*, *Senegalia bahiensis*, *Senegalia piauiensis*, *Poincianella pyramidalis* and *Trischdium molle* (Fabaceae). Herbaceous and sub-shrub strata are dominated by *Richardia grandflora*, *Diodela teres* (Rubiaceae), *Sida galheirensis*, *Herissantia crispa* (Malvaceae) and legumes as *Zornia grandflora* e *Aeschnomine martii*.

Experimental protocol

We sampled 10 paired blocks composed by an exclosure and a control plot distributed side-by-side (20 x 20 m each plot). Exclosures were installed in 2015 and plant functional traits survey was performed 1 ½ year later during peak of growing season in 2016. In each plot, all herbaceous species were sampled considering 5 individuals per species and 1-3 individuals in the case of rare species (Paine et al. 2015). We considered the following traits related to resources use, herbivores defense and plant performance: 1. specific leaf area (SLA, cm^2 g^{-1}); 2. leaf dry matter content (LDMC, g g^{1}); 3. leaf thickness (LT, mm); 4. maximum height (H*max*, cm); and 5. apical dominance index (ADI, 0-1 range). Three to five mature leaves per individual were used for trait measurements. We calculated means per individual and species for each species in exclosure and control plots. All measurements followed Pérez-Harguindeguy et al (2013) and details of their measurement and biological significance can be found in the supplemental material. We also measured relative abundance for each species in each plot.

We considered four variables (two related to herbivores pressure and two related to vegetation structure) able to mediate herbivores effects on plant functional diversity: 1. in each block we recorded goats density (ind/ha) informed by each herd owner; 2. We calculated distance from exclosure to corral (m) using a GPS. Corral distance is a measure that considers different spatial use patterns among domestic goats since the management of goat herds in this region involves gathering animals to corral for health and reproduction control as well as for food and water supply, more intensively during drought. It is a metric that takes into account that these animals present a central point of foraging and thus is expected a strong habitat use in areas surrounding corrals and houses - central point of goat dispersion (Santos et al. – *in preparation*); 3. Considering high heterogeneity of Caatinga dry forest, we recorded woody vegetation density in each block (exclosure and control) through four horizontal photos taken in each plot following Marsden et al. (2002) protocol; 4. Aboveground biomass of herbs measured in 5 quadrats (1x 1 m) per plot as a proxy for productivity.

Statistical analysis

To test if herbivores induced shifts on plant functional traits we assessed the variation of single traits among communities using the mean of each trait weighed for relative abundance per species by calculating the Community Weighed Mean (CWM) for each herbaceous community and treatment (control and exclosure). Significant differences between treatments were tested by using paired t-tests for each plant functional trait.

To test if herbivores shift functional profile of herbaceous communities we used three independent components of functional diversity using all functional traits: FD - functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis) (Mason *et al.* 2005; Villéger *et al.* 2008; Laliberté & Legendre 2010; Mouchet *et al.* 2010). FRic informs the functional space occupied by species in the community, i.e. given an idea of ecological niches that are being used; FEve indicate how even are the abundance distribution on niche space and FDis is the mean dispersal of individual species to the centroid of all species in the community considering their relative abundance. These indices were calculated based on species abundance in each plot and the 'Gower' distance matrices from using all five traits measured in control and exclosure plots, using the 'FD' package (Laliberté & Shipley 2010) in R. To test differences between treatments (control and exclosure) paired t-tests for each functional diversity indices were performed.

To test if functional composition of herbaceous plants differ between control and exclosures, we used total CWM using all functional traits for performing the Procrustes analysis (least-squares orthogonal mapping). The procrustes analysis compares the shape of two Principal Coordinates Analysis (PCoA) plots by optimize rotating and scaling one plot to best fit the other, with the goodness of fit measured by the M^2 statistic (Mardia et al. 1979). P values are generated using a Monte Carlo simulation in which sample identifiers are shuffled (1.000 times) and the M^2 statistic is compared to the distribution drawn from these permutations. The differences in the axes values between the two ordinations (control and exclosure) paired for each block were transformed in a variable (effect size) and correlated with herbivore pressure and vegetation structure variables. All analysis was performed using R version 3.4 (R Core Team 2017).

RESULTS

Functional traits were measured into 32 herbaceous plant species. Control plots (free access to herbivores) presented 25 species while exclosure plots presented 30 herbaceous species. Both treatments shared 72 % of plant species, including all species with more than five individuals recorded in all survey (Appendix 2).

The density distribution of community weighted mean (CWM) for 2 out for 5 functional traits differed between control and exclosures plots with herbivores decreasing maximum height and increasing branching architecture. Herbivores did not change functional distribution of traits related to resources use SLA, LDMC and LT (Fig. 1, Tab. 1). The exclosure of herbivores increase marginally functional richness but decreased functional dispersion (Fig. 2, Tab. 2). Functional evenness did not differ between exclosures and control plots.

Functional composition in exclosures and control areas were strongly different ($m^2 = 0.513$, $p = 0.02$, Fig. 3), but their differences were not related to any variable related to herbivores pressure or vegetation structure (Fig. 4).

DISCUSSION

Livestock herbivores are able to impose strong taxonomic and functional effects on plant communities in ecosystems where there are introduced (Carmona et al. 2012). Even in plant communities with similar taxonomic composition, we found important functional shifts drove by exclusion of exotic herbivores. The exclusion of introduced herbivores increased ecological niches (FRic) occupied by herbaceous species while traits dispersion of traits within used niches was reduced (FDis). The decreasing in FRic in areas grazed by goats was likely to be due to disappearance of extreme traits values of H*max* and less branched individuals from community distribution of these traits since functional evenness remained similar in both treatments. Our findings suggest that in dry habitats where species tend to converge in traits of resistance to drought, herbivory by goats can boost effects of environmental constraints by reducing niches occupied by species. This pattern was found in dry systems in severe water limitation when combined effects of grazing and drought conditions led to a reduction in functional diversity (Carmona et al. 2012).

Although the same species were found in both control and exclosure areas, functional composition and functional diversity were quite different between areas used by goats and fenced areas. This occurred mainly due to shifts in traits related to plant performance (i.e. maximum height, branching), not in traits related to use of resources (i.e. SLA, LDMC and LT). This indicates that goats did not select species based in more nutrient intake since species with high SLA and low LDMC and LT tend to have high nitrogen concentration and less investment in chemical and structural defenses (Perez-Harguindegay et al. 2013), thereby herbivory by goats seems not change plant strategies for resources use, which seems probable in a community dominated by short-life species that must maximize their growing and reproduction during short growing season. In contrast, plant performance was affected by herbivory with species presenting smaller and more branched individuals. This new selective pressure on individual plants is able to impose shifts in abundance by modifying plant performance which can result in the displacement of occupied niches by species (Lau et al. 2008). It’s a consequential outcome of herbivores exercising differential selection on attributes, which may alter species traits functions modifying community assemblies and their functioning (Salgado-Luarte & Gianoli 2012).

Changes in the community average of traits that expressed plants performance such as H*max* and ADI traits suggest also a structural simplification of communities. Such convergence was on direction of small herbs with tussock architecture showing that goats filtering more tolerance strategies (Carmona et al. 2014). These observed effects after short-time exclosure are in accordance with previous studies who found herbivores effects becoming stronger size on lower-productive ecosystems and driest conditions (Carmona et al. 2012, Young *et al.* 2013). Exclusion of herbivores have already been shown to increase plant height, late flowering species and perennial species (Peco et al. 2005) where herbivory in annual-dominated systems such as in Caatinga ecosystem favors early flowering species which can be an avoidance strategy in relation to grazing (Briske et al. 1996, Peco et al. 2012). Decreases in plant height by herbivory can negatively affect both survival and growth (Horvitz & Schenske 2002) and change relative abundance of species. High variation in plant size was found as a key factor for productivity in short-life species (Roscher & Schumacher 2016), thus goats reducing values distribution for plant size help to explain the mechanisms related to increase in aboveground biomass observed in this same study area (Menezes et al., *in preparation*) after exclusion of herbivore.

Analyses of functional traits offer the potential for advanced in the mechanisms by herbivores change communities because they can detect disturbance impacts before species loss and extinctions occur (Mouillot et al. 2013). Even though the taxonomic composition of herbs was similar between control and exclosures areas, the procrustean analysis showed that functional composition of communities is already differentiated indicating herbivores are imposing selective pressures on species traits able to promote species turnover over time. The effect size on functional composition was independent of our measurements of grazing intensity and vegetation cover suggesting that differences between control and exclosures areas can be context dependent. This indicates that multiple functional trajectories may be observed under effects of herbivores which are an indication that local plant community is an important variable to be considered when evaluated effects of herbivores in highly heterogeneous environments such as the seasonally dry forest studied.

Our findings highlight that introduced herbivores promote important functional changes in herbaceous plant communities even though assemblies in control and exclosures are quite similar in taxonomic composition. Goats modified traits related to plant performance but not affected traits related to plant strategies for resources acquisition, which is an interesting find considering a short-lived species-dominated system. With a short growing season, herbaceous species in seasonally dry forests maintain their strategies for resource use, but their performances are compromised by herbivory, with possible consequences for reproduction and renewal of their populations. Future assessments must access how shifts in traits can affect species fitness and which drivers at the local scale are able to predict functional changes in plant communities under effects of introduced herbivores.

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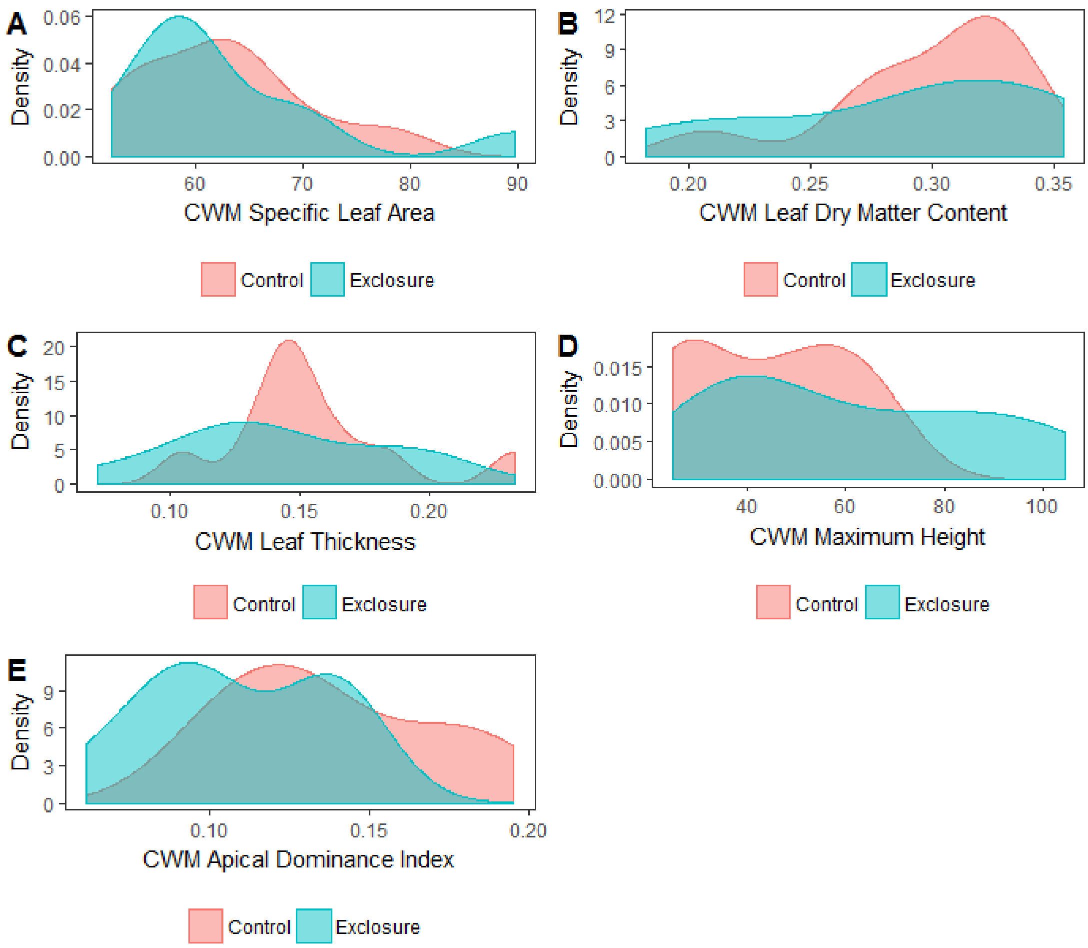

Figure 1: Density distribution of Community-Weighted Mean (CWM) of herbaceous functional traits between treatments with free access to herbivores (control) and fenced areas (exclosure).

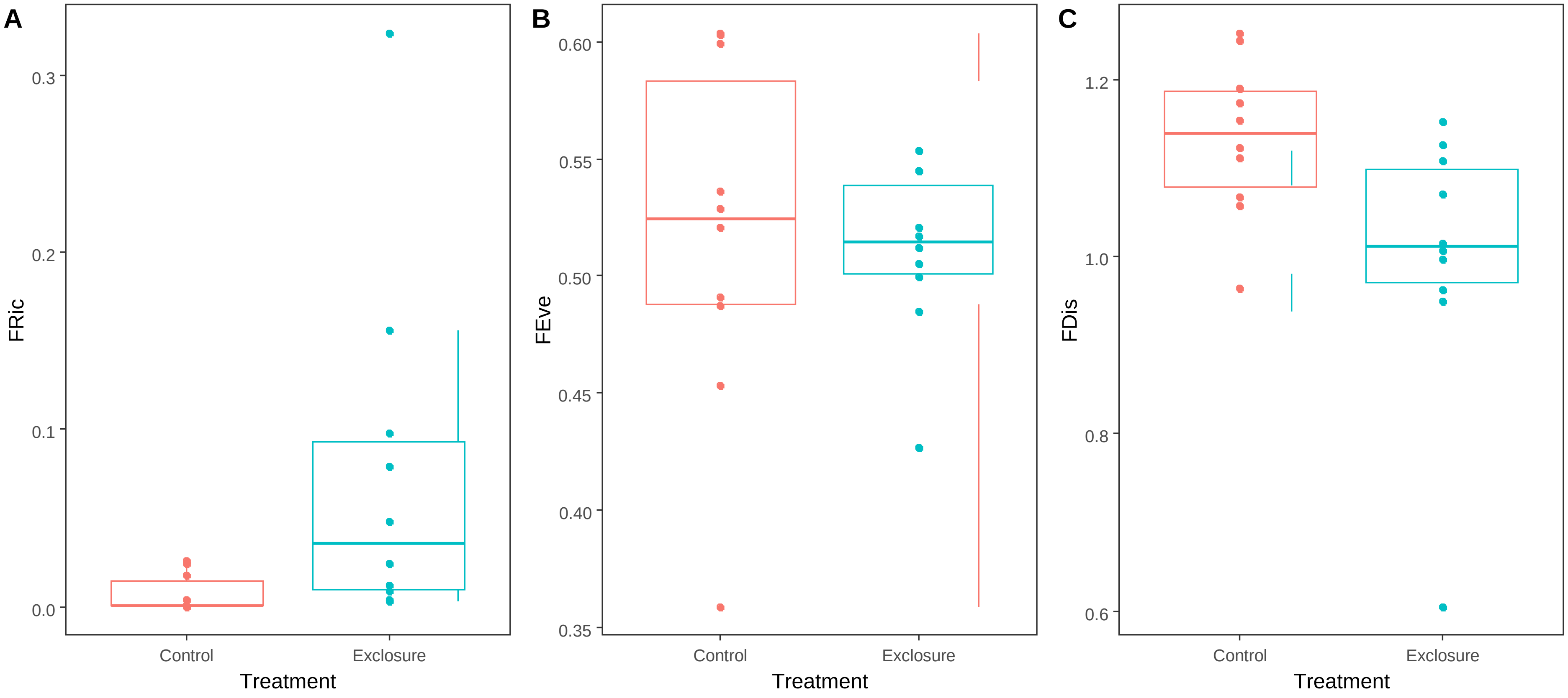

Figure 2: Comparisons between treatments with free access to herbivores (control; red dots and boxplots) and fenced against goats (exclosure; cyan dots and boxplots). (A) Functional Richness (FRic); (B) Functional Evenness (FEve) and (C) Functional Dispersion (FDis) of herbaceous plants. Shown are median, 25% and 75% quantiles.

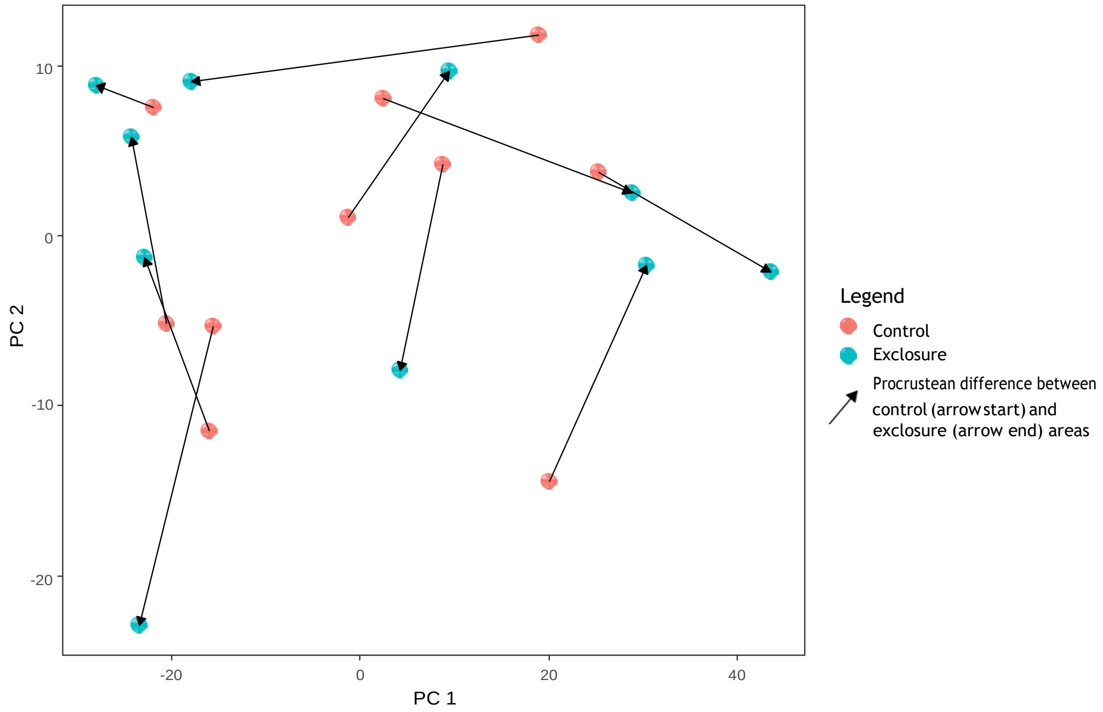

Figure 3: Procrustes analysis comparing CWM of six functional traits of herbs between ten paired areas; each composed by a plot with free access to goats' herbivory (control) and their respective exclosure. A lower distance between the circles indicates a higher degree of concordance between the plots.

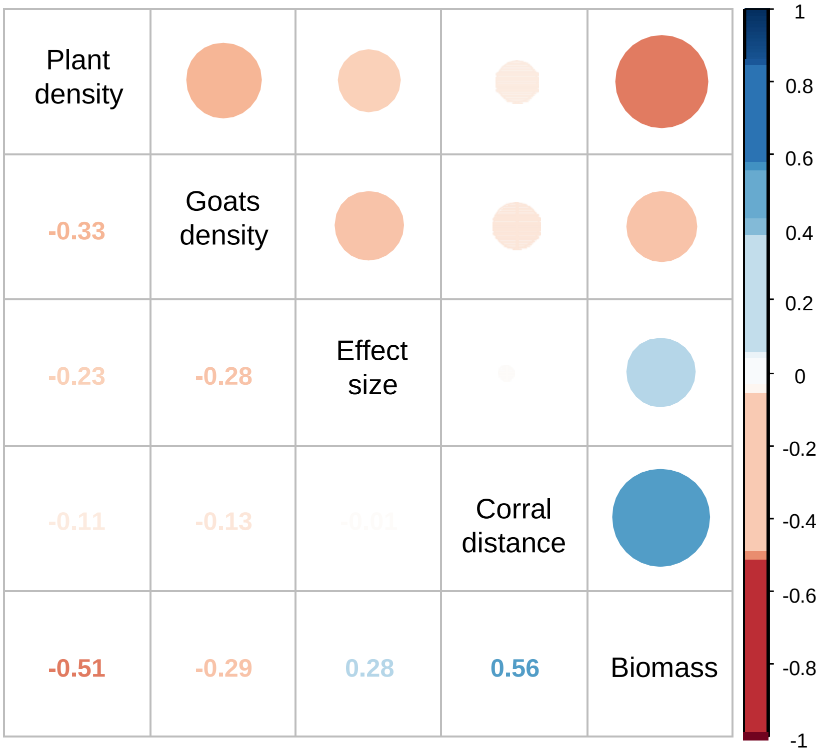

Figure 4: Correlations between the effect size of the herbivory by goats on functional traits of herbaceous plants and variables related to herbivores pressure (goats density and corral distance) and vegetation structure (woody plant density and herbaceous biomass) in a seasonally dry forest in Brazil.

Table 1: Results of paired t-tests comparing free access to goats (control) and fenced (exclosure) areas regarding Community Weighed Mean (CWM) of functional traits of herbaceous plants in a seasonally dry forest in Brazil. SLA - Specific Leaf Area, LDMC - Leaf Dry Matter Content, LT - Leaf Thickness, H*max* - Maximum height and ADI - Apical Dominance Index).

	CWM		
	t	**df**	**P**
SLA	-0.165	9	0.871
LDMC	0.652	9	0.530
LT	1.270	9	0.235
H*max*	**-3.000**	**9**	**0.014**
ADI	**2.959**	**9**	**0.015**

Table 2: Results of paired t-tests of functional diversity indices of herbaceous plants between fenced areas (exclosure) and free access to goats (control) areas in a seasonally dry forest in Brazil. FRic – Functional Richness, FEve – Functional Evenness, FDis – Functional Dispersion.

	t	**df**	**P**
FRic	-2.073	9	0.06*
FEve	0.326	9	0.75
FDis	2.403	9	**0.03**

SUPPLEMENTARY MATERIAL

List of measured functional traits and their respective biological significances.

Trait	**Functional role**
Specific leaf area – SLA	Leaves with high SLA tend to have high potential relative growth rate and low SLA correspond to high investment in structural defences and long leaf lifespan. Positively related with leaf nitrogen (N) concentration, and negatively with leaf longevity and C investment in defence.
Leaf dry-matter content - LDMC	Leaves with high LDMC tend to be relatively tough and assumed to be more physically resistant to herbivory and also tends to decompose more slowly. Correlate negatively with potential relative growth rate and positively with leaf lifespan.
Leaf thickness – LT	Plays a key role in determining the physical strength of leaves and is related also with chemical defences as latex.
Maximum height – *H*max	Competitive vigour, maximum potential.
Apical dominance index - ADI	Highly branched plants can be better defended against vertebrate herbivores, primarily by making feeding less efficient; 0 - no branched, >100 - extreme ramified.

4 CONCLUSÃO

World ecosystems are experiencing intensive land-use changes and conversion of natural areas into human-dominated landscapes. Among the major sources of disturbances is the livestock breeding which represent an important source as livelihood in tropical dry ecosystems. Introduced herbivores may affect a set of aspects from plant communities to ecosystem functioning. The thesis addressed the complexity of drivers shaping effects of large herbivores from individual to ecosystem level and highlighted interesting changes on plant communities after exclusion of introduced herbivores (goats) in Caatinga seasonally dry forests.

We proposed a conceptual framework to describe drivers influencing effects of herbivores at each ecosystem level and how different outcomes can be found according to interaction among such mediating factors. Some combinations of drivers such as high stocking rate in low productive and highly seasonal ecosystems are more likely to impose negative feedbacks on ecosystem productivity and functioning. We also emphasized that effects of herbivores can broadly varied between grasslands and trees-forbs systems in which local vegetation structure should be considered since contrasting changes on structural complexity able to influence effects on community and ecosystem may be expected in both systems. Understanding how such drivers are connected each other and produce different ecosystem trajectories can be a useful tool for biodiversity conservation and ecosystem management.

Our experimental findings suggested that introduced herbivores are important drivers of plant community assembly modifying both taxonomic and functional diversity. We found herbivores decreasing productivity and taxonomic and functional diversity of herbaceous plants. Moreover, their effects were mediated by seasonality of rainfall and time after exclosure. These results reinforce that in dry habitats, herbivory may promote negative feedbacks in productivity leading these ecosystems to less productive states, therefore threatening biodiversity maintenance and ecosystem services provision. Research efforts should be directed to assessment of vegetation responses in different grazing regimes and productivity variation within dry forests in order to access extensive livestock breeding viability in such vulnerable ecosystems.

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APÊNDICE A – LISTA DE ESPÉCIES DE PLANTAS

List of herbaceous species recorded in plots free access to goats (control) and fenced plots (exclosures) follow by occurrence number during study period (720 days) in the Catimbau National Park, Brazil.

FAMILY/SPECIES NAME	CONTROL	EXCLOSURE
ACANTHACEAE		
Ruellia		12.5
AMARANTHACEAE		
Amaranthaceae	12.5	12.5
Amaranthus viridis L.	12.5	
Gomphrena vaga Mart.	37.5	37.5
AMARYLLIDACEAE		
Habranthus sylvaticus Herb.	25	25
ASTERACEAE		
Ageratum conyzoides L.	12.5	12.5
Emilia sonchifolia (L.) DC. ex Wight		12.5
Lepidaploa chalybaea (Mart. ex DC.) H.Rob.	12.5	25
Sonchus	12.5	12.5
Tridax procumbens L.	25	50
BORAGINACEAE		
Boraginaceae	12.5	12.5
Heliotropium angiospermum Murray		12.5
BROMELIACEAE		
Bromeliaceae	12.5	
CACTACEAE		
Tacinga inamoena (K.Schum.) N.P.Taylor & Stuppy	87.5	100
Tacinga palmadora (Britton & Rose) N.P.Taylor & Stuppy	37.5	100
CYPERACEAE		
Bulbostylis capillaris (L.) C.B.Clarke	50	75
Cyperus	12.5	12.5
CLEOMACEAE		
Tarenaya	12.5	12.5
COMMELINACEAE		
Callisia		12.5
Commelina obliqua Vahl	75	75
Commelinaceae	12.5	12.5
CONVOLVULACEAE		
Evolvulus	12.5	12.5
EUPHORBIACEAE		
Cnidoscolus urens (L.) Arthur	37.5	37.5
Tragia		12.5
FABACEAE		
Aeschynomene martii Benth.	12.5	0

Aeschynomene viscidula Michx.	50	62.5
Chamaecrista rotundifolia (Pers.) Greene	37.5	62.5
Crotalaria		12.5
Indigofera suffruticosa Mill.	12.5	
Macroptilium	50	25
Stylosanthes viscosa (L.) Sw.	12.5	12.5
Zornia afranioi Vanni	50	62.5
MALVACEAE		
Herissantia crispa (L.) Brizicky	100	100
Herissantia tiubae (K.Schum.) Brizicky	37.5	62.5
Pavonia blanchetiana Miq.	12.5	12.5
Pavonia cancellata (L.) Cav.	12.5	
Pavonia varians Moric.	50	62.5
Sida cordifolia L.	25	
Sida galheirensis Ulbr.	87.5	100
Waltheria rotundifolia Schrank	12.5	
MOLLUGINACEAE		
Mollugo verticillata L.	62.5	62.5
NYCTAGINACEAE		
Boerhavia coccinea Mill.		12.5
ORCHIDACEAE		
Orchidaceae		37.5
PHYLLANTHACEAE		
Phyllanthus sp.		12.5
PHYTOLACCACEAE		
Microtea paniculata Moq.	25	50
OXILADACEAE		
Oxalis sp.	12.5	12.5
POACEAE		
Aristida sp;	12.5	50
Cenchrus ciliaris L.	37.5	75
Chloris sp.	75	62.5
Ichnanthus sp.	50	37.5
Poaceae sp.	12.5	12.5
Setaria sp.	12.5	12.5
Tragus berteronianus Schult.		12.5
Urochloa mollis (Sw.) Morrone & Zuloaga	100	100
PORTULACACEAE		
Portulaca elatior Mart.	87.5	100
Portulaca oleracea L.	75	87.5
Portulaca sp.		12.5
Talinum paniculatum (Jacq.) Gaertn.	62.5	75
PLUMBAGINACEAE		
Plumbago scandens L.	12.5	12.5
RUBIACEAE		
Ayenia erecta Mart. ex K.Schum.	12.5	25

Borreria sp.	12.5	12.5
Diodella teres (Walter) Small	50	37.5
Mitracarpus sp.	12.5	25
Richardia grandiflora (Cham. & Schltdl.) Steud.	62.5	50
SOLANACEAE		
Schwenckia americana Rooyen ex L.	12.5	12.5
Solanum americanum Mill.		12.5
Solanum rhytidoandrum Sendtn.	12.5	12.5
URTICACEAE		
Pilea hyalina Fenzl	12.5	12.5
TURNERACEAE		
Piriqueta sp.	25	25
Turnera diffusa Willd. ex Schult.	37.5	25
Turnera subulata Sm.	25	50

APÊNDICE B – LISTA DE ESPÉCIES HERBÁCEAS

List of herbaceous species used to functional traits measurements in areas free access to goats (control) and fenced areas (exclosures) in Caatinga dry forest, Brazil. Gray shadows indicate species occurrence within treatments.

Species	Treatment	
	Control	Exclosure
Aeschinomne viscidula	■	■
Aristida	■	■
Asteraceae	■	■
Ayenia		■
Boehavia diffusa	■	■
Chamaecrista rotundifolia		■
Cnidoscolus loefgrenii	■	■
Commelina	■	■
Cyperaceae		■
Dichanterium		■
Diodela teres	■	■
Fabaceae sp.		■
Gomphrena	■	■
Herissantia crispa	■	■
Herissantia tiubae	■	■
Ichnanthes	■	■
Macroptilium		■
Microtea paniculata	■	■
Pavonia	■	■
Plumbago	■	■
Portulaca umbriticola	■	■
Richardia	■	■
Sckwenckia	■	
Setaria		■
Sida cordifolia	■	
Sida galheirensis	■	■
Stilosanthes viscosa	■	■
Talinum	■	■
Tragia	■	■
Tragus	■	■
Urochloa	■	■
Zornia affranioi	■	■