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NATHÁLIA FERNANDES CANASSA

COBERTURA FLORESTAL E DEFAUNAÇÃO NA CAATINGA, O MAIOR NÚCLEO DE FLORESTA SAZONALMENTE SECA DA AMÉRICA DO SUL

João Pessoa,

Agosto de 2023

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Tese apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Zoologia) da Universidade Federal da Paraíba, como requisito parcial para a obtenção do título de Doutor em Ciências Biológicas.

Orientador: Prof. Dr. Helder Farias Pereira de Araujo

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Ata da 167ª Apresentação e Banca de Defesa de Doutorado de Nathália Fernandes Canassa

Ao(s) vinte e oito dias do mês de agosto de dois mil e vinte e três, às 14:00 horas, no(a) Ambiente Virtual, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a tese de doutorado de **Nathália Fernandes Canassa**, candidato(a) ao grau de Doutor(a) em Ciências Biológicas. A banca examinadora foi composta pelos seguintes membros: **Dr. Helder Farias Pereira de Araujo (Orientador - UFPB/PB); Dr. Juliano Bogoni (UNEMAT/MT); Dra. Lenyneves Duarte Alvino de Araújo (UFPB/PB); Dr. Pedro Cordeiro Estrela de Andrade Pinto (UFPB/PB); Dr. Bráulio Almeida Santos (UFPB/PB).** Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra ao(à) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Nathália Fernandes Canassa**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"Cobertura florestal e defaunação na Caatinga, o maior núcleo de floresta sazonalmente seca da América do Sul".** Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito Aprovado. Perante o resultado proclamado, os documentos da banca foram preparados para trâmites seguintes. Encerrados os trabalhos, nada mais havendo a tratar, eu, orientador(a), como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 28/08/2023.

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NATHÁLIA FERNANDES CANASSA

COBERTURA FLORESTAL E DEFAUNAÇÃO NA CAATINGA, O MAIOR NÚCLEO DE FLORESTA SAZONALMENTE SECA DA AMÉRICA DO SUL

Esta tese foi julgada e aprovada para obtenção do Grau de Doutor em Ciências Biológicas, área de concentração Zoologia no Programa de Pós-Graduação em Ciências Biológicas da Universidade Federal da Paraíba.

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Cobertura florestal e defaunação na Caatinga, o maior núcleo de floresta sazonalmente seca da América do Sul.

Resumo

As flutuações climáticas do Pleistoceno contribuíram para a grande extinção da megafauna, porém a presença de seres humanos na época acelerou para contribuição dessa grande extinção. Muitos desses animais eram herbívoros e contribuíam para funções ecológicas dentre elas, as relações mutualísticas. Esses animais exerciam a função de dispersores de sementes, permitindo a permanência de espécies de plantas em diversas regiões e contribuindo para composição de formações vegetacionais. No Domínio Caatinga, atividades no antropoceno, como a caça e a pecuária, vêm ocasionando perda na diversidade de espécies de mamíferos de médio e grande porte (defaunação), como o caso da anta (*Tapirus terrestre*), atualmente extinta na região, além de perda da diversidade de plantas. A perda dessas diversidades afeta as interações ecológicas como dispersão de sementes e estocagem de carbono. Para entender como a antropização tem interferido na Caatinga, fizemos 1) reconstruímos modelos de distribuição de vegetação florestal e vegetação aberta no domínio pelo algoritmo MaxEnt, avaliando efeitos do tipo de solo e de variações climáticas do Quaternário, com base na distribuição de aves florestais e fósseis da megafauna. Encontramos que a região exibiu áreas de clima e solo capazes de suportar mais cobertura florestal do que atualmente existe, restando apenas 4,34% desse tipo vegetacional; 2) verificamos a predição da defaunação e o efeito de downsizing causado pela mesma utilizando o algoritmo MaxEnt e a distribuição espacial das espécies perdidas, bem como os fatores subjacentes que contribuem para o seu declínio através do algoritmo Random Forest. Encontramos uma drástica defaunação, com ~80% das espécies extintas localmente, suportando o efeito downsizing, sendo a caça o principal indicador para esse declínio; e por último 3) verificamos a relação entre plantas zoocóricas com remoção de carbono e biomassa acima do solo, a relação de riqueza de mamíferos frugívoros de médio e grande porte e a defaunação com remoção de carbono, gerados por modelos lineares generalizados. Encontramos relações positivas com dados de plantas zoocóricas e riqueza de mamíferos frugívoros. Resultados que vão contribuir para a conservação da biodiversidade do domínio considerando os efeitos das mudanças climáticas e das atividades humanas que impactam a região de forma não sustentável.

Palavras-chave: antropoceno, aves, carbono, mamíferos e plantas zoocóricas.

Abstract

Pleistocene climatic fluctuations contributed to the great extinction of the megafauna, but the presence of human beings at the time accelerated the contribution of this great extinction. Many of these animals were herbivores and contributed to ecological functions, amongst them, mutualistic relationships. These animals acted out as seed dispersers, allowing plant species to remain in different regions and contributing to the composition vegetation formations. In the Caatinga domain, activities in the Anthropocene such as hunting and livestook raising have been causing a loss in the diversity of species of medium and large mammals, as the case of the tapir (*Tapirus terrestre*) is currently extinct in the region, in addition to loss of plant diversity. The loss of these diversities affects ecological interactions such as seed dispersal and carbon storage. To understand how anthropization has interfered in the Caatinga, we did 1) we reconstruct distribution models of forest vegetation and open vegetation in the domain by the MaxEnt algorithm evaluating effects of soil type and Quaternary climate variations, based on the distribution of forest birds and fossils of the megafauna. We found that the region exhibited areas of climate and soil capable of supporting more forest cover than currently exists, with only 4.34% of this vegetation type; 2) we verified the prediction of defaunation and the downsizing effect caused by it using the MaxEnt algorithm and the spatial distribution of lost species, as well as the underlying factors that contribute to their decline by the Random Forest algorithm. We found a drastic defaunation, with ~80% of species extinct locally, supporting the downsizing effect, with hunting being the main indicator for this decline; and 3) we verified the relation between with carbon removal and aboveground biomass, the relation richness of medium and large frugivorous mammals and defaunation with carbon removal, generated by generalized linear models. We found positive relationships with zoochoric plant data and richness of frugivorous mammals. Results that will contribute to the conservation of the domain's biodiversity, considering the effects of climate change and human activities that impact the region in an unsustainable way.

Key words: anthropocene, birds, carbon, mammals and zoochoric plants.

Sumário

Introdução geral

As flutuações climáticas do quaternário correspondem às mudanças climáticas de um passado relativamente recente (Aleixo *et al.*, 2010). A extinção em massa da megafauna nessa época associadas tanto às alterações climáticas como as ações humanas, reduz funções ecológicas (Barnosky *et al.*, 2004; Lima-Ribeiro e Felizola Diniz-Filho, 2013). Existem evidências de que as mudanças climáticas causadas por ações antropogênicas estão impactando os sistemas biológicos em todo o mundo (Hoffmann *et al.*, 2019; Yeakel *et al.*, 2014). A interação do homem com a biodiversidade tem provocado impactos severos na fauna e na flora ao redor do planeta (Silva 2004). Os impactos não ocorrem só diretamente devido ao desmatamento, à pecuária e à caça (Barboza *et al.*, 2016), mas tem acelerado processos climáticos indiretamente durante o período conhecido como Antropoceno (Silva, 2004). Na Austrália, por exemplo, alterações na duração de períodos de secas, incêndios florestais, doenças, temperaturas extremas e condições das chuvas estão sendo associadas às mudanças climáticas causadas por ações antropogênicas (Hoffmann *et al.*, 2019).

Embora períodos de estiagem sejam eventos climáticos naturais em regiões semiáridas, a Caatinga, região semiárida localizada no nordeste brasileiro, sofreu uma das maiores estiagens recentemente, entre 2012 e 2017 (Marengo *et al.*, 2013; Marengo, Torres e Alves, 2017). No entanto, mesmo durante esse período, áreas naturais atuaram como sumidouro de carbono tanto na curta estação chuvosa como na estação seca (Mendes *et al.*, 2020). Desse modo, mesmo em períodos críticos, florestas secas na Caatinga retiram gases de efeito estufa da atmosfera e os armazenam. Possivelmente, a manutenção de grandes áreas naturais na região foi responsável por uma estabilidade de sua distribuição durante mudanças climáticas do Quaternário (Werneck *et al.*, 2011). No entanto, atualmente, florestas na Caatinga encontram-se distribuídas em pequenas manchas, abrigando, por exemplo, espécies de aves endêmicas em populações separadas (Araujo e Silva, 2017). Ainda, a manutenção de florestas tropicais está fortemente associada às interações entre animais e plantas, como dispersão de sementes e, portanto, a perda dessas interações afeta essa manutenção (Camargo-Sanabria *et al.*, 2014).

Durante o Antropoceno, animais que hoje vivem em outras regiões do Brasil foram totalmente extintos em várias localidades na Caatinga, como é o caso de *Tapirus terrestre* (anta), *Myrmecophaga tridactyla* (tamanduá-bandeira), *Panthera onca* (onça pintada), *Dicotyles pecari* (queixada) (Barboza *et al.*, 2016; Feijó e Langguth, 2013). Há também animais cujas populações vêm sendo reduzidas ao longo dos anos, como é o caso de *Pecari tajacu* (porco do mato), *Cuniculus paca* (paca), *Nasua nasua* (quati), *Alouatta belzebul* (guariba) (Barboza *et al.*, 2016; Feijó e Langguth, 2013). Um dos principais motivos dessas extinções é a caça (Barboza *et al.*, 2016). Além da caça, a pecuária e o desmatamento também estão associados a essas extinções e redução populacional desses animais (Alves *et al.*, 2016). Além da megafauna, muito desses animais atuam como dispersores de sementes e a perda deles também afeta a manutenção de áreas florestais e serviços ecossistêmicos como a remoção de carbono.

Nesse contexto, a proposta dessa tese é explorar três objetivos associados à relação entre a diversidade de fauna e a distribuição da vegetação na Caatinga. 1) O primeiro capítulo tem como objetivo reconstruir e avaliar os efeitos do tipo de solo e de condições climáticas na distribuição potencial de florestas e vegetação aberta, com base na distribuição atual de aves florestais e na distribuição de fósseis de grandes herbívoros pastadores. 2) O segundo capítulo tem como objetivo predizer a extensão da defaunação de mamíferos de médio e grande porte e o efeito downsizing ocasionado por ela e quais fatores contribuem para a defaunação. 3) O terceiro capítulo tem como objetivo testar se há relação de plantas zoocóricas com biomassa acima do solo e remoção de carbono, bem como se há relação da riqueza atual e da defaunação de mamíferos frugívoros de médio e grande porte com a remoção do carbono. Os capítulos estão organizados no formato de artigos a serem publicados em periódicos científicos.

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CAPÍTULO 1

Submited to Scientific Reports

Human disturbance the major driver of vegetation changes in the Caatinga dry forest region and climate conditions can exacerbate them.

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Human disturbance the major driver of vegetation changes in the Caatinga dry forest region and climate conditions can exacerbate them.

Abstract

Drastic changes in vegetation structure caused by exceeding ecological thresholds have fueled the interest in tropical forest responses to climate and land-use changes. Here, we examine the potential successional trajectories experienced by the largest dry tropical forest region in South America, driven by climate conditions and human disturbance. We built potential distribution models for vertebrate taxa associated with forest or shrub habitats to estimate natural vegetation cover. Distribution patterns were compared to current vegetation across the entire region to identify distinct forest degradation levels. Our results indicate the region has climatic and soil conditions suitable for more forest cover than is currently found, even in some areas with limited precipitation. However, 11.04% of natural cover persists across such an immense region, with only 4.34% consisting of forest cover. Forest degradation is characterized by the dramatic expansion of shrubland (390%), farming, and non-vegetation cover due to changes in land-use, rather than climatic conditions. Although different climate conditions have been the principal drivers for natural forest distribution in the region, forest seems unable to resist the consequences of land-use changes, particularly in lower precipitation areas. Therefore, land-use change has exceeded the ecological thresholds for the persistence of forests, while climate change may exacerbate vegetation type transitions

Introduction

Climate and land-use change are expected to drastically alter patterns of natural vegetation cover, particularly in the tropics [1–3]. This emerging trend is not just related to the replacement of natural vegetation by other types of anthropogenic land-uses (e.g., agriculture, pasture, urban areas), but is also related to drastic changes in vegetation structure and functionality as ecological thresholds (i.e., tipping points) are exceeded [4–6]. In general, projections indicate dry forests may be replaced by deserts (bare soils) in response to reduced precipitation and increased human disturbance, such as habitat loss and fragmentation, logging, harvesting of forest products, fire, and other chronic disturbances [7]. Such trajectories are expected to change the ability of natural vegetation to deliver ecosystem services, with impacts on both regional and global sustainability. Accordingly, there has been increasing interest in the drivers of changes in vegetation cover and their local- and global-scale effects, including the relative contribution of both climate and local human pressure on native vegetation.

Drylands have been expanding across the globe since 1960s, and are projected to expand further throughout the 21st century under future climate changes [8–10] [11]. This transition towards treeless vegetation states is argued to emerge as a result of reductions in precipitation [12,13]. However, such projections are based on the associations between present-day tree cover distribution and precipitation data, without the consideration of anthropogenic pressures, which may lead to a misinterpretation of the importance of climate for the distribution of natural semiarid vegetation, i.e. precipitation being assumed to be the main driver determining the distribution of natural vegetation in dry forests, when long-term anthropogenic land-use is a critical factor [14]. When ecohydrological characteristics and plant physiological regulations in natural drylands are considered, adverse effects of warming and drying can be mitigated by reducing water losses from soils [15,16]. Therefore, the real contribution of land-use and climate conditions to current and future changes in natural vegetation cover needs to be verified at the local- and regional-scale for drylands.

Land-use change has converted 50% of the world's natural land cover over the last 300 years [17]. Drylands in the Neotropics, for instance, are old colonization frontiers that are mostly covered by second-growth vegetation [18]. Empirical data suggests that long-term land-use has reduced the resilience of the remaining natural vegetation in semiarid regions, with the rainy season offering little in the way of a boost to rates of recovery [19]. Landscape structure also plays a major role in controlling and defining successional vegetation trajectories in dry tropical regions, as faster recovery occurs in sites surrounded by higher forest cover [20]. Therefore, in addition to desertification, second-growth vegetation can represent a degradation-driven alternative stable state in dry forest regions [21]. Forest degradation is defined as a state of anthropogenically-induced arrested succession, where ecological processes that underlie forest dynamics are disturbed or severely constrained [22]. Consequently, alternative stable states via forest-to-shrub conversions can be found [23], and these phenomena can mask the real interaction between climate and natural vegetation cover in semi-arid regions.

The Caatinga region is one of the most populated and biodiverse seasonally dry tropical forests (SDTF) globally, which has undergone intense transformations (including desertification) over the past five centuries, increasing its vulnerability to climate change [24]. Historical records from the 18th and 19th centuries demonstrate that the Caatinga was characterized by extensive dry forests with high levels of biodiversity [25,26]. However, slash-and-burn agriculture, free-ranging livestock, exploitation of forest products, and cycles of intensive agriculture (e.g., cotton) have converted large tracts of old-growth forest into vegetation mosaics dominated by shrubby vegetation and regenerating forest stands, areas of bare soil, and agricultural fields and pastures, across extensive areas during the 20th and 21st centuries [27]. Based on remote sensing data, some estimates suggest that the Caatinga has more than 60% natural vegetation cover [28,29], but these estimates consider all shrubland as natural vegetation and do not consider historical forest degradation caused by forest-to-shrub conversions (Table 1). Thus, the potential ecosystem services provided by undisturbed natural vegetation may be underestimated in the Caatinga, since soil and vegetation carbon stocks drop drastically following land-use change, even from dry forest to shrubland, for instance [30]. Nevertheless, we recognize that distinguishing between degradation-induced forest-to-shrub conversion and undisturbed natural shrubland is hard, since this is also a natural vegetation type throughout the region, remains a challenge.

In this context, paleoecological patterns (including faunal composition) can provide insights into the relationships between climate and natural vegetation types [31]. Due to past climate change, larger-sized mammals were narrowly distributed across scattered patches of suitable habitats in South America throughout the late Quaternary [32]. In the Holocene, the loss of larger-sized mammal lineages was related to the decrease of open vegetation areas and an increase in dry forests in South American semiarid regions [33]. On the other hand, the life-history traits by current endemic bird species associated with different vegetation types (forest or shrubland, for instance) supports the occurrence of a natural gradient from forest to open vegetation composing the original cover in South American drylands [34]. However, some current species associated with open vegetation are able to increase their distribution because they benefit from anthropogenic disturbance, and, therefore, these contemporary changes hamper efforts to identify current patterns of natural vegetation distribution.

Here, we (1) estimate the potential distribution of natural Caatinga vegetation cover, considering climate and soil; (2) estimate land-cover change; and (3) identify the relative contribution of human and climate as drivers of these land-cover changes. Three questions guided the study: (a) What would the expected distribution of dry forest and shrubland be in the absence of acute human disturbance? (b) How much of the natural distribution has been modified? (c) What are the relative contributions of human activities and climate conditions to vegetation change in distinct degradation transitions (forest to shrub, forest/shrub to farming, forest/shrub to non-vegetation) (Table 1)? To answer these questions, we used potential distribution models of strictly forest-dependent endemic birds as a proxy of forest habitats and potential distribution models of extinct larger-sized mammals for LGM, projected to current climate conditions, as a proxy of shrubland distribution across the region. Further, (1) these models were contrasted with the present-day vegetation across the entire region, and (2) the documented vegetation changes were contrasted with anthropogenic and climatic variables.

Results

Potential vegetation distribution

Our vegetation distribution models indicated high probability of potential forest distribution stretching across the south, center, and west of the Caatinga region, and patches in the east. On the other hand, our models indicated a high probability of shrub habitats occurring in the Caatinga, particularly in the center and east of the region (Figure 1) (Supplementary Figure S1). All models were influenced by environmental variables, with area under the curve (AUC) values greater than 0.8 for all models (i.e., a non-random distribution of vegetation types). Of the environmental variables we assessed, mean temperature of wettest quarter (25.3%), temperature seasonality (16.9%), and annual precipitation (13.5%) were the most important, explaining 55.7%

of forest distribution. While annual precipitation (57.3%) and annual mean temperature (10.7%) explained 68% of the distribution of shrub habitats (Supplementary Table S1).

Change in vegetation cover

Considering the spatial limits of the Caatinga biota (i.e., 863,752 km^2), we predicted a total potential area of 731,211 km² for forest cover, and 132,195 km² for shrub cover, which correspond to approximately 84.6% and 15.3% of the entire region, respectively. However, our analysis of present-day cover indicated that only 31,793 km² is covered by forest, 63,639 km² by natural shrubland, and 766,235 km² by degraded vegetation (452,128 km² by forest to shrubland, 300,822 km² by forest/shrubland to farming, and 13,284 km² by non-vegetation cover) (Figure 2). These scores indicated an extensive loss of forest, i.e., only 4.34% of their potential distributions remaining. On the other hand, shrubland has expanded by 390% by grouping undisturbed natural shrubland and forest to shrubland change (Figure 2). Furthermore, 35% was modified to farming and 1.6% to non-vegetation cover; i.e desertification areas.

Drivers of vegetation cover change

Our random forest model predicted c. 73% ($R^2 = 0.73$, MAE = 0.14, RMSE = 0.20) vegetation cover change. Human footprint was the variable with the highest relative importance (100%), consistently appearing in all models and in the best performing model. On the other hand, climatic variables (precipitation seasonality, annual precipitation, and temperature seasonality) contributed less than 15% each (Figure 3). However, the highest degradation levels were weakly associated with areas where current temperature seasonality is higher, annual precipitation and precipitation seasonality are lower (Supplementary Figure S2).

Discussion

Our results indicate that the Caatinga has climatic and soil conditions able to support more forest cover than is currently found throughout the region, regardless of the current occurrence of low-precipitation areas (Supplementary Figure S3). However, our estimates indicate that only 11.04% of native vegetation cover persists across the whole region, with only 4.34% being forest cover. On the other hand, forest degradation is characterized by the dramatic expansion of shrubland (390%), farming, and non vegetation cover due to changes in land-use, rather than climatic conditions. Climate conditions have been the major driver for forest and natural shrubland distribution in the Caatinga region, with areas climatically suitable for both vegetation types. However, forest seems unable to resist the consequences of land-use changes, particularly in those areas where the temperature seasonality is high and annual precipitation is low. Therefore, the percentage of land-use change has exceeded ecological thresholds (i.e., tipping points) for the persistence of forest, while further climate changes can exacerbate this. The patterns we have uncovered highlight the resistance the Caatinga has to different climatic conditions, while reinforcing the protagonism of land-use change as the main driver of the rapid decline in forest cover and the proliferation of reduced tree-cover vegetation types such as shrublands.

Although our approach was able to identify the potential forest distribution across areas with past forest occurrence, confirmed by historical records from the 18th and 19th centuries [25,26], it is worth mentioning the potential limitations of the model sensitivity. Even using climate extremes and soil variables to predict potential vegetation distribution cover at a regional scale (Supplementary Table S2), local conditions may support particular vegetation types, which are not detected by regional-level assessments. However, our findings indicated that the forest and shrubland could potentially occur across a wide range of climate conditions, which naturally reduces the protagonism by local conditions (particularly soil conditions) as the main driver of vegetation type. This perspective is supported by the present-day occurrence of Caatinga dry forest across a wide range of soil conditions, such as deep sandy soils to shallow and clay-based relatively rich soils.

Globally, precipitation and water availability are the major drivers of vegetation distribution [35] by controlling biological processes from plant physiology to ecosystem dynamics and structure [36]. In the Caatinga region, the precipitation regime is mainly associated with warm and humid air masses coming from the west (Continental Equatorial), southeast (Atlantic Tropical), and north-northeast (Atlantic Equatorial), as well as with the relief which contributes to the occurrence orographic rains [37]. The Caatinga biota dates back to the Miocene and since then it has experienced climate changes [38,39]. Moreover, the Caatinga dry forest stretches over a wide spectrum of soils and precipitation conditions, which results in gradients of water availability occurring from local to regional spatial scales. In addition to successive climate changes, the Caatinga biota has long been exposed to frequent droughts, commonly associated with

El Niño Southern Oscillation events [40]. This evolutionary and ecological context has probably favored plant lineages able to cope with increased ecological filtering such as those with conservative resource-use strategies, high plasticity, and the ability to resprout as previously documented [41]. However, the Caatinga has been submitted to intense human disturbances since the arrival of Europeans in the 16th century [42]. We refer to an immense package of disturbances including slash-and-burn agriculture, extensive cattle raising, and the exploitation of forest products. Such disturbance is varied and intense including the collection of firewood, wood for charcoal production, timber and fodder, plus the periodic cycles of commercial agriculture devoted to commodities such as cotton [43–45]. In fact, the resistance of the Caatinga to different climatic conditions and its ability to cope with climate oscillations through time has been considered a key asset in a global change scenario [46]. This perspective highlights the particular ways tropical biotas may respond to climate change and climatic tipping points. However, this apparent resistance to climate oscillations, has not been sufficient to resist local human disturbances, resulting in the expansion of shrublands and deserts [47].

Our findings confirm land-use change as the main driving force of forest loss and distinctive successional trajectories towards shrublands and anthropogenic-induced deserts. This trajectory affects ecosystem services provided by the natural vegetation cover, such as soil/vegetation carbon stocks, which drastically drop in the case of biomass, when forest, for example, is converted to shrublands [30]. [4647]Present-day satellite data indicates [48]that aboveground forest biomass can reach 80–130Mg/ha in the Caatinga, but such a high-biomass forest covers only about 7% of the region today, while 73% of its area support aboveground biomass < 40 Mg/ha [48]. Landscape-level data obtained through direct measurements have also found reduced aboveground forest biomass across successional mosaics resulting from slash-and-burn agriculture [27], with several sites exhibiting low rates of biomass recovery (i.e. reduced resilience). We refer to secondary/regenerating forest stands (up to 70-yr old) limited to 50 Mg/ha on average [49][48]. In fact, dry forest regeneration and dynamics are influenced by local land-use and landscape context, where long-term land-use affects the potential for recovery, particularly when soils are degraded [50], regeneration mechanisms (e.g. seeds and sprouts) are compromised, and sites are located far from old-growth forest patches [19,20]. In other words, forest persistence has already been compromised across the majority of the Caatinga region, because more than 90% of the potential forest distribution has already been modified, as a result of disruptions in forest regeneration mechanisms at regional scale. This scenario demands active forest restoration initiatives across the entire region, if society is to have any chance of protecting the irreplaceable biodiversity and ecosystem services of the Caatinga.

Considering the socioecological context of the Caatinga, with the prevalence of subsistence farming, we argue that this transition of dry forests naturally dominated by single-stem tree species towards deserts (i.e. bare soils) or vegetation type dominated by multi-stemmed shrubs (here defined as shrubland) is a response by the forest ecosystems to a continuous exposition to conversion into pastures[17,51], slash-and-burn agriculture [52], shifting cultivation [27,53], coppicing [23], and browsing by livestock [45,54] , as well as the exploitation of forest products. Such an alternative successional trajectory is not exclusively related to tree species replacement by shrub species, but also by the predominance of tree species occurring as multi-stem shrub-sized individuals, as is already occurring with almost all dominant tree species in human-modified Caatinga landscapes. [55][5657]Such forest transition towards shrublands as an alternative successional trajectory has been previously proposed for other dry forests exposed to intensive land use [58]. However, to what extent regeneration favoring shrubs rather than trees (one of the stages towards human-induced desertification in the Caatinga) meets the concept of alternative stable states, remains to be investigated.

In synthesis, natural cover in the Caatinga has been replaced by deserts [47] and shrublands due to historical and current anthropogenic land-use. Land-use intensification is already causing tree cover and aboveground biomass decline, not only due to deforestation, but also due to changes in the structural status of the remaining vegetation, such as the spread of shrublands, at the expense of forests. This transition toward treeless land cover reduces ecosystem services, as is already occurring in tropical dry forests around the world (i.e. forest degradation), affecting billions of people that directly depend on forest products and their regulating services [7,12,58]. Although much attention has been given to the occurrence of potential precipitation thresholds which, if exceeded, may permanently reduce tree cover and biomass, comparatively little attention has been paid to land-use intensification, which is already causing fast declines in tree cover and biomass. However, climate change may be a synergistic force that will intensify (where precipitation is reduced and drought events are more frequent) or retard (where precipitation increases) regeneration dynamics representing alternatives trajectories in human-modified landscapes.[15] In this context, it might be misleading to adopt current patterns of vegetation distribution across human-modified landscapes as a reliable indicator to infer vegetation sensitivity to climate change. Finally, we propose that landscapes composed of a combination of forests and crop and/or cattle farming may allow high food productivity, biodiversity, and ecosystem services, even during extreme drought events [59,60]. However, dry forest restoration and adoption of better practices to prevent further degradation are urgently needed to help the recovery of ecosystem productivity and resilience for the sake of global sustainability.

Methods

Study area

The Caatinga region in northeast Brazil is one of the world's largest SDTFs [61], which originally covered almost one million km^2 [62]. This biota is restricted to the Brazilian territory, and it covers crystalline basement surfaces and sand sedimentary basins supporting flattened surfaces cut by narrow valleys, residual hills, and high-altitude plateaus (Supplementary Figure S4). Soil types are diverse, ranging from shallow, rocky and quite fertile to deep, sandy and unfertile. The climate is classified as BSh (hot semi-arid) and As (with dry summer) across most of the region [63]. Most of the rainfall is concentrated in three consecutive months, but the region experiences spatial and annual variations. Due to the great inter-annual variability of precipitation, droughts can endure for years [37].

At the regional level, the Caatinga dry forest was originally a vegetation mosaic dominated by dry forest stands of varying structure (high- to low-statured forests) [64], which also supported enclaves of both semideciduous rainforest and Cerrado (i.e. Brazilian savanna), particularly due to the occurrence of patchy orographic rain. The Caatinga dry forest is highly diverse, with levels of species endemism ranging from 5% to 25% [64]. This unique biota has been intensively modified since the arrival of Europeans in the 16th century by a combination of (1) slash-and-burn agriculture, (2) cycles of intensive agriculture devoted to commodities across particular sites, (3) free-ranging livestock (principally goats and cattle), and (4) exploitation of forest products, such as firewood for domestic use and for charcoal production, fodder, and poles for farming facilities [43]. Rural smallholdings are prevalent throughout the region, with residents' livelihoods depending on natural resources and ecosystem services such as nutrient provision for subsistence agriculture

To address our questions, three complementary and integrative steps were performed as described below.

Potential distribution of forest and shrub vegetation

The potential forest and shrub distribution at biota scale under current climatic conditions was estimated using (1) taxa associated with forest habitats under present climate conditions, and (2) vertebrate taxa associate with open vegetation during the Last Glacial Maximum (LGM; 21 ka BP). More precisely, we used records of strictly forest-dependent endemic bird species as a proxy, since these species do not benefit from anthropogenic changes in the landscape. In the Caatinga, 31% of bird species are forest-dependent and such habitat filtering reduces the influences of spatial dynamics associated with the conservation status of the region [34]. Our database consisted of occurrence records of six endemic bird species: *Conopophaga cearae, Hylopezus ochroleucus, Xiphocolaptes falcirostris, Lepidocolaptes wagleri, Phylloscartes roquettei, Arremon franciscanus*. Species' occurrences were retrieved from the avifauna literature and the following online databases: Global Biodiversity Information Facility (Gbif - https://www.gbif.org), Species link (http://www.splink.org.br), and Wikiaves (https://www.wikiaves.com.br).

We did not use present-day endemic species to model open vegetation cover because these species can benefit from anthropogenic processes that reduce forest cover [34]. Therefore, we used extinct megafauna occurrences in the Caatinga to model potential shrub-dominated environments. Occurrences of megafauna taxa that lived at the end of the Pleistocene were collected from papers on animal paleoecology. The interpretations of paleoecology were based on dental morphology and studies involving carbon isotopes. Taxa were selected based on literature focusing on grazing behavior, C4 plant-based diets (grasses), and occurrence in open areas (Supplementary Table S3). Our database consisted of occurrence records of eight species: *Equus neogaeus, Glossotherium sp., Glyptodon clavipes, Glyptotherium cylindricum, Pampatherium humboldtii, Panochthus greslebini, Panochthus jaguaribensis,* and *Xenorhinotherium bahiense*. The occurrences of the species were collected from bibliographic surveys of fossil findings in the Caatinga, paleontology collections (Department of Geology of the Federal University of Pernambuco, Vertebrate and Paleontology Laboratory of the Federal University of Paraíba), Federal University of Bahia (from Prof. Dr. Mario Dantas), and Paleobiology networks (https://www.paleobiodb.org).

Distribution modeling was carried out using 393 geographic points in the Caatinga region, 196 from forest cover indicators under current climatic and soil conditions, and 197 from shrub environment indicators under LGM (21 ka BP) climatic conditions. We used 19 climatic variables obtained from Worldclim (www.worldclim.org) and PaleoClim (www.paleoclim.org). The climatic variables used to model forest cover, obtained through present-day forest bird occurrence, were selected after an autocorrelation analysis of the current climatic conditions in the Caatinga region. Variables used for shrub environments, were selected after an autocorrelation analysis of the LGM climatic conditions (Supplementary Table S2). We included in the models the variables with a correlation < 0.8 to avoid redundancy of climatic variables. We used Pearson's correlation, calculated using the *Vegan* package for R (version 3.5.3). Physical soil properties (Clay and Sand content in g/kg) also were used as variables to model current forest cover. These variables were obtained from digital soil mapping (SoilGrids) based on a global compilation of soil profile data (WoSIS) and environmental layers (www.soilgrids.org). Further information about the SoilGrids and WoSIS projects is available on isric.org.

The distribution models were generated with the Maximum Entropy (Maxent) algorithm [65], which models a probability distribution where each grid cell has predicted suitability of conditions, from a set of environmental variables and georeferenced occurrence records. The highest value of area under the curve (AUC) was used to select the best models. An AUC ≥ 0.75 indicated that the modeled distribution was not random but influenced by environmental variables. We use Receiver Operator Characteristic statistics (ROC) to assess model accuracy with 10 repetitions of 10,000 interactions, with 10% of replicas being randomly selected as test data and the remaining 90% used for model training in each replica.

To map the potential distribution of natural vegetation cover, we summed the raster file of the current potential distribution of forest with the reprojected raster file of the current potential distribution of shrubs, derived from the LGM model. For that, we reproject the LGM model to the current climate scenario using Maxent and used the raster calculator to multiply the likelihood of shrub occurrence by -1. So, we summed the positive probability (0 to 1) for the potential distribution of forest with the negative probability (0 to -1) that represents the potential distribution of shrub environments.

Estimating vegetation cover change

To assess regional changes in vegetation cover, the potential distribution of forest and shrub vegetation for current conditions were compared with present-day vegetation cover, assessed by MapBiomas[29] for the year 2021. We use current forest-bird occurrence data to calibrate the threshold expected of the probability distribution of forest, transforming the raster file of the potential distribution of natural vegetation covers into a binary map (forest vs shrub). This binary map was compared with MabBiomas land-use and land-cover type, and the difference was categorized in forest degradation levels (0 – no change, when forest or shrub remained in Forest and Savanna Formation by MapBiomas, respectively; 1 – forest to shrub, when Savanna Formation occur where forest was predicted; 2 - forest/shrub to farming, when Pasture or Agriculture occur where forest or shrub was predicted; 3 - forest/shrub to non-vegetation, when Non-Vegetated Areas occur where forest or shrub was predicted (Table 1).

Drivers of vegetation cover change

To identify the relative contribution of human and climate as drivers of the land-cover changes, we used a hexagonal grid covering the entire Caatinga. We use 12,976 hexagons with a side of 5km (area 64.95 km^2), and statistical zonal to obtain information from degradation level as response variable and human footprint and climate as predictor variables. The degradation level raster was obtained from the previous step, where each pixel (30 × 30m) has a value between 0 and 3 (0 – no change, 1 – forest to shrub, 2 - forest/shrub to farming, 3 - forest/shrub to non-vegetation). The Human Footprint (hfp) was used as a human pressures variable and was obtained from global map terrestrial Human Footprint[66] (1 km^2 resolution). The Human Footprint map indicates human pressure weighted within that range according to estimates of their relative levels of human pressure for the extent of built environments, population density, electricity infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways[66]. Climate variables used as predictors were precipitation seasonality (pss), annual precipitation (pre), temperature seasonality (tss), max temperature (tma), and min temperature (tmi) (1 km^2 resolution). These climate data were obtained from Worldclim[67]. We extracted the mean value of each variable from each hexagon (Figure 4).

To evaluate the relationship between the predictor variables and the response variable, we used the Random Forest (RF) predictive analysis (Predictive Model with Machine Learning)[68]. In general, the RF algorithm is robust and one of the most used in predictive model analysis. It has few assumptions and data pre-processing and generation of predictive models with high performance, designed to avoid overfitting[68]. Through decision tree algorithms, RF produces classifications or regression models, as in the case evaluated here. Tuning of the model parameters was carried out to increase the performance of the model. In our RF analysis, hfp, pss, pre, tss, tma, and tmi are used as predictor variables and degradation level (0 to 3) as the response variable. Analyses were performed using the caret package in R[69].

To evaluate the performance of the models, RMSE (Root Mean Square Error), R^2 and MAE (mean absolute error) were used. We selected the best model using the bestTune and finalModel functions from the caret package. In the final model, the selected variables are organized in order of importance. The importance of the variable is a value that measures the number of times the performance of the model increased when a specific predictor was included in the model. Therefore, the importance of the variable is closely related to the performance of the model and the relative values are scaled between 0 and 100 [69].

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Author contributions

HFPA and CCCM conceived the ideas; HFPA, NFC, and CCCM analyzed the data; all authors drafted and included relevant intellectual contributions to improve and conclude the manuscript.

Additional Information (including a Competing Interests Statement)

The authors do not have any competing interests.

Legends

Main table

Table 1: Ground and aerial views of the land-uses and land-covers (LULC) found in the Caatinga region. The LULC types used in this paper were classified in degradation levels (italic) and contrasted with LULC types derived from current satellite data (MapBiomas [29]).

Main figures

Figure 1 Potential distribution of forest and shrubland in the Caatinga for current climatic and soil conditions.

Figure 2 Distribution and amount of each forest degradation level in the Caatinga region. Forest degradation is defined as a state of anthropogenically induced arrested succession, where ecological processes that underlie forest dynamics are diminished or severely constrained [22].

Figure 3 Importance values of human footprint (hfp) and climate variables on the forest degradation in the Caatinga region. Importance values were calculated based on a Random Forest model that explained 73% of the variation in the data. Climate variables were: precipitation seasonality (pss), annual precipitation (pre), temperature seasonality (tss), max temperature (tma), and min temperature (tmi).

Figure 4 Distribution of the degradation levels (as a response variable) and human pressure and climate variables (as predictor variables) in the Caatinga region. The relationship between the predictor variables and the response variable was evaluated using a Random Forest predictive model (see results and Fig.3).

Data availability

The datasets used in this study are available from the corresponding author upon reasonable request.

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Table 1: Ground and aerial views of the land-uses and land-covers (LULC) found in the Caatinga region. The LULC types used in this paper were classified in degradation levels (italic) and contrasted with LULC types derived from current satellite data (MapBiomas [29]).

View		**LULC Type**	
Ground	**Aerial**	**Present paper**	**MapBiomas**
		Forest (*no change*)	Forest formation
		Shrub (*no change*)	Savanna Formation
		Forest to Shurb (*degradation – level 1*)	Savanna Formation
		Forest/Shurb to Farming (*degradation – level 2*)	Pasture or Agriculture
		Forest/Shurb to non vegetation (*degradation – level 3*)	Other non Vegetated Areas

Figures

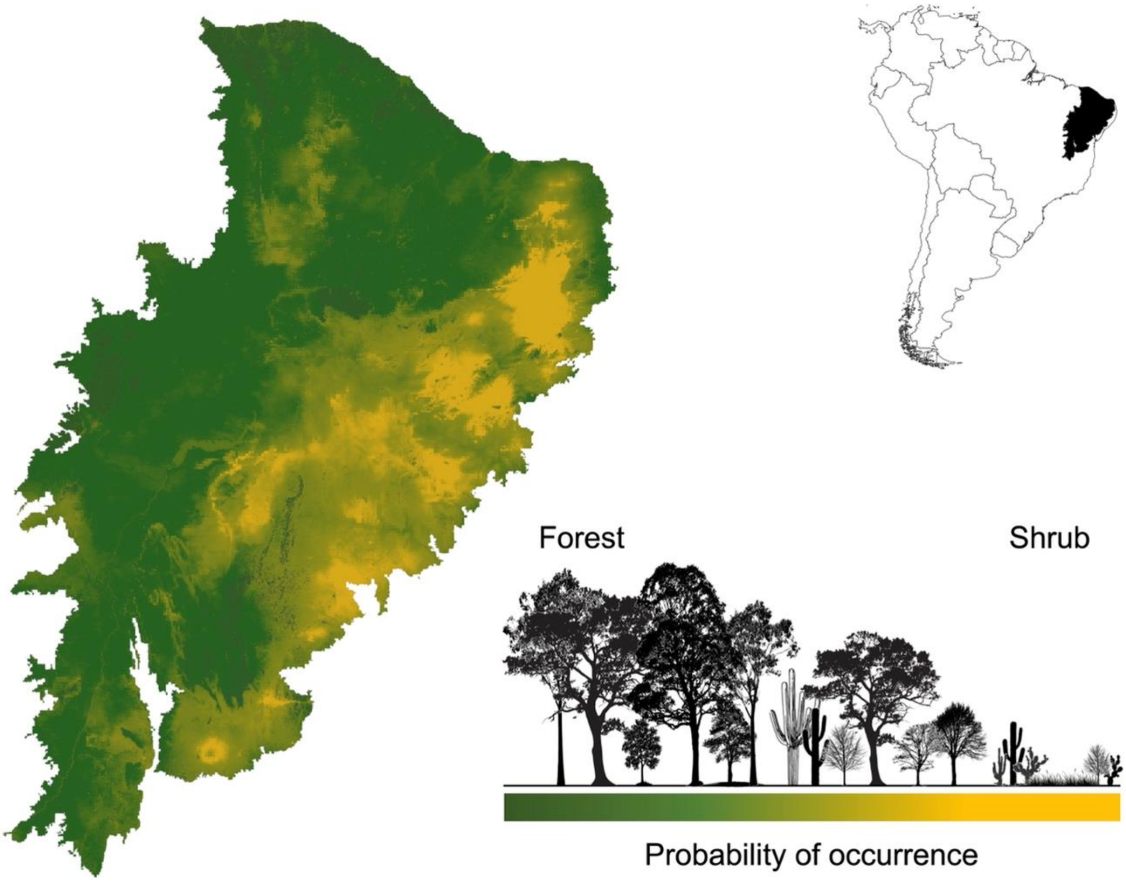

Fig.1. Potential distribution of forest and shrubland in the Caatinga for current climatic and soil conditions

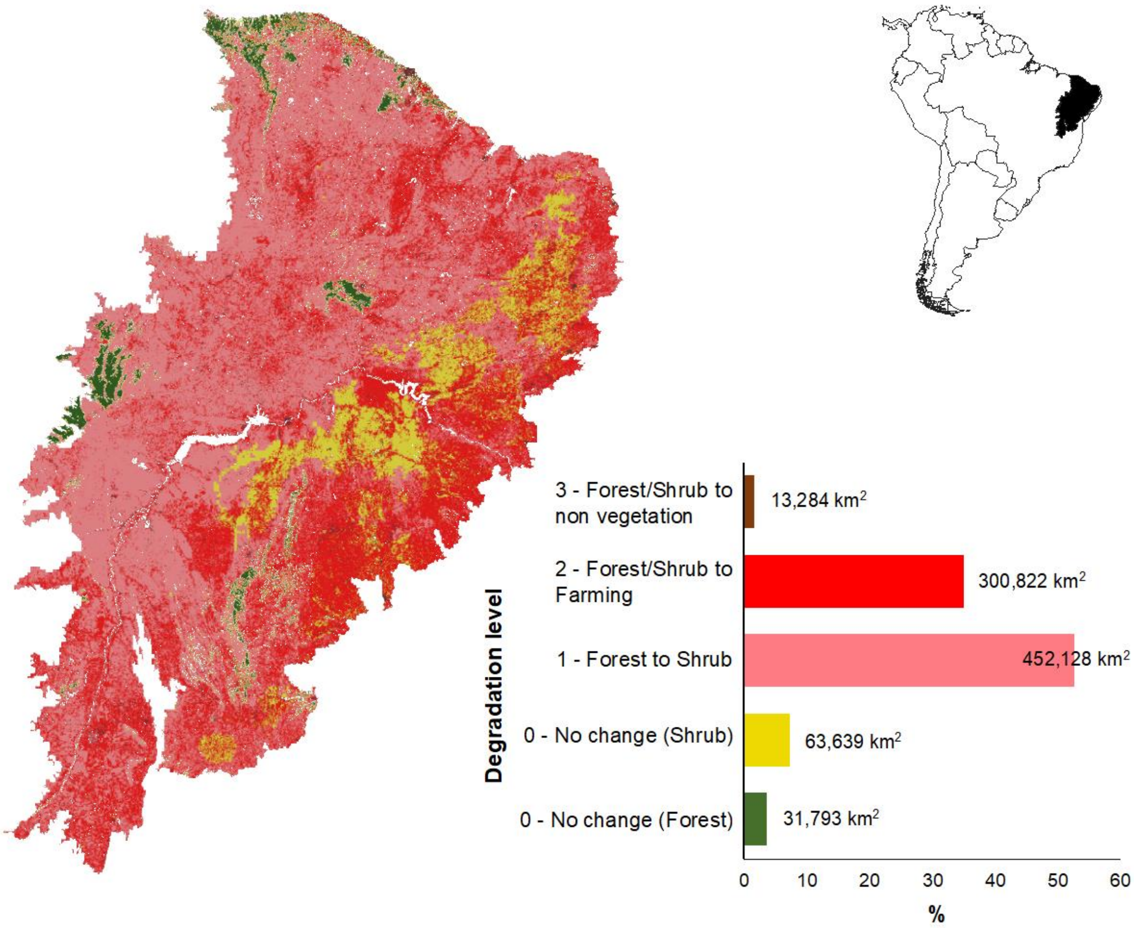

Fig. 2. Distribution and amount of each forest degradation level in the Caatinga region. Forest degradation is defined as a state of anthropogenically induced arrested succession, where ecological processes that underlie forest dynamics are diminished or severely constrained [22]

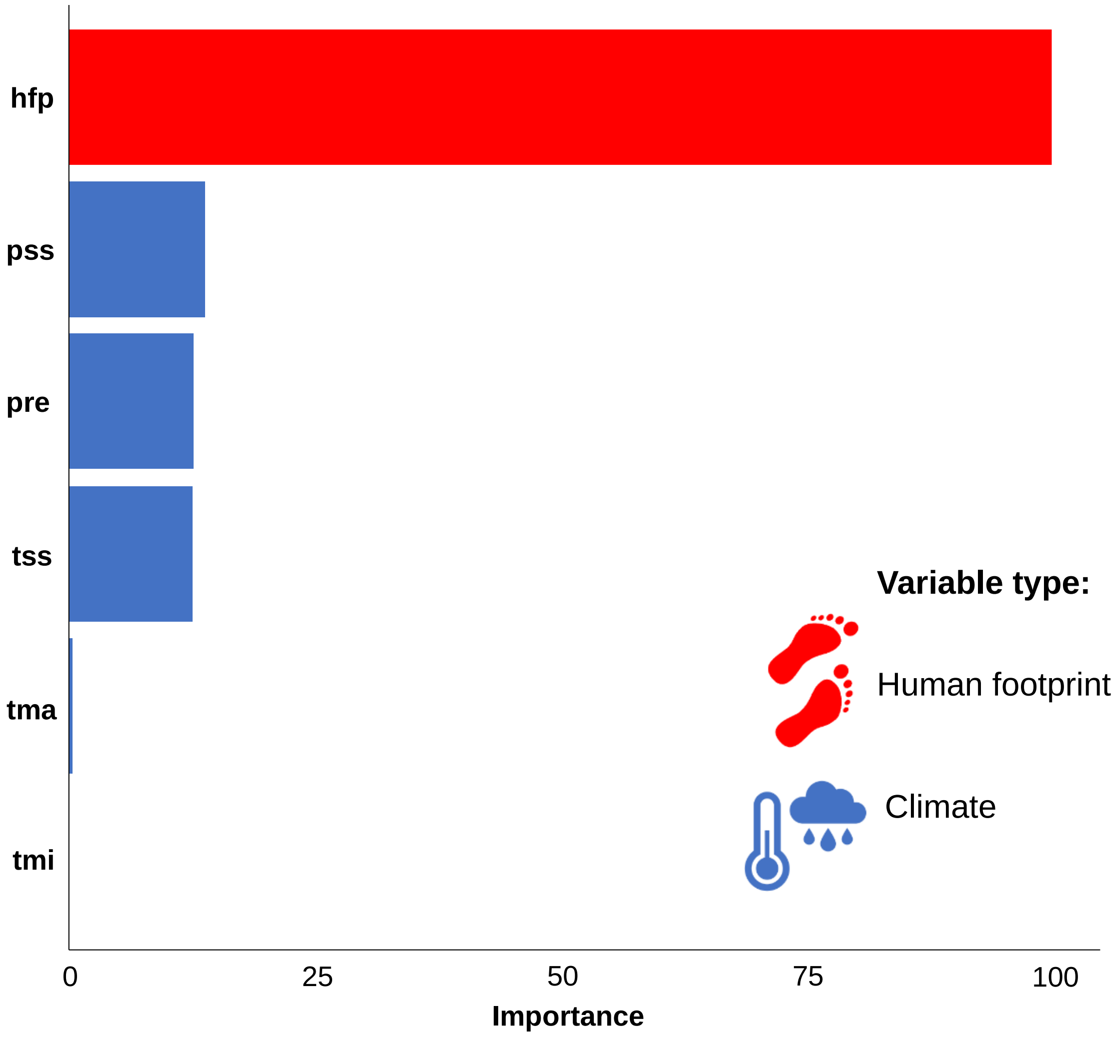

Fig. 3. Importance values of human footprint (hfp) and climate variables on the forest degradation in the Caatinga region. Importance values were calculated based on a Random Forest model that explained 73% of the variation in the data. Climate variables were: precipitation seasonality (pss), annual precipitation (pre), temperature seasonality (tss), max temperature (tma), and min temperature (tmi).

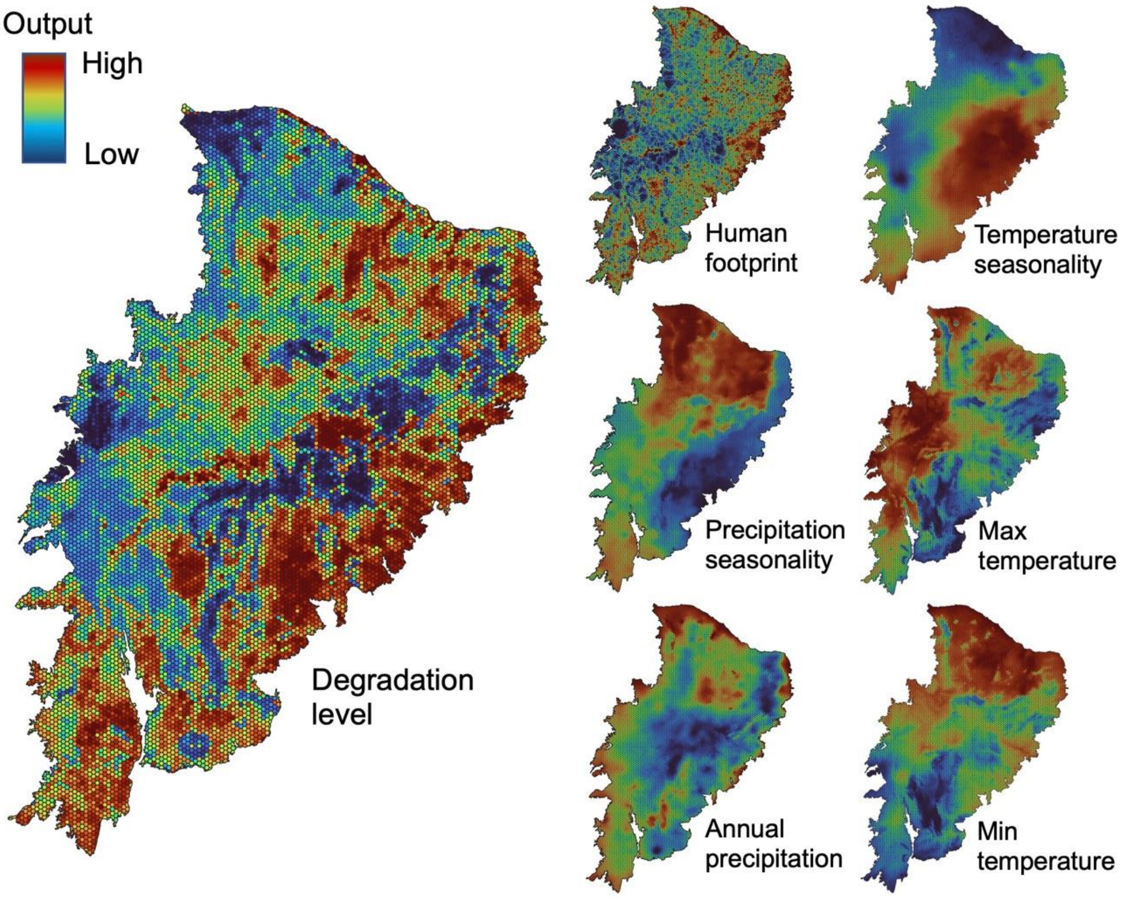

Fig. 4. Distribution of the degradation levels (as a response variable) and human pressure and climate variables (as predictor variables) in the Caatinga region. The relationship between the predictor variables and the response variable was evaluated using a Random Forest predictive model (see results and Fig.3).

Supplementary Information for

Human disturbance the major driver of vegetation changes in the Caatinga dry forest region and climate conditions can exacerbate them

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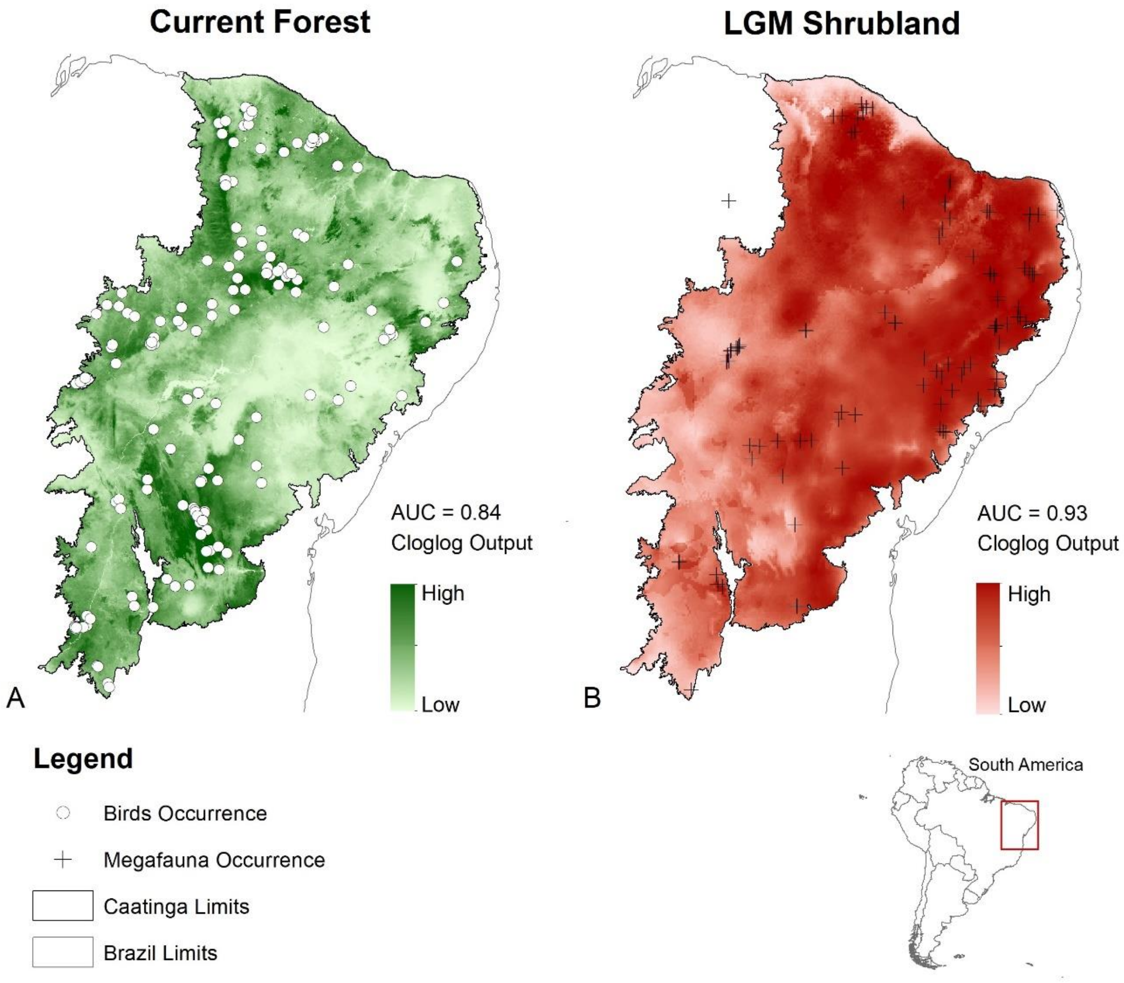
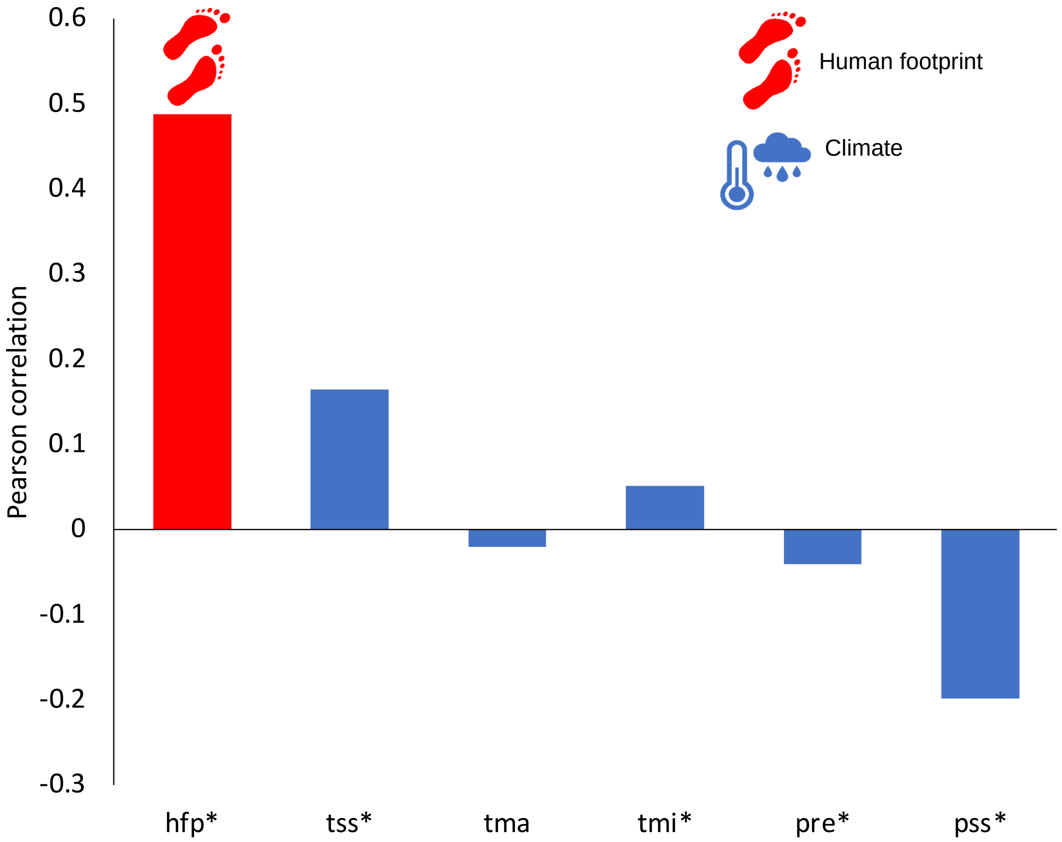
Figures S1 to S4

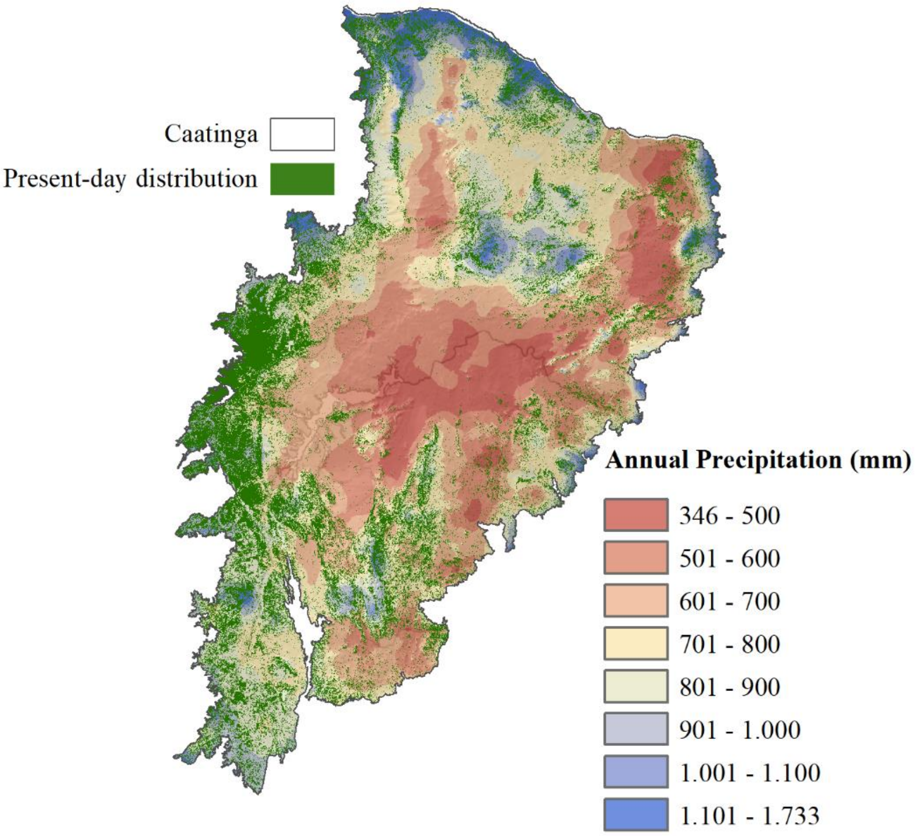
Tables S1 to S3



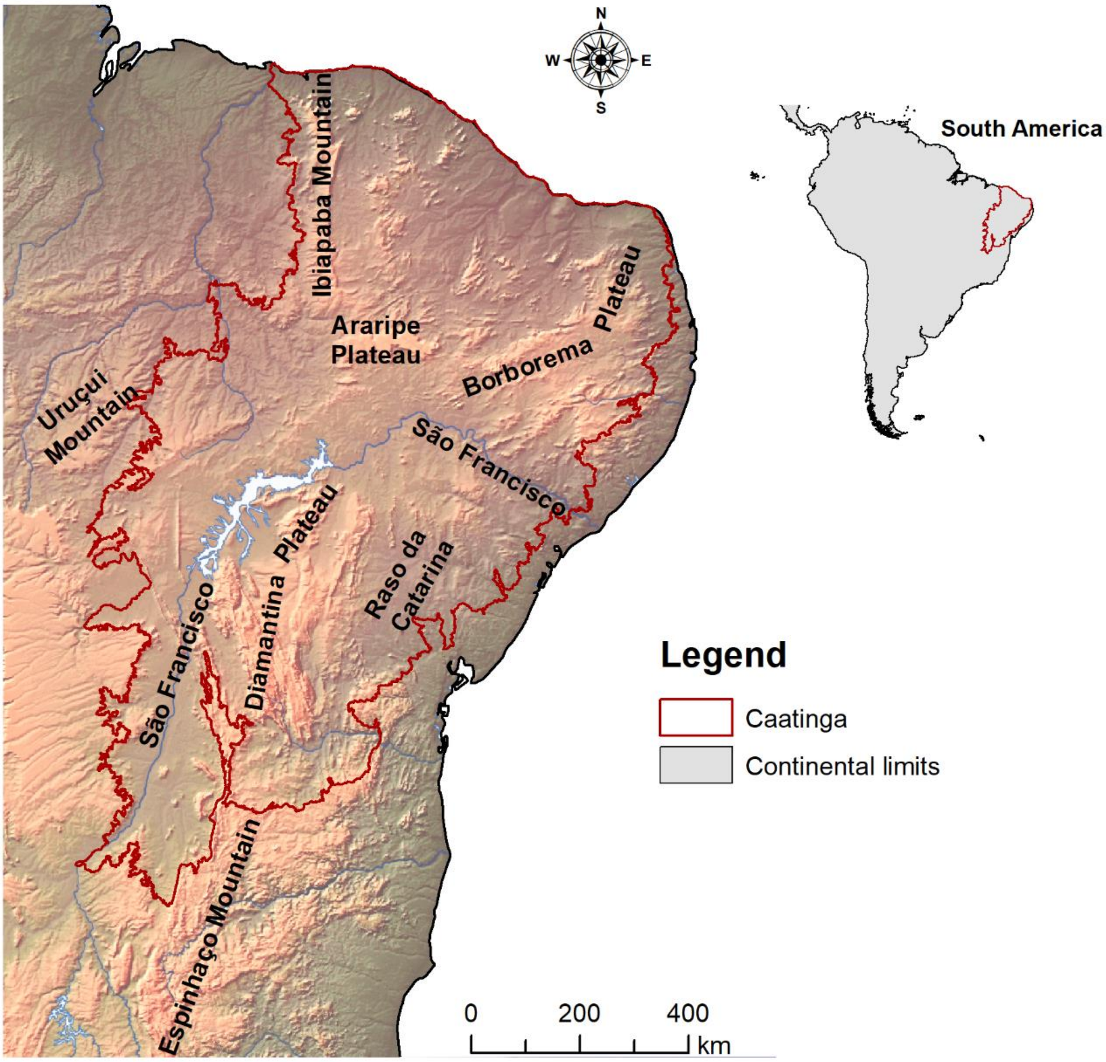
Supplementary Figure S1. Potential distribution of forest for the current period (A) based on forest-dependent bird species, and shrubland for Last Glacial Maximum (LGM) (B) based on megafauna occurrence. The colors in the cloglog output for each map represent the probabilities of the potential distributions.



Supplementary Figure S2. Pearson correlation values demonstrating possible associations between forest degradation and potential drivers (human footprint (hfp) and climate variables in the Caatinga region. Climate variables refer to temperature seasonality (tss), max temperature (tma), min temperature (tmi), annual precipitation (pre), and precipitation seasonality (pss). (*) means significant association (p<0.001).



Supplementary Figure S3. Present-day distribution of forest and woodland (green), and average annual precipitation distribution across the Caatinga region.



Supplementary Figure S4. The Brazilian dryland popularly and scientifically referred as Caatinga, the South American largest and more biodiverse tropical dry forest. It is a region with various landforms like flattened surfaces cut by narrow valleys, residual hills, high-altitude plateaus, and mountains that influence local precipitation distribution.

Supplementary Table S1. Contribution from the e environmental variables for forest distribution models in the current period and shrub habitats during the Last Glacial Maximum (LGM).

Variables	**Time**	**Cover**	**Contribution (%)**
Annual Mean Temperature	Current	Forest	-
	LGM	Shrub	10.7
Mean Diurnal Range	Current	Forest	5.4
	LGM	Shrub	7
Isothermality	Current	Forest	2.1
	LGM	Shrub	1.4
Temperature Seasonality	Current	Forest	16.9
	LGM	Shrub	-
Temperature Annual Range	Current	Forest	-
	LGM	Shrub	7
Mean Temperature of Wettest Quarter	Current	Forest	25.3
	LGM	Shrub	-
Mean Temperature of Driest Quarter	Current	Forest	10.9
	LGM	Shrub	-
Annual Precipitation	Current	Forest	13.5
	LGM	Shrub	57.3
Precipitation of Wettest Month	Current	Forest	1.8
	LGM	Shrub	-
Precipitation of Driest Month	Current	Forest	5
	LGM	Shrub	-
Precipitation Seasonality	Current	Forest	6.9
	LGM	Shrub	0.1
Precipitation of Driest Quarter	Current	Forest	-
	LGM	Shrub	8
Precipitation of Warmest Quarter	Current	Forest	3.1
	LGM	Shrub	8.6
Precipitation of Coldest Quarter	Current	Forest	3.1
	LGM	Shrub	-
Soil (clay content)	Current	Forest	1.8
Soil (sand content)	Current	Forest	4.2

Supplementary Table S2. Environmental variables adopted for modeling potential distribution. Only uncorrelated variables were adopted. The current period was used to represent climate conditions used in the forest models. The Last Glacial Maximum (LGM) period was used to represent the climate conditions used in the open vegetation. The potential distribution from LGM was re-project to current for comparison. The “x” indicates which environmental variables were adopted in each period.

Description	**Current (1970-2000)**	**LGM (21k years BP)**
Annual Mean Temperature		x
Mean Diurnal Range		x
Isothermality		x
Temperature Seasonality	x	
Max Temperature of Warmest Month	x	
Min Temperature of Coldest Month		
Temperature Annual Range	x	x
Mean Temperature of Wettest Quarter	x	
Mean Temperature of Driest Quarter		
Mean Temperature of Warmest Quarter		
Mean Temperature of Coldest Quarter		
Annual Precipitation	x	x
Precipitation of Wettest Month		
Precipitation of Driest Month		
Precipitation Seasonality	x	x
Precipitation of Wettest Quarter		
Precipitation of Driest Quarter		x
Precipitation of Warmest Quarter	x	x
Precipitation of Coldest Quarter	x	

Supplementary Table S3. Extinct megafauna species in the Caatinga used to model the potential distribution of open vegetation. Palaeoecological information adopted as proxies for open environments, which were associated with diet, grazing behavior, and habitat use (dental morphology, carbon isotopes, grazing behavior, diet of C4 plants (grass), and occurrence in open areas).

Species	**Paleoecology proxy**	**Source***
Equus neogaeus	Dental morphology and diet of C4 plants	1
Glossotherium sp.	The lips coupled with the tongue were used to pull out grass and herbaceous plants	2
Glyptodon clavipes	Habitat use like savannas and grazing behavior	3, 4
Glyptotherium cylindricum	Habitat use like savannas and grazing behavior	4
Pampatherium humboldtii	Dental morphology, carbon isotopes, and diet of C4 plants	5
Panochthus greslebini	Habitat use like savannas and grazing behavior	3, 4, 6
Panochthus jaguaribensis	Habitat use like savannas and grazing behavior	3, 4, 6
Xenorhinotherium bahiense	Scratch in dental morphology	7

*Source:

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CAPÍTULO 2

Model PLoS ONE

Reconstructing mammal defaunation throughout the Caatinga seasonally dry tropical forest biome

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Abstract

Wild mammal diversity worldwide has been threatened by anthropogenic drivers such as overhunting and natural habitat loss. These threats can alter the structure of local mammal communities and, consequently, their associated ecological interactions. Here, we assess the degree to which mammal faunas have been defaunated throughout the 863,752 km² Caatinga seasonally dry tropical biome of northeastern South America. Specifically, we examined (1) potential changes in the structure of medium- to large-bodied mammal assemblages, (2) broad spatial patterns of local extinctions, and (3) the role of hunting, habitat loss and protected areas in mammal defaunation. We compiled empirical data on a total of 73 modern mammal assemblages that could be defined as exhaustively sampled across the region and compared distribution estimates between contemporary and historical species incidences. Our results show that ~80% of the Caatinga mammal fauna has experienced local extinctions, which on average downsized local assemblages by 76.9%. Among all 51 species recorded, 37 lost over 50% of their incidence area across the region. Human population, road density, and habitat loss explained over 75% of local defaunation responses. This study provides valuable insights in support of conservation efforts across the region, including habitat set-asides, restoration, and refaunation initiatives, thereby assisting the recovery of both mammal- and habitat-mediated ecosystem services.

Key-words: hunting, habitat loss, downsizing, medium to large.

Introduction

The Anthropocene is characterized by human profound impacts on Earth's natural landscapes, mainly leading to the loss of biodiversity, as manifested by local to regional scale, if not global, extinctions [1]. In the last 300 years, there has been a loss of over 50% of Earth's natural tree cover [2]. Moreover, 515 species of terrestrial vertebrates at the brink of extinction hold global populations of fewer than 1000 individuals, 30% of which are in South America. Since 1900, 48 mammal species with under 1000 individuals have lost 95% of their geographic distribution in the world [3]. These biodiversity losses affect ecological functions, such as dispersal, pollination, and population control via top-down regulation [4].

Defaunation refers to the decline or extinction of animal populations induced mainly by anthropogenic activities [1]. Some of these activities have resulted in the loss of natural habitats due to perennial changes in land use, driven by factors such as food and fiber commodity production, afforestation, shifting agriculture, and urbanization [5]. These land use changes not only fragment and decrease the area and quality of remnant habitats but also alter the structure and composition of ecological communities, ultimately leading to a biodiversity decline [6,7]. In addition to the loss of natural habitat, defaunation also results from direct human overexploitation for trade, subsistence, or sport [1]. One of several phenomena related to population declines and extirpations is the "downsizing effect", in which individuals within an assemblage on average become much smaller.

Assemblage downsizing is a result of widespread human propensity to target and hunt larger-bodied species compared to smaller ones. If larger animals are consistently depleted from a community, it can result in density compensation by smaller-bodied species [8]. Likewise, predictable selection of larger individuals within a population by harvesting can result in a shift in the gene pool towards faster life-histories and smaller-bodied individuals [9]. Over time, both of these processes can lead to predictable changes in the average size of individuals within an assemblage. This overall downsizing can have pervasive ecological consequences, since larger animals often play essential roles in ecosystems as top predators or keystone species, influencing the dynamics of their habitats, disrupting ecological relationships and leading to cascading effects on overall ecosystem structure and function [4,10]. For example, heavily hunted areas in Amazonian forests host an average vertebrate biomass density of 200 kg/km², compared to >700 kg/km² in non-hunted areas [11]. Prey body mass is an key indicator of preference, as larger animals provide more meat per unit of hunting cost, which can be associated with high economic or energy returns [12]. Therefore, studies on the effects of human harvesting have shown a global reduction in the average body size of mammal assemblages [13].

In semi-arid regions, the decline in mammal abundance and species diversity can be attributed to anthropogenic drivers such as conversion into livestock pastures and croplands, which are further aggravated by even drier conditions as aligned with global climate trends [14]. In these xeric regions, the combination of extreme land use and climate change often reduces overall primary productivity as a response to markedly low precipitation [15], further suppressing habitat carrying capacity to sustain large animals. In addition to the degradation of the natural landscape, these regions face significant hunting pressure for both commerce and subsistence [16]. In the Brazilian semi-arid biome known as the Caatinga, for example, subsistence hunting frequently subsidizes the subsistence of poor households or is associated with commercial and recreational practices [17]. This practice has already induced regional scale extinctions of large mammals white-lipped peccary (*Tayassu pecari*), and widespread local extinctions of large rodents such as paca (*Cuniculus paca*) [18,19].

Although only about 11% of original vegetation cover is currently retained in the Caatinga (Araujo et al. 2023 unpublished data), hunting remains a pervasive extractive activity [18,20], resulting in high rates of defaunation [9]. However, significant knowledge gaps persist concerning the magnitude, species composition and geographic patterns of large vertebrate losses, thhe scale of the downsizing effect, and the underlying factors contributing to regional defaunation . We therefore here assess: 1) the magnitude and spatial extent of defaunation among all medium to large-bodied mammals of the Brazilian Caatinga; 2) the resulting changes in terms of the size structure of contemporary mammal assemblages; 3) the degree to which the geographic range of these species have been reduced; and 4) the relative importance of either habitat loss or overhunting as contributing factors to this defaunation process. Finally, we discuss the effects of regional scale defaunation on the conservation status of different species and possible functional extinctions that may affect the natural resilience of Caatinga ecosystems.

Methods

Study area

The Caatinga is a 863,752-km² semiarid region in Brazil [21] characterized by a diverse vegetation mosaic encompassing four biomes: Tropical Seasonal Dry Forest, dominating most of the region; enclaves of Tropical Rain Forests, located in mountain ranges; Savannas, located in areas with poor soils and low pH; and Rupestrian Grassland, limited to a section of Chapada Diamantina, Bahia [22]. The region experiences marked variation of annual precipitation ranging from 400 to 1200 mm, resulting in distinct local climates, with more arid environments in the central region and wetter portions along coastal and montane area, due to an orographic effect [23]. Approximately 94% of the Caatinga is at risk of desertification due to human disturbance [24], including livestock farming, croplands, and mineral extraction, which have been the main drivers of environmental degradation in the Caatinga [25].

Study species and defaunation estimates

We selected species of medium to large bodied mammals (mlbm) that occur in the Caatinga based on their large home ranges (>5km^2), high trophic levels, and relatively small population size compared to small mammals [26]. To do so, we conducted a bibliographical survey using "Google Scholar" "Scielo", "Web of Science", and "ScienceDirect" databases, employing word combinations such as "medium to large bodied mammals", "check-list", "checklist", "Caatinga", "hunting", "ethnofauna" to access all available information on MLBM assemblages across the Caatinga. We also used the Global Biodiversity Information Facility (GBIF – https://www.gbif.org) and Specieslink (https://specieslink.net) platforms to supplement spatially explicit data on species occurrences. From the data compiled, we grouped species that were georeferenced to the same locality and selected assemblages with a richness of at least five species, based on both the contemporary literature [27] and field records. This process resulted in the compilation of 73 mammal assemblages distributed throughout the region, amounting to a total of 51 species (Fig. 1).

We estimated a measure of defaunation in by subtracting values from a raster file containing information on the historical distribution of each of the selected mammal species as of 1500 AD (the onset of Brazil's colonial period) and a raster with an estimate of the current distribution. Next, we provide details on how these rasters were generated.

Historical distribution

The potential historical distribution of the 51 MLBM species selected in this study were obtained by species distribution modelling (SDM) based on current climate and topographic conditions. SDMs were obtained using occurrence data for each selected species throughout South America, with subsequently clipped to match the Caatinga boundaries [21] (Fig 1). We therefore estimated the unadulterated distribution of these species without land use and land cover layers (i.e. without restrictions induced by post-1500 habitat modification). We used 19 climatic variables plus elevation (m.a.s.l.) extracted from Worldclim (www.worldclim.org), at a spatial resolution of 2.5 arc-minutes. To avoid redundancy, we included in the models all variables that we correlated with one another by less than 0.8, using Pearson correlations calculated using the "vegan" R package (version 3.5.3). At the end of this process, we considered the following 10 variables: diurnal range of mean temperature (BIO2), temperature seasonality (BIO4), mean temperature of the wettest (BIO8) and the driest quarter (BIO09), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of the driest (BIO17), warmest (BIO18), and coldest quarter (BIO19), and elevation.

We used the Maximum Entropy algorithm v.3.4.1 (MaxEnt) [28] to generate the modelled geographic distributions of each selected species. MaxEnt models comprise a probability distribution in which each grid cell predicts the suitability of conditions for the species [28]. We used the Receiver Operator Characteristic (ROC) statistic to assess model accuracy, with 10 repetitions of 10,000 iterations maximum; 10% of the average repetitions were randomized as test data, whereas the remainder was randomized for training the model in each replication. Each species predictive map was transformed to a binary map (0 absent, 1 presence) that was delimited using the MaxEnt thresholds (Supplementary Information S2). We selected the thresholds that defined the smaller potential habitat following a conservative approach to preclude overestimates of species geographic distributions. To obtain the final raster layer containing the potential species richness and composition representing past conditions, we summed all binary maps.

Contemporary distribution

Based on the georeferenced points of the assemblages, we performed an interpolation using the "inverse distance weighting" (IDW) method to generate a continuous probability surface (raster) of contemporary species richness across the Caatinga. IDW is a mathematical method that estimates a value for an unsampled location using the average of data values within a neighbourhood weighted by the inverse of the distance between any interpolated points.

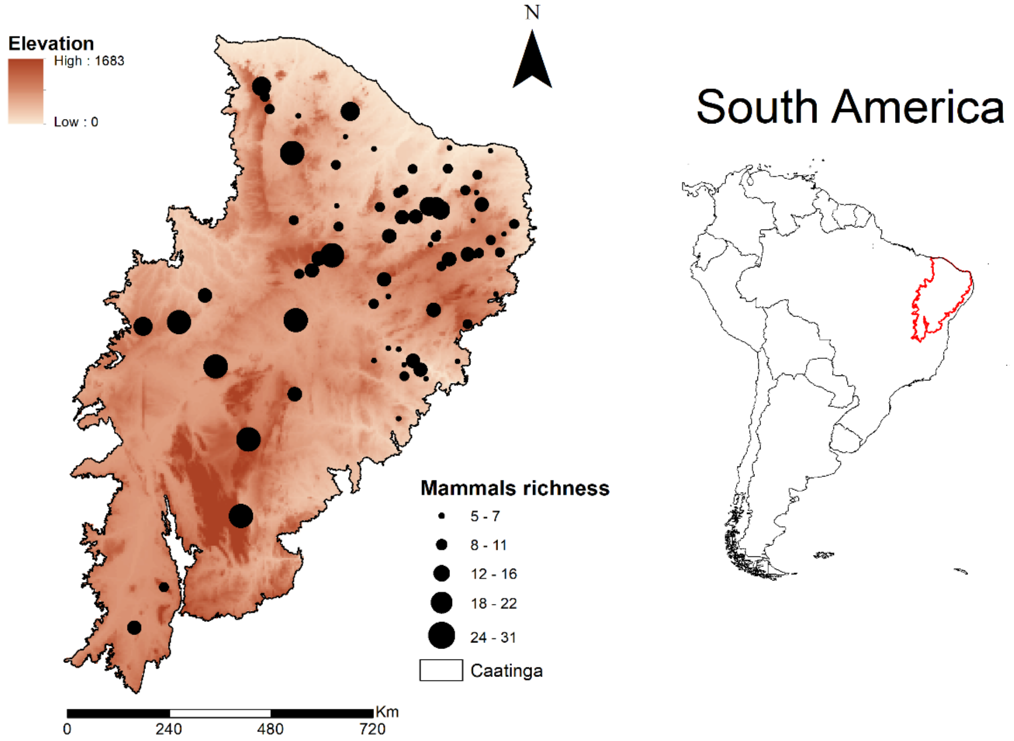

Figure 1 – Geographic distribution of representative assemblages of medium- to large-bodied mammal species within the semiarid Caatinga region of northeast Brazil and their respective species richness based on a maximum local coexistence of 51 MLBM species. The boundaries of the Caatinga is shown by the red outline in a map of South America

Species composition and size downgrading

We compiled information on the body mass of the 51 selected species from the literature [29,30]. To create a contemporary body mass raster, we summed the body mass of all species present within each of the 73 assemblages. To obtain the expected historical body mass raster, we first reconstructed the species composition of each past assemblage using the binary maps of the likely distribution on each species, and then summed their body mass accordingly. Changes in size structure were then estimated for each of the 73 assemblages by comparing their contemporary and historical body mass distributions. Assemblage downsizing therefore occurs if the mean species body mass of historical assemblages is greater than that of the contemporary assemblage for the same locality. Following the same logic, the expected historical species composition of each assemblage was also compared with their contemporary analogues.

Drivers of defaunation

Habitat loss

Since agriculture has been the main driver of natural vegetation conversion in the Caatinga, especially since the bovine cattle economic cycle that began in 1549 [31], we used the extent of land allocated to livestock farming as a regional scale indicator of habitat loss. We therefore assumed that areas containing a larger number of livestock establishments are likely associated with greater natural habitat loss in the Caatinga. To this end, we adopted the proportion of livestock enterprises (Ls) per municipal county as an indicator of habitat loss. This variable represents the proportion of rural enterprises dedicated to livestock husbandry relative to the total number of agricultural establishments in each county, obtained from Brazil’s 2017 agricultural census.

Hunting pressure

The degree of hunting intensity was estimated using two indicators of wildlife harvesting in their natural habitat: 1) increment in human population density (Pd); and 2) available accessibility infrastructure (Roads - Ro). Changes in human population density were estimated by subtracting the population density data between the years 2017 and 1700. For this purpose, we employed a consistent combination of up-to-date historical population estimates over the past 12,000 years, extracted from the Hyde 3.2 database [32], which provides raster maps representing the rural, urban, and total population size (persons)and population density (persons/km^2). A detailed road map (Ro) was obtained from ‘OpenStreetMap’ (https://www.openstreetmap.org). This database consists of open-source data developed by a community of volunteer mappers who continuously update spatial data on several public utility services, including the mapping of paved (highways) and unpaved (dirt) roads under federal, state and municipal jurisdiction.

Suitable habitats availability

To assess habitats that may protect local faunas and potentially preclude defaunation, we analysed the availability of suitable habitats using indicators of legally protected areas using hierarchical protection criteria: 1) Fully Protected Conservation Units (FPCUs), 2) Sustainable Use Conservation Units (SUCUs), and 3) Permanent Preservation Areas (PPA). We expect a higher species richness of MLBM in the most intact sites. Data on protected areas (in Brazil, Conservation Units) were extracted from the Ministry of the Environment (MMA), which provides vectors of federal, state, and municipal protected areas for both fully protected and sustainable use reserves. To identify and map PPAs, we considered slopes greater than 45°, as prescribed in the Brazilian Forest Law (Law 12.651, 25th May 2012; Brasil, 2012). Native vegetation remnants throughout the Caatinga areas are predominantly restricted to these areas due to limited accessibility for mechanized croplands. We used a digital elevation model (DEM) from the Shuttle Radar Topography Mission (SRTM) with a spatial resolution of 1 arc sec (30 m) to generate a slope map using the spatial analysis tools in QGIS version 4.4.14 Madeira.

Data analysis

We employed a hexagonal grid system with cells measuring 5 km in edge length (hexcell area = 64.95 km^2), amounting to ~13.240 hexcells covering the entire extent of the Caatinga biome. Within each hexcell corresponding to the 73 assemblages, we extracted several metrics describing potential drivers of defaunation, including the cumulative proportion of Ls, mean increase in human density, the cumulative road network (in meters), and the areas (m^2) of suitable habitat indicators (FPCUs, SUCUs, PPA). As a response variable, we considered the reduction in local species richness in each of the 73 assemblages. In addition, we examine the environmental and socioeconomic determinants of the degree to which the size structure of mammal assemblages changed from historical to modern times, for which we consider our metric of community downsizing. All vector and matrix spatial analyses were performed using the open-source software QGIS version 4.4.14 Madeira.

To assess the relative importance of each of the drivers on the defaunation of medium to large-bodied mammals in the Caatinga, we employed the Random Forest (RF) algorithm, which generates predictive models based on randomized decision trees [33]. RF provides effective predictions because it rarely overfits the data, and the higher degree of randomness amounts to an accurate classifier and regressor [33]. RF models have been widely discussed due to their high precision and stability when applied to nonlinear data and their ability to relate highly divergent parameters in ecology [34]. The classifier requires two parameters, the number of classification trees to be generated, and the number of predictor variables considered as candidates for defining each node (mtry). To evaluate the performance of the models, RMSE (Root Mean Square Error) and R^2-values were used. In the end, the variables selected by the model are ranked according to their importance, and relative values are scaled between 0 and 100. Variable importance measures the number of times the model performance increased when any given predictor was included in the model (Araujo et al. 2023 chapter 1 this thesis). We fitted RF models using the *caret* R package [35] and results show the ‘best’ model, including the number of trees used in the default (500). To plot the relative variable importance in the model obtained, we used the *vip* R package [36].

Results

Defaunation

The medium large body mammals currently has a maximum local richness of 33, a minimum of 5, and an average of 13 (± 3.95). Projections from the past showed a maximum local richness of 48, a minimum of 9, and an average of 33 (± 6). The estimated defaunation showed a maximum local loss of 41 species (80%), and the average regional loss was 20 species (39%). In general, this species loss covers all Caatinga region, with higher rates observed in the central-east and central-north regions. The localities where there was less defaunation were in conservation units, such as, Serra das Confusões National Park (5), Boqueirão das Onças National Park (6), Ubajara National Park (7), Serra das Almas Natural Reserve (7) and Serra da Capivara National Park (9). On the current map they are dark green in color (Fig 2A). On the other hand, the highest concentration of defaunation is found in urban centers. In the defaunation map represented by red (Fig 2B).

Loss of body mass and species composition

According to past projections, the local accumulate biomass varied from 160.14 kg to 707.60 kg, with an average of 389.78 kg (± 1.66). On the other hand, the current accumulate biomass varied from 7.72 kg to 468.95 kg, with an average of 90.103 kg (± 7.5) per locality (Fig 3). The highest value of biomass accumulation is currently also found in areas of conservation units, as in these places there is a greater richness of species, proving the importance of these protected areas for the region. These results suggest a body loss of about 76.9% per locality, which characterize a mammal downsizing pattern in the Caatinga region.

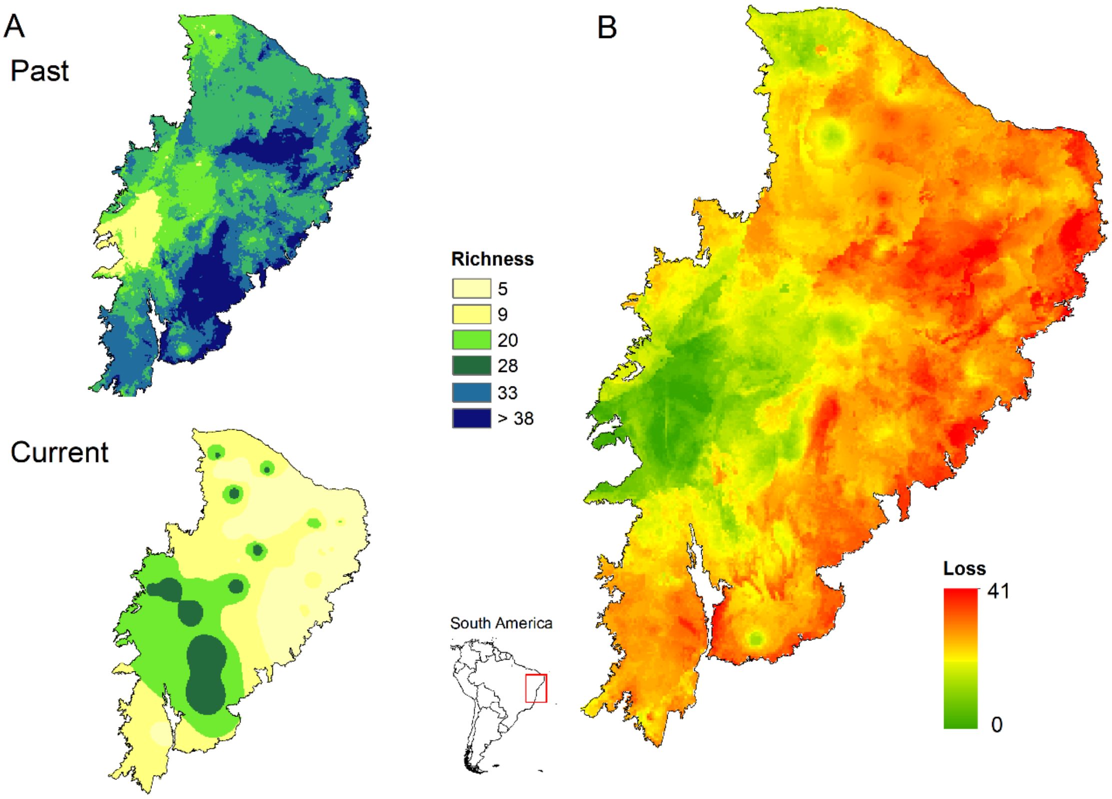

Figure 2. (A) Distribution of past and current potential species richness of medium to large-bodied mammals in the Caatinga. B) Defaunation of medium to large-bodied mammals (defaunation) in the Caatinga.

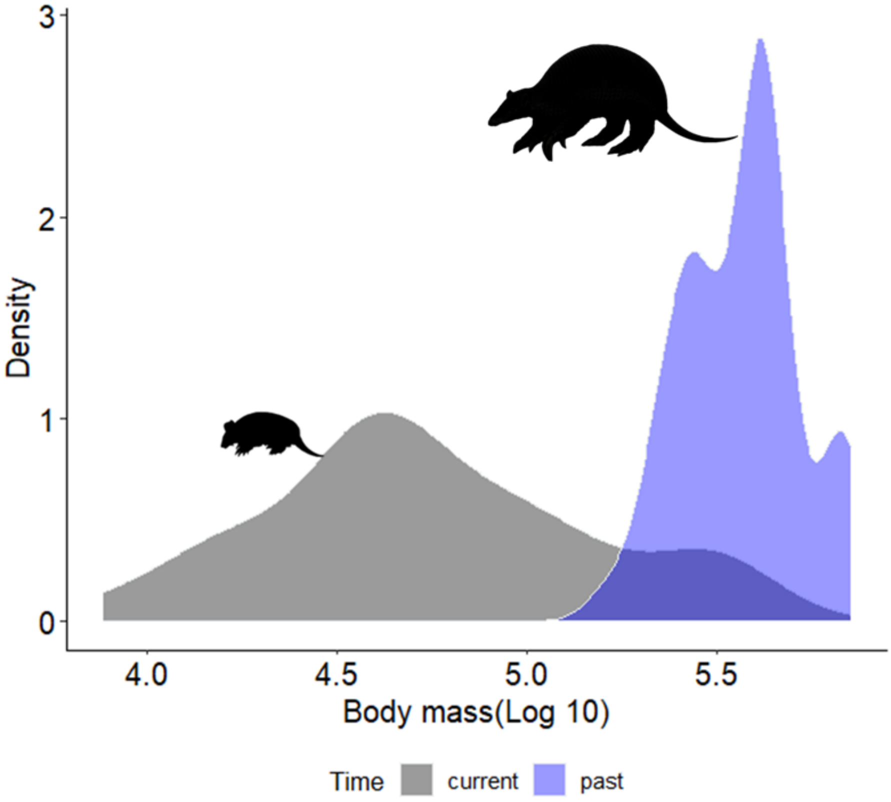

Figure 3. Body mass by locality of medium to large-bodied mammals generated by the potential model (past) and contemporary mammals (current) in the Caatinga region.

Among the 51 species surveyed, a staggering 37 showed a loss of more than 50% in their occurrence area in the Caatinga. *Sapajus xanthosternos* (buff headed capuchin) and *Priodontes maximus* (giant armadillo) showed the highest local extinction (95% each) surpassing other species (Figure 4), the first one being endemic and critically endangered, and the other one being vulnerable, according to the IUCN. Species such as *Tapirus terrestres* (lowlander tapir), *Tayassu pecari* (white-lipped peccary), *Cuniculus paca* (agouti), among others were locally extinct in over 80% of their predicted occurrence areas. These species are especially important for the development of the ecosystem, maintaining ecological interactions such as dispersal. Even seemingly common species, such as the crab-eating fox (*Cerdocyon thous*) and the yellow armadillo (*Euphractus sexcinctus*), were found to be locally extinct, albeit with relatively low loss rates (Fig 4).

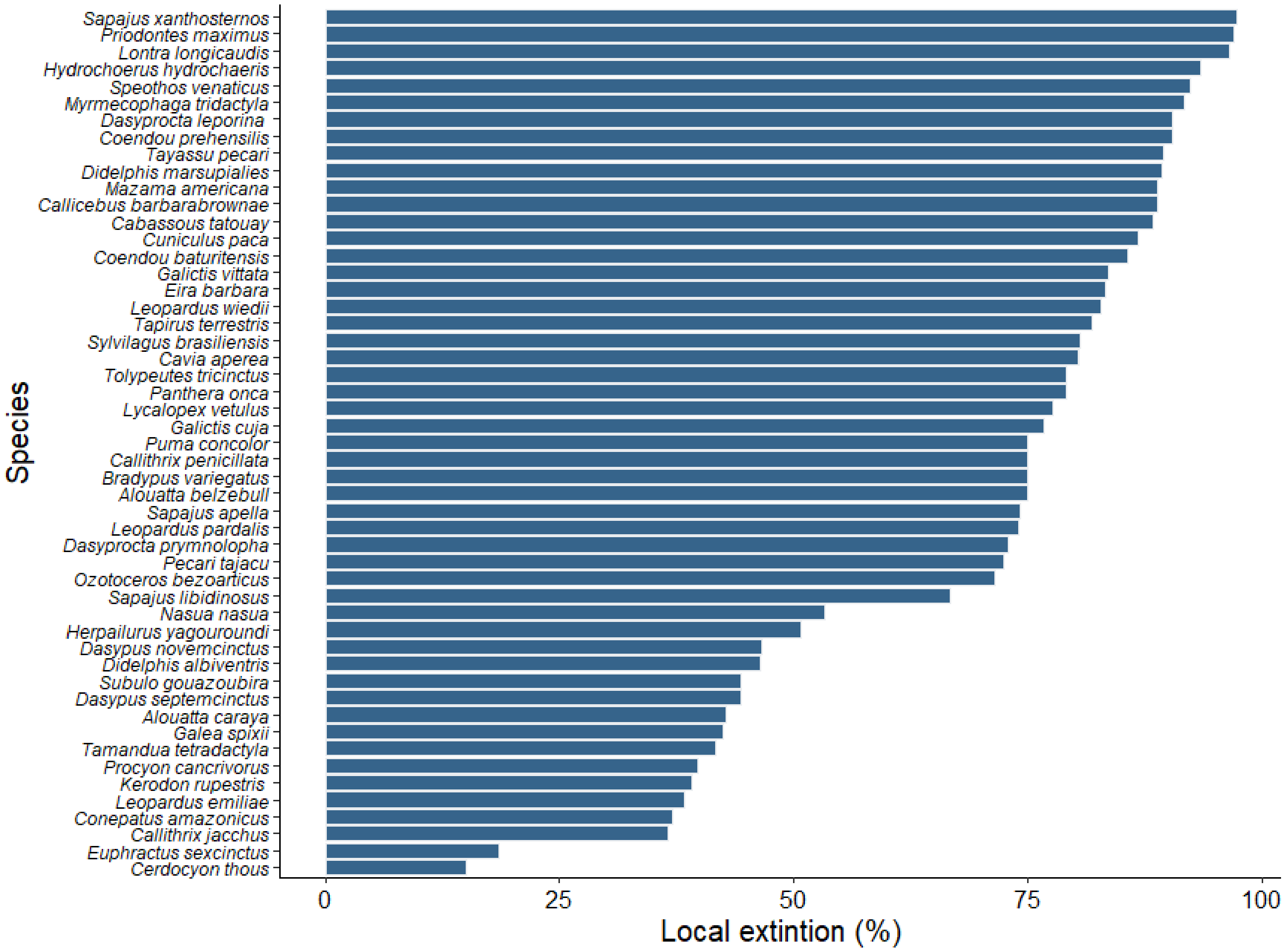

Figure 4. Observed rates of site occurrence of medium to large-bodied mammal species across 73 mammal assemblages distributed throughout the Caatinga. Species are listed from top to bottom from the highest to the lowest local extinction rates.

Drivers of defaunation

Human population density, roads and livestock were the main variables associated with defaunation in the Caatinga, representing more than 75% of relative importance when compared to protected area indicators (Fig 5). Thus, hunting and habitat loss were together the most important drivers for defaunation in the Caatinga region. The random forest results were Mtry=2, RMSE =6.9 and R^2 =0.08.

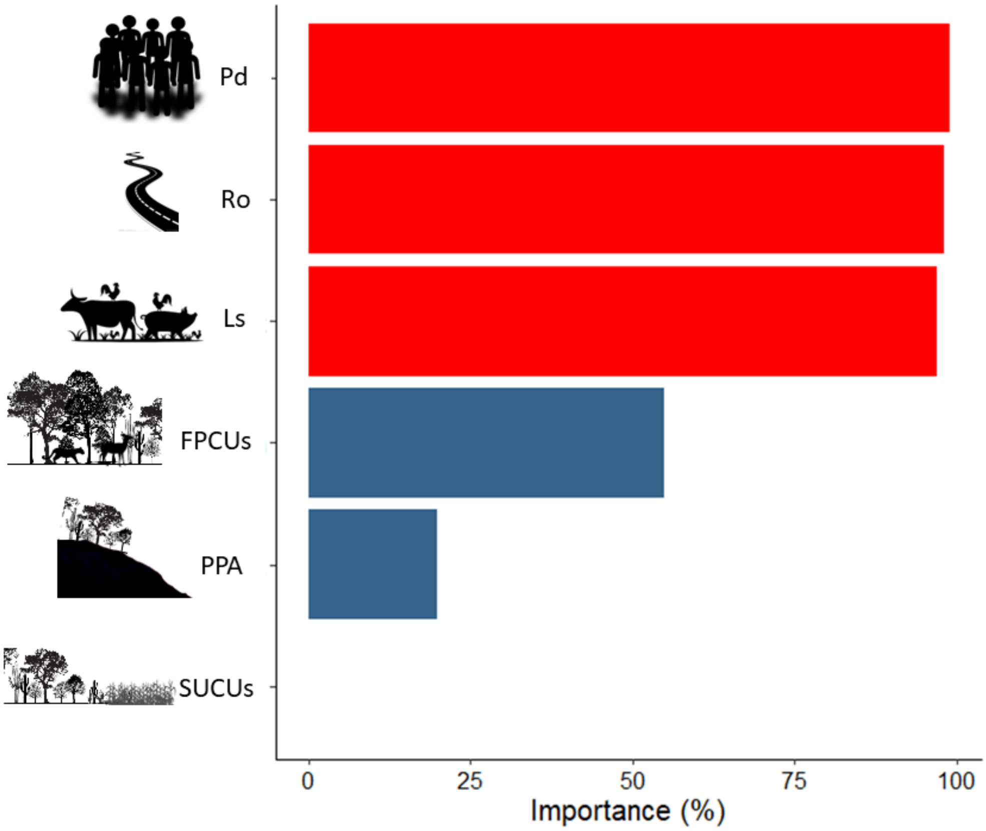

Figure 5. Importance value of variables on the defaunation in the Caatinga region. Population density (Pd), Roads (Ro), Livestock (Ls), Fully Protected Conservation Units (FPCUs), Sustainable Use Conservation Units (SUCUs), and Permanent Preservation Area (PPA). The red color represents in positive relation with defaunation and blue negative relation.

Discussion

Our results reveal a drastic defaunation scenario with around 80% of species being locally extinct across the semi-arid region of northeastern South America. Although neglected by researchers until now, this defaunation exhibits a clear downsizing effect, with a significant shift in the body size structure of mammals in most of the region, which is currently a refuge to lower-mass animals. Hunting indicators were the main factors associated with this loss of species and, therefore, suggesting tha the continuation of this practice currently has as its main target the few remaining medium-sized species, such as *Euphractus sexcinctus* and *Kerodon rupestris*. The historical/current conversion of natural habitats into pasture areas for livestock emerged as another significant driver associated with this defaunation, highlighting the classic effect of habitat loss on fauna distribution across most of the region. On the other hand, the limited presence of fully protected conservation units underscored the relative importance of suitable habitat availability for mlbm. This scenario exacerbates the dire need for reforestation and refaunation efforts in one of the most threatened ecosystems in the Americas, considering the loss of essential ecological functions and ecosystem services [37].

According to Bogoni et al [9], in the Neotropics, the historical average local richness of mlbm species was 32 and the current average richness is 12, thus there was an approximate average loss of 63%. The same authors, estimate that local reduction in the Caatinga was 75%. Our result shows an estimate of a slightly greater reduction in local richness (80%) in the Caatinga, which reinforces and corroborates its status as the region with the highest intensity of defaunation in the entire Neotropics [9]. Therefore, the current mlbm fauna present in most of the Caatinga represents only a fraction of its former potential. This scenario exacerbates a history of local extinctions that has been overlooked so far and exacerbates the ongoing trend of local replacements in the mammalian assemblage's structure, leaving only small and some medium-sized mammals.

The downsizing effect is evidenced along with the defaunation of mammals in tropical regions [11,38]. Likewise, our results show that in the past, the sum of the masses of mlbm assemblages in Caatinga was, on average, four times greater than the current sum. Large species (> 30 kg), such as *Priodontes maximus, Hydrochoerus hydrochaeris* and *Tayassu pecari*, were locally extinct in over 80% of their distributions areas within the region. Given that the downsizing effect is mainly associated with the presence of hunting [38,39], we can suggest that hunting was the main cause of the local extinction of larger species like these in the Caatinga. Hunting continues to be a prevalent issue in the region, with animals weighing only 0.3 kg being slaughtered in the region [18]. Characterized by a low human development index (HDI) and a high population density[40] the Caatinga is considered economically disadvantaged, which contributes to the prevalence of subsistence hunting cultures in the region. additionally, many animals are hunted for other purposes, such as religious rituals (*Tamandua* *tetradactyla*), as pets (C. *barbarabrowne*), for medicinal reasons (*Herpailurus yagouaroundi*) and for control purposes (*Puma concolor*) [16,41,42].

The medium to large bodied mammals have a large home range compared to small-sized ones (< 500g), which suggests that these animals depend on a large habitat [26,43]. However, habitat loss alters the population size and diversity of these animals. [44–46]. In the dry regions of the world, habitat loss is mainly associated with large-scale agricultural practices, since, with the increase in population size in these regions, there is an increase in the demand for food to sustain humans. The Caatinga has an average of 60% of its area dedicated to raising cattle and goats [47]. Livestock in the region has stood out since the 18th century, and the demand for beef increased driven by the establishment of mills and access to metropolitan cities [48]. The introduction of domestic animals presents a series of problems such as competition for space, predation and transmission of diseases with native fauna, and these reasons further accelerate the defaunation process [1]. This scenario is a portrait of what currently occurs in the Caatinga, where landscapes historically characterized by agricultural activities maintain more than 60% of mlbm records composed of only two species: exotic goats and native crab-eating fox [49].

One way to mitigate landscape changes and interactions between domestic and native fauna is the creation of more conservation units in the region. The Caatinga has only 1.92% of the area destined for conservation units and, according to article 8° of the Convention on Biological Diversity, the minimum expected would be 17% of the territory [50]. Furthermore, our results show that strict protection units play a role in mitigating defaunation in the region, an effect not observed in sustainable use units. Although Brazil has more areas designated for sustainable use, the strictly protected areas in the Caatinga prevent deforestation by 27%, and those of sustainable use do not. [50]. Therefore, our data support the need to create more fully protected conservation units to effectively mitigate defaunation in the region.

Thirty-seven species out of the 51 that we recorded lost more than 50% of their places of occurrence. Among them, three are endemic and one is classified as threatened with extinction: the blond titi monkey (*Callicebus barbarabrowne*), the Brazilian porcupine (*Coendou baturitensis*) and the rock cavy (*Kerodon rupestris*) [51]. In addition to being critically endangered, our estimate points to a current reduction of less than 20% in the potential occurrence of blond titi monkey. Although recently described and with a very restricted occurrence [26], our estimates also point to a loss of over 75%

of the potential occurrence of the brazilian porcupine, also highlighting the urgent need for conservation measures. Nationally, the rock cavy is considered a species in vulnerable and endangered status. Our results suggest a reduction to less than 50% of its potential occurrence. Although it is an easily registered species, mainly in rocky places, it is an easy prey for hunters [20,52]

The few species that still manage to survive in most of the region can be considered winner species, as they have better adaptations in anthropized environments. [53]. Examples of these species are: 1) crab-eating fox (*Cerdocyon thous*), considered a generalist animal, being adaptable in degraded environments and with a varied diet [54,55], and 2) six-banded-armadillo (*Euphractus sexcinctus*), because it is tolerant to changes in landscape cover and has a fossorial habit [56]. Even though they are considered winner animals, these species still show a loss of area of occurrence in the region, either due to pedestrians being run over on highways [56] or even higher frequency of hunting in the region [18,20].

Conclusions

Our results show a drastic local extinction of mlbm in the Caatinga, mainly caused by illegal hunting, which is currently no longer for subsistence purposes and has become a recreational activity in the region. Defaunation in the region affects the structure of mlbm assemblages in relation to the size of the species, replacing large and medium-sized animals with smaller ones. This shift influences the loss of critical ecological functions, such as the dispersal of fruits with large seeds, for example. Our findings align with the historical context and the effect of the loss of forest cover on the local extinction of species that this region presents. Therefore, we urgently recommend the creation of full protection conservation units in areas such as Serra de Santa Catarina - PB, Serra de Santana - BA, São João do Piauí - PI, São Fernando - RN, Paulista - PB e Lagoa Grande - PE since in these areas a greater diversity of species is still found. Futhermore, we suggest implementing refaunation initiatives in areas that have a large biomass, but considered as empty forests, since the fauna has already been locally extinct by hunting.

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Supporting information

Reconstructing mammal defaunation throughout the Caatinga seasonally dry tropical forest biome

Nathália Fernandes Canassa, Célia Cristina Clemente Machado, Carlos A. Peres, Helder Farias P. de Araujo

S1 Table-Threshold values–Threshold of values used for generated of mammal species potential models.

Species	Threshold	Values
Alouatta belzebull	Equate entropy of thresholded and original distribuitions Cloglog threshold	0.1664
Alouatta caraya	Fixed comulative value 10 Clolog threshold	0.2691
Bradypus variegatus	Equal training sensitivity and specificity Clolog threshold	0.4175
Cabassous tatouay	Fixed comulative value 10 Clolog threshold	0.1769
Callicebus barbarabrowen	Minimun training presence Clolog threshold	0.1770
Callithrix jacchus	Maximun test sensitivity plus specificity Cloglog threshold	0.2183
Callithrix penicillata	Equal training sensitivity and specificity Clolog threshold	0.3097
Cavea aperea	Maximun test sensitivity plus specificity Cloglog threshold	0.3372
Cerdocyon thous	Maximun test sensitivity plus specificity Cloglog threshold	0.1852
Coendou baturitentsis	10 percentile training presence Cloglog threshold	0.6237
Coendou prehensilis	Equal training sensitivity and specificity Clolog threshold	0.2566
Conepatus amazonicus	Fixed comulative value 10 Cloglog threshold	0.2211
Cuniculus paca	Fixed comulative value 5 Cloglog threshold	0.2291
Dasyprocta leroporina	10 percentile training presence Cloglog threshold	0.3009
Dasyprocta prymnolopha	10 percentile training presence Cloglog threshold	0.3453
Dasypus novemcinctus	Minimun training presence Clolog threshold	0.0474
Dasypus septemcinctus	10 percentile training presence Cloglog threshold	0.2202
Didelphis albiventris	Balance training omission, predicted area and threshold value	0.0912
Didelphis marsupialis	10 percentile training presence Cloglog threshold	0.3733
Eira barbara	Equate entropy of thresholded and original distribuitions Cloglog threshold	0.2749
Euphractus sexcinctus	10 percentile training presence Cloglog threshold	0.3483
Galea spixii	Fixed comulative value 1 Cloglog threshold	0.1139
Galictis cuja	Fixed comulative value 1 Cloglog threshold	0.0304
Galictis vittata	10 percentile training presence Cloglog threshold	0.2710

Herpailurus yagouaroundi	10 percentile training presence Cloglog threshold	0.2881
Hydrochoerus hydrochaeris	Minimun training presence Clolog threshold	0.1464
Kerodon rupestris	10 percentile training presence Cloglog threshold	0.3063
Leopardus emiliae	10 percentile training presence Cloglog threshold	0.1889
Leopardus pardalis	Balance training omission, predicted area and threshold value	0.1565
Leopardus wiedii	Fixed comulative value 5 Cloglog threshold	0.1437
Lontra longicaudis	Fixed comulative value 5 Cloglog threshold	0.1921
Lycalopex vetulus	10 percentile training presence Cloglog threshold	0.3582
Mazama americana	Minimun training presence Clolog threshold	0.1896
Mymercophaga tridactyla	Minimun training presence Clolog threshold	0.1553
Nasua nasua	10 percentile training presence Cloglog threshold	0.4201
Ozotoceros bezoarticus	Fixed comulative value 10 Cloglog threshold	0.2406
Panthera onca	Fixed comulative value 5 Cloglog threshold	0.2263
Pecari tajacu	10 percentile training presence Cloglog threshold	0.4051
Priodonte maximus	Fixed comulative value 5 Cloglog threshold	0.1809
Procyon cancrivorus	Balance training omission, predicted area and threshold value	0.1260
Puma concolor	menor do que o treshould	0.0700
Sapajus apella	Fixed comulative value 5 Cloglog threshold	0.2363
Sapajus libidinosus	Fixed comulative value 10 Cloglog threshold	0.1598
Sapajus xanthosternos	Equate entropy of thresholded and original distribuitions Cloglog threshold	0.2477
Speothos venaticus	Minimun training presence Clolog threshold	0.1205
Subugulo gouazoubira	10 percentile training presence Cloglog threshold	0.3072
Sylvilagus brasiliensis	Fixed comulative value 5 Cloglog threshold	0.1763
Tamandua tetradactyla	Fixed comulative value 5 Cloglog threshold	0.2697
Tapirus terrestris	Fixed comulative value 10 Cloglog threshold	0.3576
Tayassu pecari	Fixed comulative value 5 Cloglog threshold	0.2266
Tolypeutes tricinctus	Minimun training presence Clolog threshold	0.5065

CAPÍTULO 3

Loss of seed dispersal interaction compromises carbon removals in the seasonally dry tropical forest region

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Abstract

The maintenance of tropical forests is strongly associated with interactions between animals and plants, such as seed dispersal. The loss of these interactions affects essential ecosystem functions such as atmospheric carbon removals and storage. In the Caatinga, the largest region of dry forest in South America, patches of native vegetation are identified as a carbon sink. However, the levels of forest degradation and defaunation of medium and large mammals that disperse seeds are very high in the region. Here, we evaluate the hypothesis that richness of zoochoric plant species is positively associated with aboveground biomass and carbon removals in the Caatinga. Furthermore, we evaluated whether the species richness of medium and large frugivorous mammals is also positively associated with carbon removals rates, as well as verifying whether the defaunation of these species alters this possible relation. Our results corroborate these hypotheses and show a typical scenario of the empty forest syndrome, where processes necessary for the maintenance of the ecosystem are compromised over time, if active measures are not implemented. We spatially characterize this scenario on a regional scale and make recommendations based on zoochoric plant diversity, aboveground biomass and species composition of frugivorous mammals that have become locally extinct throughout the Caatinga.

Key words: Caatinga, defaunation, ecosystem function, frugivores, mammals

Introduction

The proportion of zoochoric plant species, those dispersed by animals, increases from dry to humid forests, from temperate to tropical regions, and from higher to lower altitudes(Gentry 1982, 1995). Associatedly, in regions where zoochory diversity increases, there is greater diversity of wild fauna (Fleming et al. 1987). Zoochoric species play a key role in the natural regeneration of ecosystems and maintenance of plant species diversity (Herrera 1989), as well as the maintenance of these species that guarantees resources for the associated fauna (Galetti et al. 2015; Pires & Galetti 2023). This interaction between zoochoric species and disperser fauna can be compromised or lost by anthropic processes, such as hunting and habitat reduction (Dirzo et al. 2014; Young et al. 2016). While in habitat reduction, suppression has immediate and medium-term effects, in hunting, the effects of defaunation on processes associated with dispersal are slow, complex and imperceptible in the short term. In both situations there is loss of species, genetic heritage and biomass, with consequent loss of carbon storage, as they compromise the natural regeneration dynamics and functionality of ecosystems (Bello et al. 2015; Pereira Júnior et al. 2016; Pires & Galetti 2023).

The loss of ecosystem functionality in neotropical forest areas due to defaunation is known as the empty forest syndrome (Redford 1992). Empty forests may still have a high diversity of plants, but there is no presence of medium and large animals, responsible for the efficient dispersion of zoochoric species. As a consequence, the loss of this dispersion affects the structure of these forests in the long term (Terborgh et al. 2008). There is evidence of replacement of zoochoric species diversity by anemochoric or autochoric species (Peres et al. 2016). Also, over time, the dispersal pattern of some of these species may undergo changes, such as a selected reduction in seed size, as only small dispersers can occur in defaunated forests (Galetti et al. 2013, 2015). These alterations affect the structure of the forest, resulting in an increasing aggregation of individuals, low species diversity and genetic variability, with probability of extinction (Harrison et al. 2013).

Loss of seed dispersal leads to losses in aboveground biomass and, consequently, in carbon storage (Bello et al. 2015; Peres et al. 2016). Studies indicate, without dispersing species, forests cannot reach their maximum carbon storage potential, since the natural regeneration of plant species becomes limited. In rainnig forest, the effect of the defaunation of dispersing animals has already been corroborating this hypothesis, since most of the plants in these regions depend on this dispersion function (Bello et al. 2015; Peres et al. 2016). In neotropical dry forests, although plants with abiotic dispersion are the majority, around 40% of plant species with zoochoric dispersion (Griz & Machado 2001). n these areas, the anthropic effect has been acting since the beginning of the 17th century, with the expansion of agriculture and hunting, contributing to the defaunation of medium and large animals, mainly mammals (Bogoni et al. 2020a, 2020b).

In the Caatinga, the largest region of seasonally dry forest in South America, patches of native vegetation are identified as a carbon sink (Mendes et al. 2020). However, levels of forest degradation and defaunation of medium and large mammals are very high in this region (Capítulos 1 e 2). Therefore, both the reduction of aboveground vegetation biomass and the loss of seed-dispersing fauna can affect the natural carbon uptake potential in the region. However, the effects caused by the loss of these two mechanisms may have different temporal consequences. The reduction in biomass caused by forest degradation directly affects the ability to carbon removals. The loss of dispersers in areas that still have high biomass can characterize processes associated with the empty forest syndrome. Therefore, the reduction in carbon removals may not be observed, but these areas can be real time bombs regulated by the permanence of old trees and reduced recruitment rates.

Here, we tested the hypotheses that richness of zoochoric plant is positively associated with vegetation biomass in the Caatinga and, consequently, with greater carbon removals capacity. Furthermore, we evaluated whether species richness of medium and large-sized seed-dispersing mammals is positively associated with carbon removal rates, as well as whether the defaunation of these species alters this possible relation. If this process is observed, it is possible that it is evidence of observed effects of the late consequences of the empty forest syndrome.

Methods

Study area

The Caatinga, located in the semiarid region of Brazil, has an area of 863,752 km², being the largest and most continuous extension of seasonally dry tropical forest and woodland (SDTFW) in the world, with a high diversity of endemic flora (31 genus)

(Queiroz et al. 2017). The mammalian fauna presents a total of 183 species, 11 of which are endemic species, considered a heterogeneous fauna because it presents taxa with distribution in other regions and that currently live in the enclaves of other vegetation types in the region.

The Caatinga region is characterized by a diverse vegetation mosaic encompassing four biomes: Tropical Seasonal Dry Forest; enclaves of Tropical Rain Forests, located in mountain ranges; Savannas, located in areas with poor soils and low pH; and Rupestrian Grassland, limited to a section of Chapada Diamantina – BA (Queiroz et al. 2017). The region experiences a variation of annual precipitation ranging from 400 to 1200 mm, resulting in distinct local climates, with more arid environments in the central region and other rainier ones along the coastal area and in the mountains, due to the orographic effect.(de Andrade et al. 2017). Approximately 94% of the Caatinga's territory is at risk of desertification due to human interference (Vieira et al. 2015). primarily stemming from activities such as livestock farming, agriculture, and mineral extraction, which have been the main drivers of environmental degradation in the Caatinga (Alves et al. 2009).

Zoochoric plants

We conducted a bibliographical survey using "Google Scholar", "Scielo", "Web of Science" and "ScienceDirect", databases, employing word combinations such as "phytosociolog", "Caatinga", "floristic", "dispersal syndrome" to access available information on arboreal floristic composition in Caatinga. From the compiled data, we grouped locality the nearby georeferenced with a maximum distance of 2km, summing the richness of the localities. This process resulted in the registration of 34 locality in the region, accumulating a total richness of 77 arboreal species. We use just arboreal species with zoochory syndrome dispersal accumulating a total of a maximum of 52 species of zoochoric plants.

Aboveground biomass

The data aboveground biomass density megagrams per hectare was extract in the Global Forest (https://data.globalforestwatch.org/datasets/gfw::aboveground-live-woody-biomass-density/about). The global benchmark map of aboveground biomass density for the year 2000 at 30-m spatial resolution is the result of integrating ground measurements, airborne and spaceborne LiDAR data with satellite images. The basic approach follows the one developed to map tropical biomass at 500-m resolution (Baccini et al. 2012) and 30-m resolution (Zarin et al. 2016). For more information about the calculation can be found in Harris et al. (2021).

Carbon Removals

The removals carbon data was extracted for Global Forest (https://data.globalforestwatch.org/datasets/gfw::forest-carbon-removals/about).This carbon removals layer is part of the forest carbon flux model described in Harris et al. (2021). This paper introduces a geospatial monitoring framework for estimating global forest carbon fluxes which can assist a variety of actors and organizations with tracking greenhouse gas fluxes from forests and decreasing emissions or increasing removals by forests. Forest carbon removals from the atmosphere (sequestration) by forest sinks represent the cumulative carbon captured (megagrams CO^2/ha) by the growth of established and newly regrowing forests during the model period between 2001-2022. Removals include accumulation of carbon in both aboveground and belowground live tree biomass.

Species selection and defaunation estimates

We selected species of medium to large bodied mammals (mlbm) that occur in the Caatinga based on their large home range ($>5km^2$), their position at the top of the trophic level, and their relatively smaller population size compared to small mammals (Feijó & Langguth 2013). To do that, we conducted a bibliographical survey using "Google Scholar" "Scielo", "Web of Science", and "ScienceDirect" databases, employing word combinations such as "medium to large bodied mammals", "check-list", "Caatinga", "hunting", "ethnofauna" to access available information on mlbm assemblies in Caatinga. We also used the Global Biodiversity Information Facility (Gbif – https://www.gbif.org) and Specieslink (https://specieslink.net) platforms to supplement data on species occurrence points. From the compiled data, we grouped species that were georeferenced in the same locality and selected assemblages with a richness of at least five species, based on current literature (Bezerra et al. 2014) and field-collected information. This process resulted in the registration of 73 assemblages distributed throughout the region, accumulating a total richness of 51 species. But we used just species the according with your percentage diet-type where almost is frugivores and/or herbivores (Paglia et al. 2012; Wilman et al. 2014). Totaling 53 assemblages and 18 mammals with large seed dispersal potential.

We estimate the defaunation in the Caatinga by subtracting values from a raster file with information on the distribution of the selected mammalian species predicted for the recent past (550 years ago, equivalent to Brazil's pre-colonization period) and a raster with an estimate of the current distribution. Below are the details of how these rasters were prepared (Figure 1).

Past mammals

The potential distribution of the species the mlbm was considered as past distribution of these species. For this, we perform predictive species distribution modelling (SDM) considering current climate and topography conditions, for South America, and we cut at the limit of the Caatinga (IBGE 2019) (Figure 1). Thus, we estimate the distribution of these species without using layers of land use and land cover, that is, without restriction caused by human actions. We used 19 climatic variables more elevation from Worldclim (www.worldclim.org), at a spatial resolution of 2.5 arc-minutes. We included in the models the variables with a correlation < 0.8 to avoid redundancy. To do that, we used Pearson’s correlation, calculated using the “vegan” package for R (version 3.5.3). At the end, we used the variables: mean temperature diurnal range (BIO2), temperature seasonality (BIO4), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO09), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of driest quarter (BIO17), precipitation of warmest quarter (BIO18), precipitation of coldest quarter (BIO19), and elevation.

We used the Maximum Entropy algorithm v.3.4.1 (MaxEnt) (Elith et al. 2011) to generate the modeled geographic distributions of each selected species. MaxEnt models are a probability distribution where each grid cell has predicted the suitability of conditions for the species (Elith et al. 2011). We used the Receiver Operator Characteristic (ROC) statistic to assess the model’s accuracy, with 10 repetitions of 10,000 iterations maximum, 10% of the average repetitions were randomized as test data, and the remainder was randomized for training the model in each replication. Each species predictive map was transformed to a binary map (0 absent, 1 presence) that was delimited using MaxEnt thresholds (Anexo S2). We chose the thresholds that defined the smaller potential habitat following a conservative approach and do not overestimate the geographic distribution. To obtain the final raster with potential species richness representing past conditions, we summed all binary maps (Figure 1).

Current mammals

The current species were those selected from the literary database. Based on their percentage of diet, we selected 18 of the 51 species and totaled 58 assemblages of medium and large dispersing mammals (Figure 1).

Data analysis

We extracted metrics of aboveground biomass and carbon removals from boundaries of 32 localities with zoochory plant species recorded. For that, we employed 500m radios buffer from each locality as respective boundary. As the predictor variable, we considered the zoochory species richness in each of the 32 assemblages. All vector and matrix spatial analyze were performed using the open-source software QGIS version 4.4.14 Madeira (Figure 1).

For the mammal species data, we employed a 5km radios buffer corresponding to the 58 mammals assemblages, and we extracted from this limit the metrics of aboveground biomass and carbon removals. As the predictor variable, we considered the species richness of dispersers and the respective defaunation data in each of the 58 assemblages.

To verify our hypotheses, we used generalized linear models (GLMs). The GLM estimates the parameters through maximum likelihood. Therefore, it relates the distribution of the response variable (aboveground biomass and removals carbon) with linears predictors (zoochory species richness, disperser species richness and defaunation) through a link function. As our response variables are continuous data, we used Gaussian distributions. The models generated by the "mass" package and the graphics production by the "ggplot2" package on the R platform.

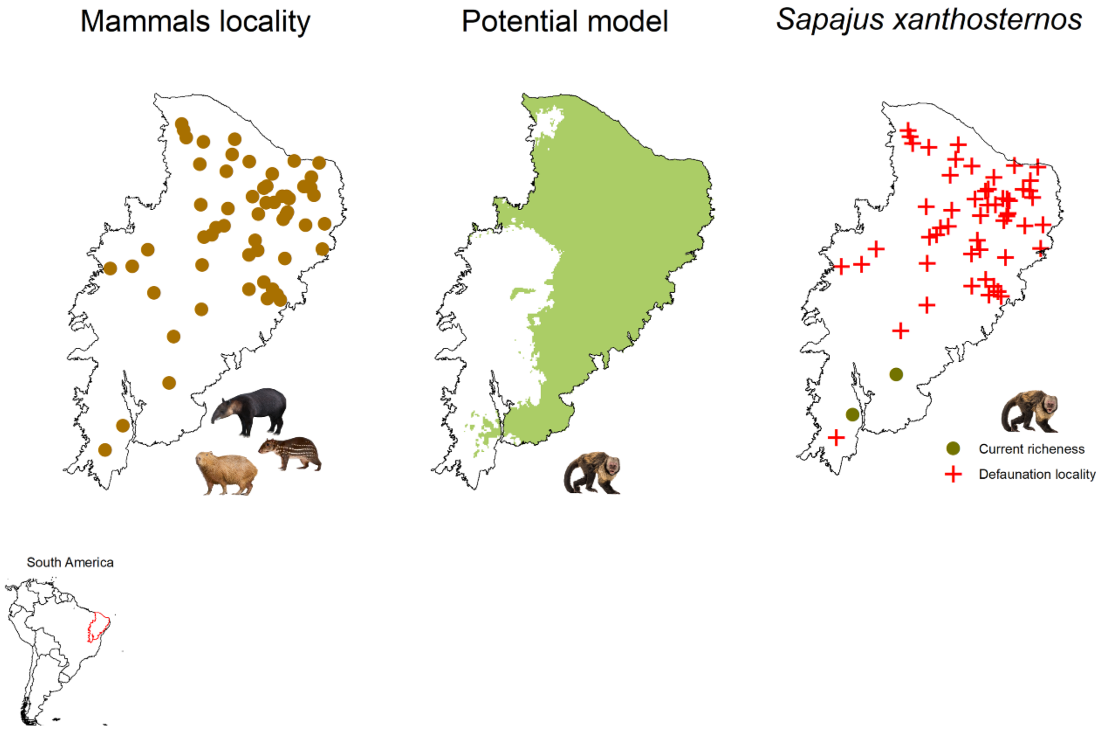

Figure 1. Map of the Caatinga. A) Boundary of the Caatinga with reference points of occurrence for seed-dispersing mammals. B) Potential model generated by MaxEnt of the species *Sapajus xanthosternos* (golden-bellied capuchin) in the limit of the Caatinga. C) Current location where *S. xanthosternos* live (olive green dot) and potential occurrence of this species in today's locations, but no longer exist (red cross).

Results

As expected, there is a positive relation between carbon removals and aboveground biomass ($p < 0.001$, estimates 574.5) in the Caatinga region (Figure 2). We also found positive relationship between species richness of zoochoric plants and aboveground biomass, and carbon removals ($p < 0.01$ in both relations, estimates 2880.45 and 1285.6 for aboveground biomass and carbon removals respective) (Figure 3). The distribution of these relationships is spread across the Caatinga region (Figure 4).

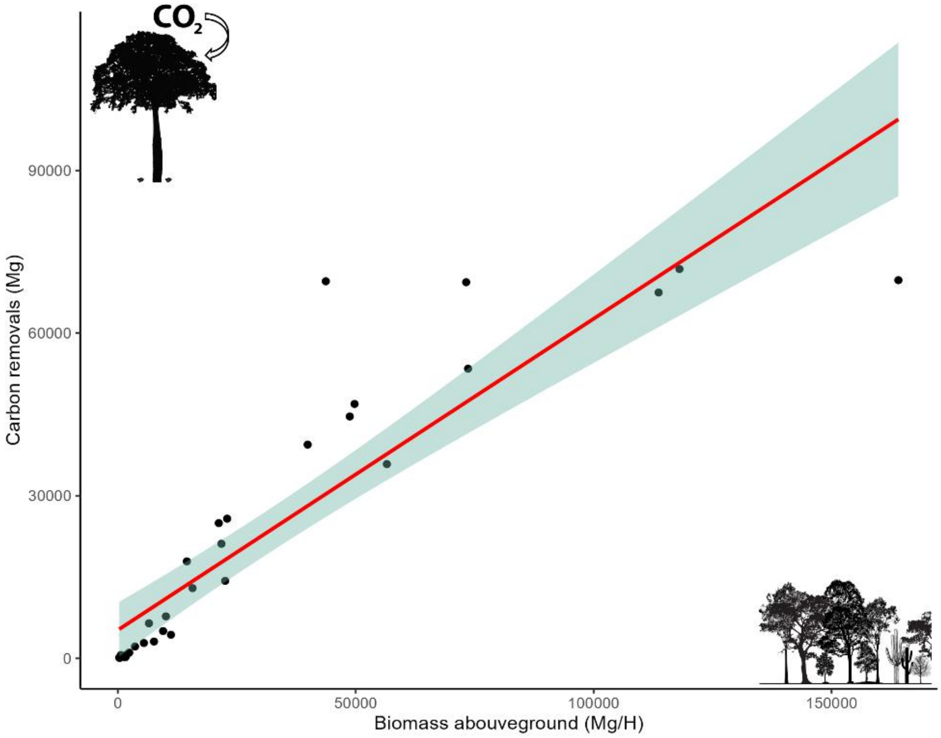

Figure 2. The positive relation between carbon removals (Mg) and aboveground biomass (Mg) in localities used in the work.

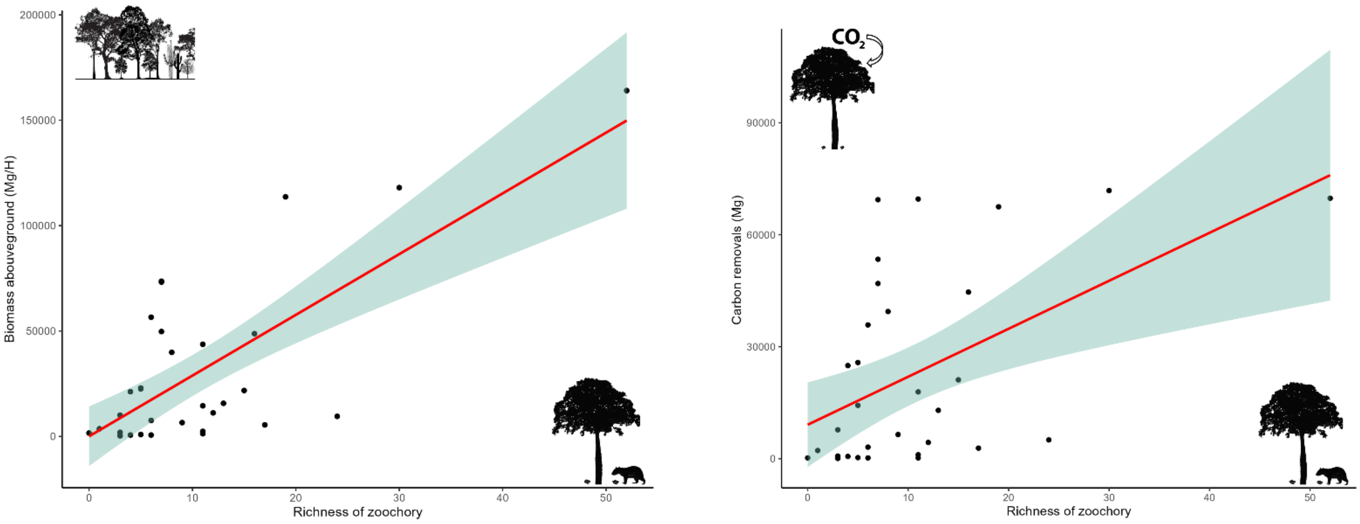

Figure 3. A) The positive relation between richness of zoochoric plants and aboveground biomass. B) The positive relation between richness of zoochoric plants and carbon removals.

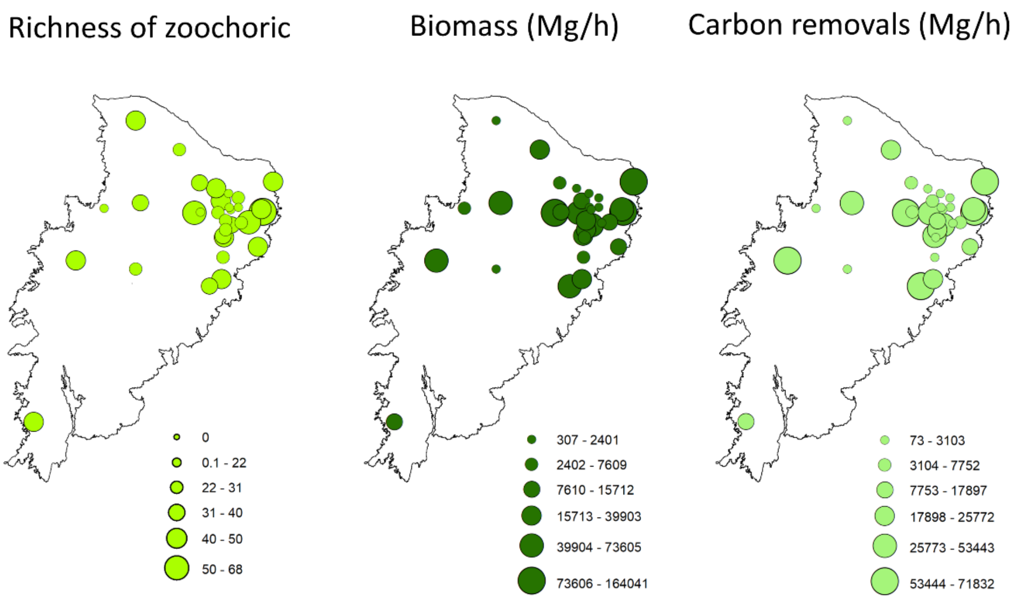

Figure 4 – Map showing the limit Caatinga with: A) species richness of zoochoric plants in the studied localities; B) aboveground biomass in the studied localities; C) carbon removals in the studied localities.

We found a positive relation between current species richness of frugivorous mammals and carbon removals ($p < 0.01$, estimates 369839). However, we did not find negative relationship between defaunation of this species and carbon removals ($p > 0.05$), although the tendency of this relationship is oppositive to the tendency of the species richness of frugivorous mammals relation (Figure 5).

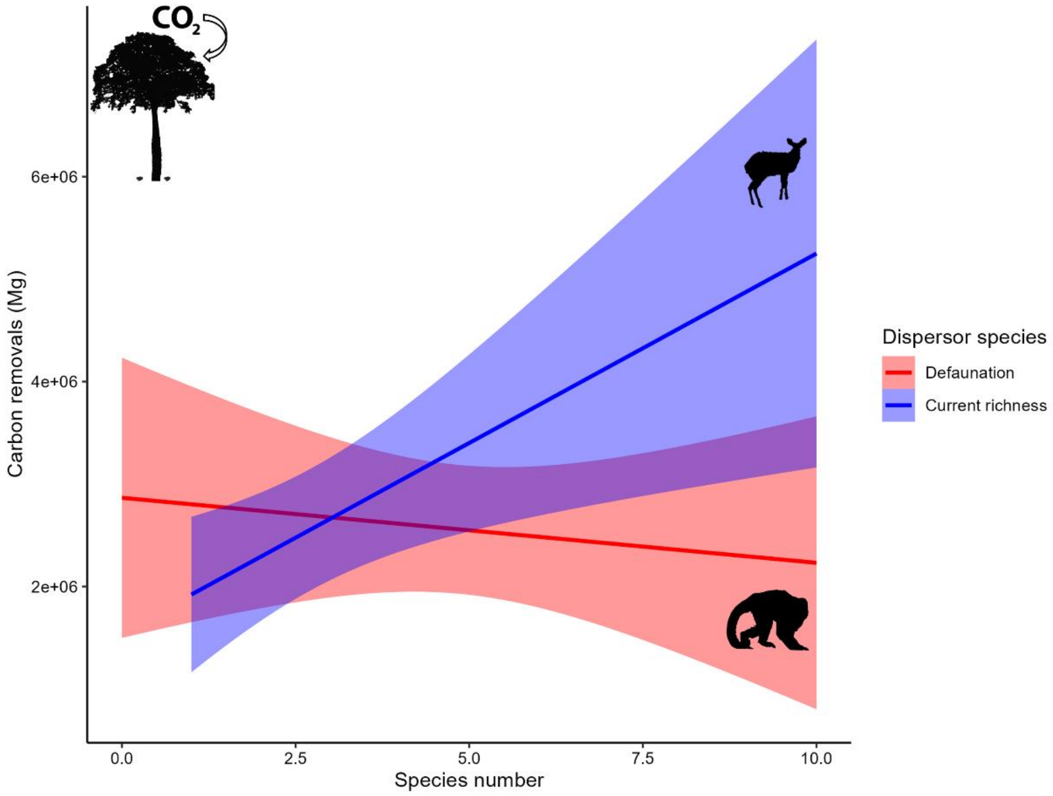

Figure 5. The positive relation between current frugivorous mammals richness and carbon removals (blue line). The null relation between defaunation these mammals and carbon removals (red line).

By analyzing the defaunation data, we identified the percentage of loss of the 18 species of frugivorous mammals in the studied localities. Of the 18 listed, 16 lost more than 50% of their occupation. Among them, the main ones are the *Sapajus xanthosternos* (~95%), endemic species in the region and critically endangered, *Hydrochoeros hydrochaeris* (~90%), and *Coendou prehensilis* (~80%) (Figure 6).

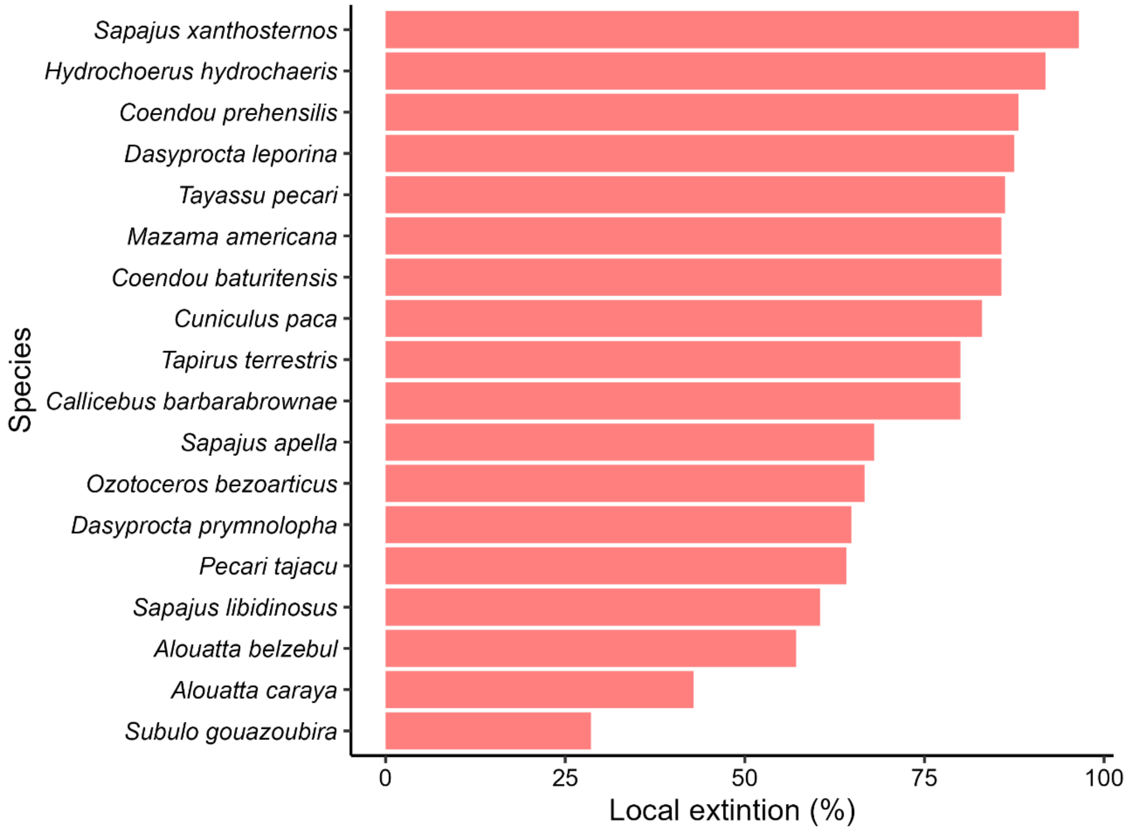

Figure 6. Observed rates of the occurrence loss of frugivorous mammals species across the 53 mammal assemblages distributed throughout the Caatinga. Species are listed from the highest to the lowest local extinction rates (top to bottom).

Discussion

Our results show that localities with the higher richness of zoochoric plants tend to remove more carbon in the Caatinga region. The increase of these plant species increases the aboveground biomass, which consequently increases the carbon removals. Our results also indicate that localities with the higher species richness of medium and large frugivorous mammals tend to remove more carbon. The defaunation of these mammals did not affect the carbon removals but show a different tendency of the positive relationship between species richness of frugivorous mammals and carbon removals. It is possible that many localities keep aboveground biomass in the Caatinga but have already lost these medium and large mammals. Therefore, this extinction is limiting to the regeneration of zoochoric plants and may result in the empty forests scenario.

Similar to the pattern found in rainnig forests (Bello et al. 2015; Peres et al. 2016; Chanthorn et al. n.d.), areas with higher zoochoric plant species richness have higher aboveground biomass and store more carbon in the Caatinga . In this region, the largest amount of carbon storage is found in forest and/or arboreal areas and the largest proportion of this stored carbon is found in the soil (Menezes et al. 2021). This higher retention of carbon in the soil decreases its emission into the atmosphere, since soils on dry land are less subject to mineralization (FAO 2004; Fu et al. 2013). Furthermore, higher carbon storage is associated with organic carbon availability and higher soil moisture retention, which is positively related to fertility and productivity in dryland ecosystems(Lal 2004; Yeboah et al. 2021). Therefore, the diversity of zoochoric species and the interactions responsible for maintaining this diversity are extremely strategic for the occurrence of fundamental functions in dry tropical forest regions, such as carbon storage and productivity. As the semiarid regions in the American continent are on the verge of collapse due to losing the functional capacity of the ecosystem (Ferrer-Paris et al. 2019), actions to recover these fundamental processes are necessary and urgent.

The zoochoric plant necessarily depend on some animal to efficiently disperse their seeds. Generally, large frugivores play an important role in this dispersion because they are characterized as wandering animals, with a greater capacity to retain seeds in the body and disperse them further away from the mother plant (Boone et al. 2015; Pires et al. 2018). There is evidence of a positive correlation between mammalian species size and seed size (Fleming & Kress 2013). In rainnig forests, many of these large seed plants absorb more carbon, and in these forests there is a greater diversity of large frugivorous mammals (Bello et al. 2015; Peres et al. 2016). The positive relationship between diversity of frugivorous mammals and carbon removals found here suggests that this pattern may also occur in the Caatinga. However, in addition to the historic forest degradation that directly reduces biomass in the region, the high rates of defaunation associated with the downsizing effect indicate that the regional potential for carbon storage has already been drastically reduced and, even so, may decrease due to the effect of the empty forest, if no action is taken to reverse this scenario.

We show that sites that still harbor a greater diversity of medium and large-sized frugivorous mammals are sites that sequester more carbon in the Caatinga. On the other hand, the places where the higher loss of these species are projected are still not the places that sequester carbon the least. This suggests that there are areas with high aboveground biomass, but that it has lost much of the diversity of these disperser species. Therefore, the reduction or loss of dispersal efficiency in these forest areas due to defaunation may characterize an effect of the empty forest syndrome (Redford 1992) in the Caatinga. Generally, with losses of frugivorous animals, there is a greater local agglomeration of plant species over time (Guimarães et al. 2008), which also generates changes in the distribution of available fruit to attract generalist dispersers, which consequently promotes loss of fruit distribution diversity of plant species (Guimarães et al. 2008). As defaunation not only generates loss of diversity of plant species, but also loss of ecosystem functionality, a process similar to a ticking time bomb can regionally characterize ecosystem functioning in the Caatinga. Several areas in the region already have collapsed ecosystem functions due to limits exceeded by the reduction of aboveground biomass (Tabarelli et al., 2023). And, even areas that still maintain high biomass, may have their maintenance processes compromised in the long term due to the loss of dispersers.

Finally, due to the scenario of reduction and loss of ecosystem functioning described here, we recommend urgent measures to reverse the trajectory of carbon and productivity losses in the Caatinga: 1) urgent forest recovery actions in areas with low aboveground biomass; 2) increase in the diversity of zoochoric plants in these recovery actions or in places that need to enrich these species; 3) refaunation project, focusing on the reintroduction of frugivorous seed-dispersing species. Some of these species (see figure 4) can still be found in the region, or in other regions of Brazil to be used in captive breeding and reintroduction programs.

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