UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

LARGE MAMMALIAN HERBIVORES MODULATE PLANT LIFE-FORM DIVERSITY IN TROPICAL FORESTS

YURI SILVA DE SOUZA

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Dissertação apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Mestre em Ecologia e Biodiversidade

Orientador: Prof. Dr. Mauro Galetti

Coorientador: Prof. Dr. Tadeu de Siqueira Barros

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This work is dedicated to those more than 250,000 people who died by SARS-CoV-2,
To nurses and doctors who are risking their lives to avoid more deaths by SARS-CoV-2,
To thousands of researchers that lose their jobs and financial support,
To hundreds of women and LGBTQ+ people that were violented or murdered,
To those that risk and lost their lives protecting our biodiversity against governmental services,
All of this in Brazil, during the government of president JAIR BOLSONARO

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“But of bliss and glad life there is little to be said, before it ends;
as works fair and wonderful, while still they endure for eyes to see,
are their own record, and only when they are in peril
or broken for ever do they pass into song.”

J. R. R. Tolkien - The Silmarillion

RESUMO

Os biomas terrestres do mundo são amplamente classificados de acordo com as formas de vida de plantas dominantes que definem a estrutura e os processos do ecossistema. Embora a abundância e distribuição dessas formas de vida possam ser fortemente determinadas por fatores como clima e composição do solo, grandes mamíferos herbívoros têm um forte impacto nas comunidades dessas plantas, portanto, a defaunação (a extinção local ou funcional de grandes animais) tem o potencial de alterar a estrutura de composição das formas de vida das plantas em ecossistemas naturais. As florestas tropicais sustentam uma grande diversidade de formas de vida, incluindo árvores, palmeiras, lianas, arbustos, ervas e bambus, todos os quais desempenham funções importantes do ecossistema. Aqui, avaliamos experimentalmente como grandes mamíferos herbívoros afetam a dominância, diversidade e coexistência de formas de vida de plantas em florestas tropicais usando um experimento de exclusão replicado de longo prazo na Mata Atlântica do Brasil. Ao longo de 10 anos, a exclusão de grandes herbívoros diminuiu a diversidade de formas de vida, aumentou a abundância absoluta de palmeiras e árvores (22% e 38%, respectivamente) e aumentou a diversidade de espécies dentro desses dois grupos, em detrimento de outras formas de vida. Além disso, todas as correlações entre formas de vida foram positivas em parcelas onde os herbívoros tinham acesso, enquanto várias relações negativas surgiram em parcelas onde os herbívoros foram excluídos. Isso ocorreu devido a diversos mecanismos temporais que afetou as comunidades de plantas em ambos os tratamentos experimentais. Nosso trabalho indica que a defaunação altera a dominância das formas de vida e diminui a diversidade e coexistência dessas plantas e, portanto, pode levar a impactos profundos em funções importantes do ecossistema e uma simplificação na estrutural vertical das florestas tropicais.

Palavras-chave: Experimento de longo prazo, herbivoria, defaunação, mudanças climáticas, dinâmicas competitivas.

ABSTRACT

The world’s terrestrial biomes are broadly classified according to the dominant plant-life forms that define ecosystem structure and processes. Although the abundance and distribution of different plant life-forms can be strongly determined by factors as climate and soil composition, large mammalian herbivores have a strong impact on plant communities, thus defaunation (the local or functional extinction of large animals) has the potential to alter the compositional structure of plant life-forms in natural ecosystems. Tropical rainforests sustain a high diversity of life-forms, including trees, palms, lianas, shrubs, herbs, and bamboos, all of which play important ecosystem functions. Here, we experimentally evaluate how large mammalian herbivores affect the dominance, diversity, and coexistence of these major tropical forest plant life-forms in a long-term replicated exclusion experiment in the Atlantic Forest of Brazil. Over the course of 10 years large herbivore exclusion decreased life-form diversity, increased the absolute abundance of palms and trees (22% and 38%, respectively), and increased the diversity of species within these two groups, in the detriment of other life-forms. Furthermore, all pairwise relationships between life-forms were positive on plots where herbivores had access, whereas several strong negative relationships emerged in plots where herbivores were excluded. This occurred despite strong background directional temporal trends affecting plant communities in both experimental treatments across the region. Our work indicates that defaunation alters life-form dominance and erodes life-form diversity and coexistence and hence might lead to profound impacts on important ecosystem functions and a vertical and horizontal structural simplification of tropical rainforests.

KEY-WORDS: long-term experiment, herbivory, defaunation, climate change, competitive dynamics.

SUMMARY

1. INTRODUCTION

The life-form of any given plant species is the outcome of its adaptive evolution history resulting from its interaction with the biotic and abiotic environment over an evolutionary time scale (Ewel and Bigelow, 1996). Through the course of its evolution, the plant kingdom has diversified, adopting a variety of strategies and traits adapted to different environments (Clarke et al., 2011). Such strategies have been crucial in allowing plants to thrive in almost every natural place on Earth (Woodward and Williams, 1987; Kreft and Jetz, 2007). At the morphological level, the vast diversity in plant strategies and traits can be simplified in different plant life-form categories, each one defining broad strategies and structural adaptations common to all species within such life-form. Beyond their adaptative value, life-forms have an important functional value, so that life-form composition influences both ecosystem structure and processes (Ewel and Bigelow, 1996; Ghazoul and Sheil, 2010). Different biomes, such as tropical and temperate rainforests, grasslands, shrubland, and tundra, are broadly classified based on the dominance of different plant life-forms, stressing the strong influence of these life-forms on ecosystem processes. For example, tropical rainforests are dominated by trees that stock large amounts of carbon and contribute to the litter layer with their leaves, branches, and fruits, promoting feedbacks on decomposition, soil nutrient cycling, and material flows (Ewel and Bigelow, 1996; Ghazoul and Sheil, 2010). In contrast, fallen fronds from palms with large volume and slow decomposition rate can prevent plant recruitment in the understory by physically damaging seedlings, suppressing the germination of many plants, and slowing down decomposition (Denslow, 1996; Beck, 2017). Thus, plant life-form dominance and diversity might influence ecosystem dynamics and function (Ewel and Bigelow, 1996).

Tropical rainforests hold the highest diversity of plants on the planet with a rich variety of life histories, growth strategies, and life-forms (Denslow, 1996; Andersen et al., 1997; Kreft and Jetz, 2007). Trees, shrubs, lianas, palms, epiphytes, and other plant life-forms coexist in a vertically and horizontally stratified and structurally complex ecosystem, where they engage in a myriad of biotic competitive, mutualistic, and antagonistic interactions (Andersen et al., 1997; Ewel and Hiremath, 2005; Ghazoul and Sheil, 2010). Natural and anthropogenic disturbances, such as climate change, forest fragmentation, and selective logging might favor some life-forms to the detriment of others (Dupuy and Chazdon, 1998; Wright et al., 2007; Feeley et al., 2020; Püttker et al., 2020). The local or functional extinction of wildlife, a phenomenon called defaunation (Dirzo et al., 2014; Püttker et al., 2020), might also affect the diversity and coexistence among plant life-forms yet its effects on life-form composition and diversity have been poorly explored. These animals sustain functions that cannot be replaced by other faunal groups and are the most susceptible to any unsustainable human activity, with knock-on consequences on ecosystem dynamics and functioning (Dirzo et al., 2014; Püttker et al., 2020).

There is growing evidence suggesting that large mammalian herbivores (LMH) modulate plant species composition and community interactions in these ecosystems. LMH consume large amounts of fruits and seeds in tropical forests, hence acting as seed predators and dispersal agents, though the net effects of the combination of these functions are still unresolved (Bodmer and Ward, 2006; Kurten and Carson, 2015; Williams and Jedediah, 2018; Villar et al., 2020). LMH also consume seedlings and damage plant tissues and physical structures through browsing, trampling, and by overturning large amounts of soil (Coley and Barone, 1996; Villar et al., 2020). Furthermore, LMHs prevent the proliferation of smaller mammalian herbivores (Galetti et al., 2015a) and affect nutrient cycling in tropical forests (Villar et al., 2020). Thus, LMH affects plant communities in tropical rainforests through many direct and indirect pathways, all of which can have a strong impact on plant recruitment, dominance, diversity, and composition, most likely benefiting some life-form adaptations to the detriment of others (Kurten et al., 2015; Malhi et al., 2016; Luskin et al., 2019; Villar et al., 2019).

Studies addressing defaunation effects on tropical rainforest life-form composition and diversity are utterly scarce, mainly focused on the balance between trees and lianas, and sometimes contradictory. For instance, defaunation has been shown to promote lianas within the seedling banks in a Central American rainforest (Wright et al., 2007). This contrasts with the findings of another study from South-East Asia, where the experimental exclusion of artificially abundant large herbivore densities has led to a temporal decline in lianas to the benefit of trees (Luskin et al., 2019). Such contradictory results highlight the need for a broader evidence base that addresses the impacts of LMH on life-form composition, diversity, and coexistence. This is also important from a functional perspective. For example, lianas have lower carbon storage capacity when compare to trees (van der Sande et al. 2013), a and therefore an increase in lianas cannot compensate for the deficits from a concomitant decrease of other carbon-rich life-forms. Yet, by an excessive focus on the dichotomy of lianas vs. trees, the limited number of studies available neglect the potentially important effects of defaunation on other dominant life-forms, such as palms, shrubs, herbs, and bamboos. Evidence suggests that the spatial distribution and demography of palms, for example, might be affected by defaunation (Fragoso et al., 2003; Galetti et al., 2006; Valverde et al., 2020).

Here we address how defaunation impacts upon plant life-form dominance, diversity, and coexistence in tropical rainforests. We used a long-term multi-site replicated large mammalian herbivore exclusion experiment to investigate if defaunation in tropical rainforests affects i) absolute and relative abundances of different plant life-forms, ii) pairwise relationships between coexisting life-forms, and iii) diversity among and within life-forms. Our hypothesis is that lianas will become the dominant life-form in defaunated rainforests since they benefit at different degrees from alternative seed dispersal strategies (wind or small birds), low seed predation rates, and low mechanical damage that occur in the absence of LMH (Wright et al., 2007). Consequently, we expect that increased dominance by lianas negatively affects life-form diversity and coexistence.

2. METHODS

2.1. Study sites

The study is part of the DEFAU-BIOTA, a long-term experiment on LMH exclusion in the Atlantic forest of Brazil. It was carried out in four evergreen forest regions in the Atlantic forest in southeastern Brazil. Two of them, Itamambuca and Vargem Grande field station (ITA and VGM, respectively), located at Santa Virgínia-Serra do Mar State Park, are in the largest continuous reserve area throughout the Atlantic forest (332,000 ha). The other two sites are Carlos Botelho State Park (CBO, 37,633 ha) and Ilha do Cardoso State Park (CAR, 13,500 ha) (Figure S1, Supplemental Material). The altitude in these areas varies from sea level to 975 m heigh, with the annual temperature average around 20-24^{o} C and precipitation around 1500-4000 mm. In these sites, tapirs *Tapirus terrestris* and white-lipped peccaries *Tayassu pecari* are the largest ground-dwelling LMHs (31). Agoutis *Dasyprocta* spp., pacas *Cuniculus paca*, brocket deer *Mazama* spp., and collared peccaries *Pecari tajacu*, amongst other ground-dwelling frugivorous species, are also present at the sites, as well as arboreal primates (e.g., howler monkey *Alouatta guariba*, woolly spider monkey *Brachyteles arachnoides,* capuchin monkeys *Sapajus nigritus*), though the effects of these is not the focus of the study. For more information about respective areas and sample design see Villar et al. (2019).

2.2. Experimental plots and plant sampling

In 2009 15 exclusion and open control paired plots, separated by 2–7 m, were established in each of the four areas, totaling 60 exclusion and 60 control plots. Each pair plot was located at least 200 m from the closest pair. The exclusion plots were fenced using a 1.6 m high metal fence, with 5 cm wire mesh, barring the entrance of all medium and large-sized ground-dwelling mammals but allowing access to small rodents and marsupials. The control plots were open, only demarcating their areas with a line and plastic piles. Due to the natural falling of trees by natural uncontrolled causes, some plots were damaged and lost. In this work, we used data from the remaining 86 individual plots (43 pairs) that survived to October 2019. CBO was the first sampled area, starting in 2009, and the other three areas started in 2010; thus, we standardized our dataset to the minor common number sampled between the areas, 108 months.

Both exclusion and control plots were 5x3 m (15 m^2) and each plot was divided by eight 1 m^2 subplots. We sampled only three 1 m^2 subplots from each plot and used the other ones for fieldwork manipulations and access, avoiding human damage or disturbance on the main sampled plots. For every plant early stage, mentioned here as sapling, between 0.1 to 1-meter height inside the three 1 m^2 subplots, we identified the family and species, and classified it as one of the following six life-forms: lianas, palms, trees, herbs, shrubs, or bamboos (Figure S2, Supplemental Material). No palms with liana habit (e.g., *Desmoncus* spp.) occurred in our sites. Out of 8,729, a total of 1,629 individuals of other life-forms were too uncommon to be included in our analyses. Since some plant families or species have more than one life-form during its life-time, we used the sapling life-form description from Souza & Lorenzi (2012) and the “Flora do Brasil” website (http://floradobrasil.jbrj.gov.br/) for classifying these individuals.

2.3. Life-forms general descriptions

2.3.1. Trees

Trees are a life-form present in almost all the land places on the earth, with exceptions only in some Icelandic areas as Antarctica, and their diversity increase in direction of the tropical forests in the tropics since these places have favorable environments as light availability and nutritive soils (Turner, 2004). The presence of a resistant wood and suber material provides most of the mechanical support and guides trees to a vertical distribution, with individuals of tall species and different stature classes with high stocked biomass, been these particularities the most important difference of trees to other life-forms (Jeronimidis, 1980; Gonzalez de Tanago et al., 2018). The vertical composition of the trees may reflect the relative illumination at different heights above the forest floor (Turner, 2004). The horizontal variation in light availability due to irregularity in canopy structure (presence of gaps, different height, etc.) could also result in the subtle environmental variations providing the many niches variation for trees and also other life-forms, as the epiphyte (Kohyama, 1993). Trees have higher levels of genetic diversity that seem to be capable of rapid adaptation to new conditions (as climate change and human disturbance) (Vieira et al., 2015). The wood structure of trees and the high resistance of their branches is important to many invertebrates and vertebrates. These structures connect trees canopy and can provide a path for arboreal species (as squirrels and monkeys) as so protection from terrestrial predators, been a great support for primates and birds nests, and also providing food for animals by producing leaf, flowers, and nutritive fruits that attract fauna to be dispersed (Turner, 2004). The dispersal of tree seeds is diverse and can also be through abiotic ways as wind and water (Sinha and Davidar, 1992; Parolin et al., 2013).

2.3.2. Palms

Geographically, palms can be found in habitats ranging from 44o north latitude to 44o south latitude, but the majority of palm species are native to the tropical regions of the earth (Johnson, 2011). Palms are the life-forms that belong to the family Palmae and morphologically have woody stem or trunk and don’t have branches (Dransfield et al. 2008). Within tropical forests, some palm species may be tall enough to be emergent and to form a part of the canopy or they may be understory species of short stature adapted to shady conditions (Johnson, 2011). Palms typically bear their leaves, frequently referred to as fronds, in a crown at the top of the stem, and the type of crown is diverse. In a forest setting, the leaves of palms are generally large making them a key aspect of identification (Dransfield et al., 2008). Some palm species may require from as little as two years to 40 years or more to reach mat maturity and begin to flower and produce fruit (Johnson, 2011). To be dominant in most tropical ecosystems palms often a key functional component, forming complex assemblages, comprising co-existing life forms, and occupy all layers of the forest (Balslev and Fay, 2016). Zoochory is a common mode of dispersal by palms and obligate and opportunistic frugivores as many birds, non-flying mammals, reptiles, insects, and fish feed on their fruits and disperses their seeds (Zona and Henderson, 1989). Palms produce huge amounts of fruits and other valuable products that can also be explored by the economy of local communities or industries (Macía et al., 2011).

2.3.3. Lianas

Broadly distributed in the trophic and correlated negatively with mean annual precipitation and positively with seasonality, lianas is a life-forms recognized by their unique ability to use other plants to climb to the forest canopy and produce large numbers of leaves that cover those of their host, generally trees, palms, and shrubs, thus competing for light (Schnitzer et al., 2014). By their tangles, lianas provide critical inter-crown pathways in the canopy and the understory, providing structure as refuges, nests, and connections for non-volant arboreal and terrestrial animals (Yanoviak, 2014). These abilities bind the forest canopy together can potentially reduce treefalls when liana connectivity is high (Schnitzer et al., 2014). However, lianas abundance is also correlated with treefall gaps and larger-scale forest disturbances, been often classified as early successional or gap-dependent pioneer species, which can arrest forest succession and alter successional trajectories by their ability to colonize and proliferate in gaps (Isnard and Field, 2014). Lianas also produce leaves, flowers, and fruits disperse abiotically and biotically by many vertebrates, which may be critical for the survival of many animal species, especially during the dry season when lianas grow more and produce more leaves and fruits than trees (Arroyo-Rodríguez et al. 2014). In the tropical forest, the lianas slender stems are capable of moving lots of water and supplying a large canopy of leaves contributing to 40% of leaf productivity of the tropical forest, but only less than 5% of total aboveground biomass (Isnard and Field, 2014). These abilities jointly make lianas an important factor that controls plant species distribution, species diversity, plant competition, large-scale structural change in tropical forests, and ecosystem functions (Arroyo-Rodríguez et al., 2014; Isnard and Field, 2014).

2.3.4. Shrubs

Shrubs can be distinguished as small woody plants either with multiple stems or with branching very close to the ground, distributed worldwide in high and low-temperature ecosystems, been dominants in those habitats that place plants under considerable stress (Turner, 2004). Since shrubs live in rapidly changing environments they are considering among the most rapidly evolving species on earth, having genetic flexibility that allows their many species to rapidly adjust to environmental fluctuations (Stutz, 1989). Woodiness must also be counted as an advantage in providing reduced palatability to herbivores and it permits shrubs to tower above most herbaceous plants layer with which they grow, obtaining an advantage in harvesting sunlight. Further, the short and medium stature of shrubs reduces transpiration costs under drought conditions, and susceptibility to damage from winds, storms, and fires. These advantages have probably been a significant advantage against tall life-forms as trees and palms (Stutz, 1989). The shrubs stem and foliage structure is also mentioned to facilitate the storage of soil moisture by the dissipation of raindrop energy reducing compaction under the shrub cover leading to lower bulk densities, which additionally facilitate better infiltration (West, 1989). The success and arrangements of shrubs also depend on their interaction with animals as pollinators, frugivores, and herbivores, since many species of shrubs have attractive, succulent, or nutritive fruits. These fruits are often dispersed by birds and small mammals (McArthur, 1989).

2.3.5. Herbs

Herb is a life-form present over all the land ecosystems and represents the herbaceous layer. Their life-form includes species of diverse phylogenetic origin that have evolved a wide range of life-history adaptations that allow them to persist and flourish in an environment that is often light-limited (Muller et al., 2003). Herbs diversity is higher in tropical forests since this forest has heterogeneity, opportunities, and niche diversification, allowing the many herb life-history strategies to have success in an environment with low light conditions (Azevedo et al., 2015). In forests dominated by trees herbs spend their entire life cycle in the forest understory continually subject to mammalian impacts including trampling and herbivory (Royo and Carson, 2005). Herbs account for a relatively small amount of the biomass and nutrient standing stocks in deciduous and perennial forests, but nutrient uptake and cycling by herbs can account for significant amounts of total ecosystem nutrient flux (Peterson and Rolfe 1982). Nutrient cycling is also related to patterns of resource allocation and is stored in roots, rhizomes, bulbs, and corms (Gross et al., 1983, Piper, 1989). Due to their superficial root system and small size, terrestrial herbs in tropical forests are subjected to severe competition for water, nutrients, and light (Mulkey et al., 1991; Chazdon et al., 1996). To avoid this problem, for many species of herbs, the allocation of nutrients is related to the seasons. During the growing season, herbs allocate nutrients for aboveground biomass as leaves, flowers, and fruits, and as the growing season progresses, nutrients are resorbed and accumulate in belowground structures (Muller et al., 1996; Whigham, 2004). Some species have been shown to have stable population structure but for most species, population structure is temporally variable due to variation in factors such as weather, disturbance, and levels of nutrient availability (Goodwillie and Jolls, 1996; Fröborg and Eriksson, 1997; Whigham, 2004). Herbs resource like pollen, leaves, and fruits, is important for the food-web of many herbivores and small frugivores vertebrates and invertebrates, as so for the human maintenance using herbs as medicines and food (Schemske, 1978; Johns, 1990; Whigham, 2004).

2.3.6. Bamboos

The bamboos life-form are the largest grasses on Earth and exhibit some of the fastest growth rates of all plants (Pearson et al., 1994). They are a diverse and ecologically important group of plants that have the potential to modulate the structure, composition, and function of forests distributed over numerous biogeographic regions (Canavan et al., 2017; Fadrique et al., 2020). Bamboos have great plasticity in their physiological traits and can present combinations of traits typical of both early successional and late-successional species; as such, many bamboos are adapted to live in open environments as well as the forest understory and human-modified environments (Clark and Oliveira, 2018). Belowground, bamboos produce extensive rhizome networks that allow for clonal growth and rapid resprouting response after disturbances (Griscom and Ashton, 2006). Life cycle length is highly variable among species and some bamboos species have a gregarious monocarpic life cycle in which an entire population flowers, produces seeds, and then subsequently dies (Franklin, 2004; Fadrique et al., 2020). Bamboos are effective at colonizing tree-fall gaps and altering regeneration often negatively affect other life-forms recruitment, survival, and growth by casting a dense shade in the forest understory providing preferred microhabitats for seed predators, also physically damaging other life-forms seedlings and saplings (Rother et al., 2009; Rother et al., 2016; Fadrique et al., 2020). Although their conservation values are often overlooked, bamboos are an important carbon sink (Veblen et al. 1980) and provide critical habitat for specialized invertebrates, birds (Rother et al., 2013a), and mammals (Dunnum and Salazar-Bravo, 2004).

2.4. Statistical analyses

To investigate the effects of the exclusion of LMH on plant life-form abundances and diversity we performed different models using a *Generalized Linear Mixed Model* (GLMM) statistical modelling approach. First, we tested for differences between experimental treatments in the absolute abundance of every life-form separately. We expected that experimental exclusion of LMH would lead to a divergence in the trajectories of the time series of abundances of open and closed plots for every life-form. Thus, the absolute abundance of every life-form was modeled as the function of the interaction between treatment and time in months as predictors (fixed effects). This approach has the advantage of accounting for pre-experimental differences in intercepts between treatments, whilst allowing for corrections for any background long-term trend across both treatments (see, e.g., Figure 1E). To account for the nested nature of our experimental design and ensure pairwise comparisons between treatments, we included site, plot, and survey month as random effects in all GLMMs. For absolute abundances, we used GLMMs with a Poisson distribution, or a negative binomial distribution when the distribution showed zero inflation.

Second, since LMH modifies the environment in many ways, defaunation may directly or indirectly affect the competitive abilities of some life-forms relative to others. To test this hypothesis, we modeled differences between treatments in the relative abundances of every life-form following a similar approach to the one described above, except that in this case a binomial distribution was used (zero-inflated models were fitted when necessary). In addition, we tested if the experimental exclusion of LMH affected pairwise abundance correlations between life-forms so as to elucidate shifts in the relative competitive and coexistence ability of life-form pairs between treatments. Thus, we modeled the absolute abundance of every life-form as a function of the log abundances of all other life-forms (after adding the value of one), one pairwise correlation at a time. We used a Poisson distribution, or a negative binomial distribution when the distribution showed zero inflation and the same random effects as for all other models.

Third, we tested how LMH exclusion affected diversity *among* and *within* life-forms. For simplicity, we focused on the Inverse Simpson Index (InvSimp) as an index of diversity. This abundance-based diversity index emphasizes evenness rather than presence/absence and is a Hill number, thus adequate for comparisons between plots with different numbers of saplings (Chao et al., 2014). The InvSimp *among* life-forms was calculated by pooling the abundances of all individuals within every life-form irrespective of the species; subsequently, we examined the effect of treatment on the diversity *among* life-forms by modeling InvSimp as a function of the interaction between treatment and time as predictors (fixed effects) and fitted the same random effects as for other models. The InvSimp *within* every given life-form was calculated considering the number of species classified into this life-form and their abundances. Subsequently, we modeled the diversity *within* life-forms with identical predictors and random effects as above. In both cases, we used a Gaussian distribution.

We reported estimates and statistical significance for single terms in the models and results from likelihood ratio tests of the treatment*time interactions. Time (months) was log-transformed in all models as exploratory analyses indicated that this was adequate (we added the value of 1 before log-transformation). All analyses were performed in R (R Core Team, 2019), using packages "*lme4"* and "*glmmTMB*" for GLMMs (Bates e al. 2014; Brooks et al., 2017), "*stats*" for likelihood ratio tests (Fox and Weisberg, 2018), and *"hillR*" to extract InvSimp values (Li, 2018). See Supplemental Material for model structures and https://github.com/souzayuri/tropical_plant_life_forms to access data tables and scripts used in our analyses.

3. RESULTS

During 108-month (from July 2009 to October 2019), we monitored the annual survival of 7,100 plants: 2,118 trees (29.83%), 2,018 palms (28.42%), 1,480 herbs (20.84%), 749 lianas (10.54%), 407 shrubs (5.73%), and 328 (4.61%) bamboos in both open and LMH exclusion plots in four Atlantic rainforests of Brazil.

3.1. Effects of LMH exclusion on the absolute abundance of plant life-forms

We found that the absolute abundances of trees and palms were favored by LMH exclusion [trees: χ^2 (1, N = 1634) =73.25, P< 0.001; palms: χ^2 (1, N = 1634) = 206.82, P< 0.001]. Tree abundances did not increase over time in the open plots, but by the 108th month, their abundances on closed plots were on average 38% higher than at the onset of the experiment (Figure 1A and Table 1). Exclusion also favored palm abundances, but in this case, the difference between treatments was due to a decline over time on open plots but not on closed ones (Figure 1B and Table 1). The trajectory of palms on closed plots changed over the course of the experiment, with an initial demographic explosion (43% increase by the 36th month) followed by a net decrease roughly parallel to the open treatment. Contrary to trees and palms, the absolute abundance of lianas increased over time, but the increase was larger on open plots (74%) [χ^2 (1, N = 1634) = 5.57, P = 0.01, Figure 1C and Table 1]. Neither shrubs [χ^2 (1, N = 1634) = 1.14, P = 0.28, Figure 1D] nor bamboos [χ^2 (1, N = 1634) = 2.38, P = 0.12, Figure 1F] experienced any net temporal increase or divergence in the trajectory between treatments. Herbs increased in both treatments over the course of the experiment, and though there was a tendency for a larger increase in open plots, differences between treatments were not significant [χ^2 (1, N = 1634) = 3.35, P = 0.067, Figure 1E].

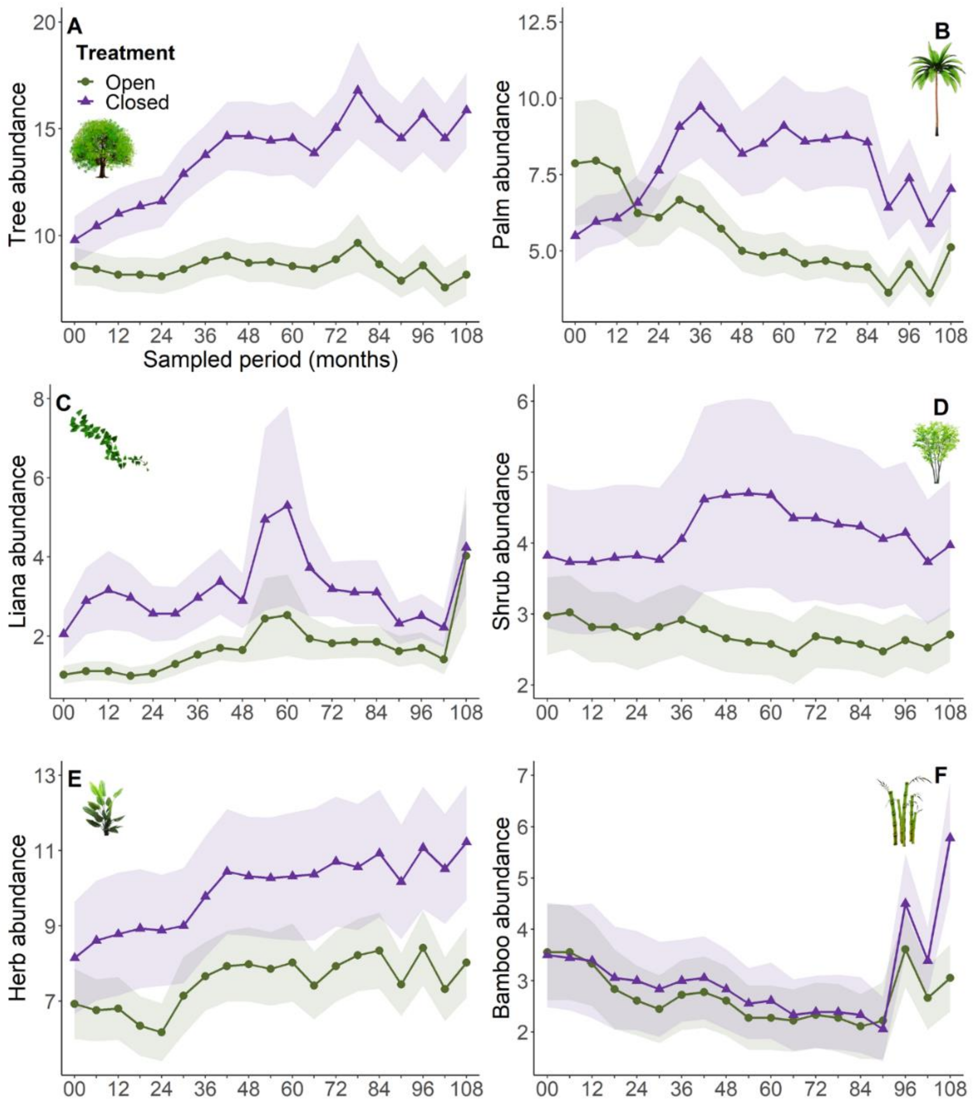

Figure 1. Mean absolute abundances of plant life-forms over the course of the 108-month experiment in the Atlantic forest, Brazil. Dark green = open plots, dark purple = closed plots, shaded area = standard error.

3.2. Dominance: Effects of LMH exclusion on plants life-form relative abundances

In order to assess how defaunation affects life-form dominance, we examined the response of relative abundances of different plant life-forms to experimental exclusion over the course of the experiment. Neither trees nor bamboos experienced a net increase in relative abundances across time in any of the treatments [χ^2 (1, N = 1634) = 1.78, P = 0.18 and χ^2 (1, N = 1634) = 0.03, P = 0.84, respectively, Figure 2A, Table 1]. Relative abundances of palms were favored by experimental exclusion plots, whilst relative abundances of lianas were disfavored [χ^2 (1, N = 1634) = 34.20, P< 0.001, Figure 2A, Table 1]. The relative abundance of palms decreased on both treatments, but in open plots this decline was steeper than in closed ones. Conversely, the relative abundance of lianas increased in the open plots, but slightly decreased in the closed treatment [χ^2 (1, N = 1634) = 34.6, P< 0.001, Figure 2A, Table 1]. The relative abundance of shrubs decreased on closed plots but did not change on controls [χ^2 (1, N = 1634) = 4.88, P< 0.02, Figure 2A, Table 1], while herbs increased in open plots more than on closed plots [χ^2 (1, N = 1634) = 15.63, P< 0.001, Figure 2, Table 1].

3.3. Coexistence: effects of large herbivore exclusion on pairwise abundance relationships between life-forms

In order to assess how defaunation affects the coexistence among life-forms, we examined how the pairwise relationships in absolute abundances between life-forms responded to experimental exclusion (see methods section for details). All possible life-form pairwise abundance correlations on open plots had positive or neutral effects (Figure 2C and Table S1, Supplemental Material). In contrast, there were six pairwise negative life-form correlations in the closed treatment. In addition, mammal exclusion significantly shifted the slopes of four pairwise correlations towards less positive values, but only one pairwise correlation (herbs vs. bamboos) towards more positive values (Table S1, Supplemental Material). There were four non-significantly pairwise correlations in the open plots and three on closed plots. Close examination of results suggested that pairwise correlations involving trees were of lower magnitude, either positive or negative, regardless of treatment. Correlations involving lianas were less strong on closed plots, yet only one (lianas-shrubs) was negative. Correlations involving palms, bamboos, and herbs (in increasing order) shifted towards more negative magnitudes with mammal exclusion. All pairwise correlations with shrubs on the closed treatment were negative (but neutral with trees).

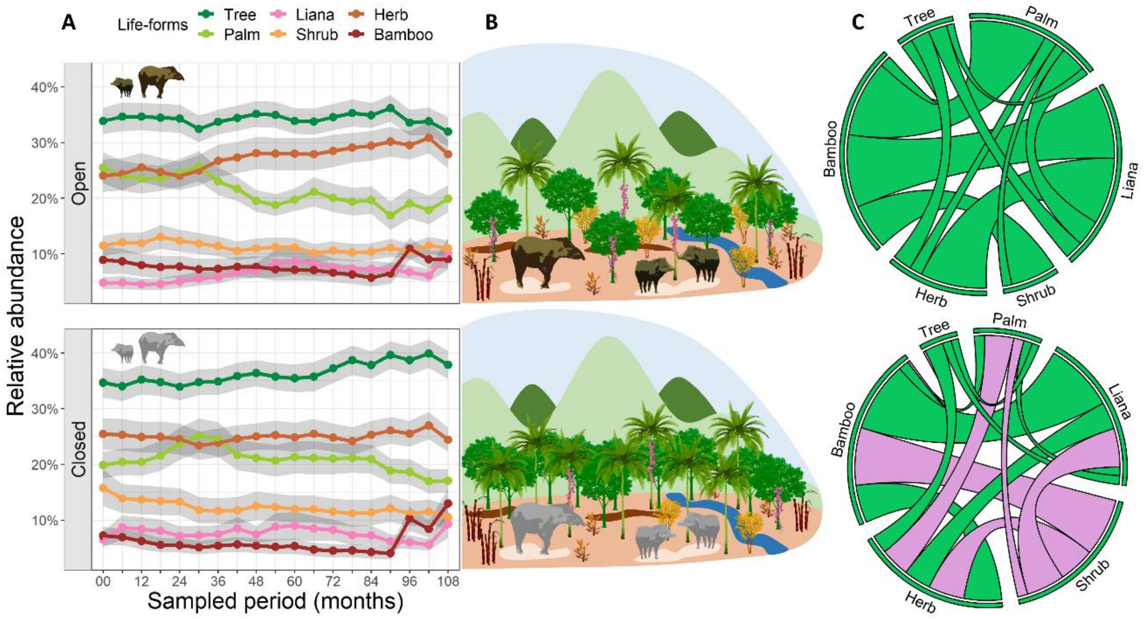

Figure 2. The relative abundance of life-forms and pairwise relationships between life-forms in the LMH exclusion experiment at the Atlantic forest (Brazil). (A) Temporal trajectories of life-form relative abundances (in %, shaded area = standard error). (B) Illustrative representation of the community structure expected in the presence of LMH (top) and under a defaunated scenario (bottom), according to the proportion of each life-form by the end of the experiment. In (C) we show the strength (line thickness) and sign (color, green=positive; pink=negative) of pairwise correlations between life-forms (only statistically significant correlations ($P < 0.05$) are displayed).

3.4. Diversity: Effects of LMH exclusion on species evenness within and among life-forms

In order to assess how defaunation affects diversity *among* and *within* life-forms, we examined, respectively, how life-form evenness and species evenness within every life-form category responded to experimental exclusion. Experimental exclusion of large mammals had a strong impact on the diversity of life-forms found in a given plant community. Evenness among plant life-forms increased substantially on open plots over the course of the experiment (Mean [S.E.] = 0.041 (0.016); χ^2 (1, N = 19) = 6.87, P = 0.008), but not on closed plots (Mean [S.E.] = -0.044 (0.022); χ^2 (1, N = 19) = 3.90, P = 0.048], so that the gap in the diversity of life-forms increased with time (Figure 3A).

The temporal trajectories and the impact of experimental exclusion on evenness within trees, lianas, shrubs, herbs, and bamboos tend to follow the same qualitative trends as the ones described for absolute abundances (Figure 3B and Table 1). However, none of the life-forms showed a statistically significant evenness decrease over the course of the experiment on any of the treatments. Evenness *within* trees strongly increased over time on closed plots, but not on control plots, so that the gap between the open and closed treatments increased over time [χ^2 (1, N = 1634) = 25.26, P< 0.001, Figure 3B and Table 1]. *Within* palms, evenness also experienced an increase on closed plots, but not on open plots [χ^2 (1, N = 1634) = 4.31, P = 0.03, Table 1]. In contrast, lianas and herbs showed a significant and positive evenness change on both treatments [χ^2 (1, N = 1634) = 0.34, P = 0.55, and χ^2 (1, N = 1634) = 0.11, P = 0.73, respectively, Table 1]. Neither shrubs nor bamboos experienced any temporal change in evenness on any of the treatments [χ^2 (1, N = 1634) = 1.78, P = 0.18, and χ^2 (1, N = 1634) = 0.30, P = 0.57, respectively, Table 1].

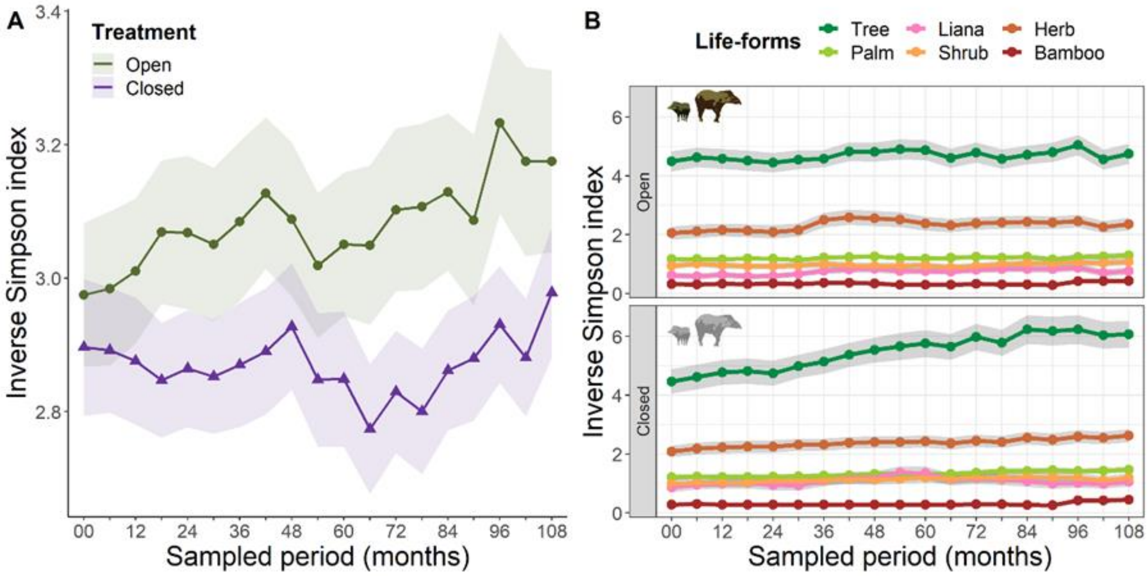

Figure 3. Temporal trajectories of species evenness *among* and *within* life-forms in the LMH exclusion experiment, Atlantic forest, Brazil. (A) Inverse Simpson index *among* life-forms (dark green = open plots, dark purple = closed plots). (B) Inverse Simpson index *within* every life-form. In both figures, shaded areas show standard errors.

Table 1. Results of statistical analyses on the effect of LMH exclusion experiment on the absolute and relative abundance and *within* life-form (species) diversity in the Atlantic forest, Brazil. The table shows the results of GLMMs and whether the net effects of LMH exclusion were positive (+), negative (-), or neutral (Ø). O = open plots (Open) and C = closed plots (Closed).

Life-form	**Absolut abundance**			**Relative abundance**			**Life-form species diversity**		
	Estimate (SE)	***p***	**Effects**	**Estimate (SE)**	***p***	**Effects**	**Estimate (SE)**	***p***	**Effects**
Trees	**Int:** 1.966 (0.12)	<0.01	+	**Int:** -0.860 (0.11)	<0.01	Ø	**Int:** 4.393 (0.47)	<0.01	+
	Treat C: 0.022 (0.05)	0.68		**Treat C:** 0.067 (0.06)	0.33		**Treat C:** -0.571 (0.28)	0.04	
	Time*O: -0.001 (0.01)	0.90		**Time*O:** 0.024 (0.01)	0.07		**Time*O:** 0.071 (0.05)	0.17	
	Time*C: 0.122 (0.01)	<0.01		**Time*C:** 0.024 (0.01)	0.18		**Time*C:** 0.373 (0.07)	<0.01	
Palms	**Int:** 1.916 (0.18)	<0.01	+	**Int:** -0.899 (0.22)	<0.01	+	**Int:** 1.143 (0.07)	<0.01	+
	Treat C: -0.547 (0.06)	<0.01		**Treat C:** -0.557 (0.08)	<0.01		**Treat C:** -0.032 (0.07)	0.65	
	Time*O: -0.149 (0.01)	<0.01		**Time*O:** -0.148 (0.01)	<0.01		**Time*O:** 0.019 (0.01)	0.15	
	Time*C: 0.247 (0.01)	<0.01		**Time*C:** 0.124 (0.02)	<0.01		**Time*C:** 0.039 (0.01)	0.03	
Lianas	**Int:** -1.216 (0.34)	<0.01	–	**Int:** -4.392 (0.39)	<0.01	–	**Int:** -0.978 (0.24)	<0.01	Ø
	Treat C: 1.059 (0.19)	<0.01		**Treat C:** 1.184 (0.16)	<0.01		**Treat C:** 0.488 (0.19)	0.01	
	Time*O: 0.189 (0.04)	<0.01		**Time*O:** 0.224 (0.03)	<0.01		**Time*O:** 0.086 (0.03)	0.02	
	Time*C: -0.116 (0.04)	0.01		**Time*C:** -0.242 (0.04)	<0.01		**Time*C:** -0.029 (0.05)	0.55	
Shrubs	**Int:** 0.400 (0.26)	0.13	Ø	**Int:** -2.791 (0.26)	<0.01	–	**Int:** 0.925 (0.12)	<0.01	Ø
	Treat C: -0.058 (0.15)	0.70		**Treat C:** 0.376 (0.11)	0.01		**Treat C:** 0.008 (0.10)	0.93	
	Time*O: -0.025 (0.02)	0.38		**Time*O:** -0.021 (0.02)	0.34		**Time*O:** 0.014 (0.02)	0.47	
	Time*C: 0.043 (0.04)	0.28		**Time*C:** -0.067 (0.03)	0.02		**Time*C:** 0.038 (0.02)	0.18	
Herbs	**Int:** 1.297 (0.31)	<0.01	Ø	**Int:** -1.745 (0.28)	<0.01	–	**Int:** 1.926 (0.35)	<0.01	Ø
	Treat C: 0.106 (0.07)	0.16		**Treat C:** 0.186 (0.07)	0.01		**Treat C:** -0.0002 (0.16)	0.99	
	Time*O: 0.047 (0.01)	0.01		**Time*O:** 0.093 (0.01)	<0.01		**Time*O:** 0.095 (0.03)	0.01	
	Time*C: 0.036 (0.01)	0.06		**Time*C:** -0.078 (0.01)	<0.01		**Time*C:** 0.014 (0.04)	0.74	
Bamboos	**Int:** -4.703 (2.36)	0.04	Ø	**Int:** -7.653 (2.30)	<0.01	Ø	**Int:** 0.298 (0.15)	0.052	Ø
	Treat C: -0.182 (0.23)	0.44		**Treat C:** -0.090 (0.16)	0.58		**Treat C:** -0.057 (0.04)	0.20	
	Time*O: -0.020 (0.04)	0.67		**Time*O:** 0.003 (0.03)	0.93		**Time*O:** 0.009 (0.008)	0.24	
	Time*C: 0.096 (0.06)	0.12		**Time*C:** 0.008 (0.04)	0.84		**Time*C:** 0.006 (0.01)	0.57	

4. DISCUSSION

Our results indicate that the defaunation shifts the dominance, impacts upon the coexistence, and erodes the diversity of plant life-forms in tropical rainforests. Over the course of the 10-year experiment, exclusion of large mammals favored palms and trees, to the detriment of other life-forms, especially lianas, by decreasing their absolute and relative abundances, rejecting our hypothesis. This occurred despite strong background temporal trends affecting sapling communities in both treatments in our experiment. We argue that this shift in dominance and reduction in diversity is probably a product of the interaction of several mechanisms operating simultaneously, including trophic (such as herbivory, seed predation and dispersal) and non-trophic (trampling) processes.

4.1. Mechanisms for LMH impacts on plant life-form communities

LMH exclusion increased the total abundance of trees and palms and reduced the total abundance of lianas. One intuitive mechanism that might explain this result is the loss of seed predation on LMH exclusion plots. In the Neotropics, large frugivores preferably feed on large fruits and seeds which are more common amongst trees than in other life-forms (Wright et al., 2007). As a consequence, seed predation by LMH is thought to strongly reduce tree recruitment and population densities (Theimer et al., 2011; Beck et al., 2013; Kurten, 2013; Kurten and Carson, 2015; Kurten et al., 2015). Indeed, whilst diversity and abundance of small mammal herbivores (rodents) increase in defaunated tropical forests (Galetti et al., 2015a), exclosure experiments show that small mammal herbivory cannot fully compensate for the magnitude of LMH seed predation (Wright et al., 2007; Kurten, 2013; Villar et al., 2020). Furthermore, large seeds are not heavily consumed by small mammals (Galetti, et al., 2015b). Thus, defaunation of LMH may release those tree species with large seeds from LMH predation and subsequently increase their recruitment and persistence in the community (Beck et al., 2013; Kurten et al., 2015). Additionally, trees with large seeds might benefit from a higher competitive advantage at sapling stage, which might contribute to dominate sapling communities in the absence of LMH (Wright et al., 2007). A similar mechanism might explain the increase of absolute and relative abundances of palms after the exclusion of LMHs. Like trees, many palms produce large seeds with relatively high germination rates and vigor (Pizo et al., 2006; Beck et al., 2013; Kurten et al., 2013). Furthermore, palms have higher fecundity and are hyper-dominant in various Neotropical regions including the Atlantic and the Amazon Forest (ter Steege et al., 2013; Staggemeier et al., 2017). As consequence, LMH are strongly attracted to palm stands (Bodmer, 1990; Beck, 2017; Akkawi et al., 2020). In defaunated areas where LMH are absent, most palm seeds accumulate beneath reproductive adults (Wright et al., 2000; Martínez-Ramos et al., 2016; Valverde et al., 2020).

Seed dispersal limitation is another mechanism that might have contributed to the patterns observed. Compared to trees, lianas have a large number of species with abundant small wind-dispersed or bird-dispersed seeds (Terborgh et al., 2001; Wright et al., 2007; Harrison et al., 2013; Schnitzer et al., 2014). Thus, in the presence of LMH, lianas might have a competitive dispersal advantage over trees and palms since the predation of liana seeds might be proportionally lower, and fecundity much higher. Our results showing that the relative abundances of lianas increase when LMH are present support this hypothesis. Furthermore, the most abundant lianas in the open plots were two wind-dispersed (*Schnella microstachya* and *Serjania communis*) and one bird-dispersed species (*Paullinia seminuda*).

The mechanical impact of LMH on sapling tissues through trampling, leaf, and sapling consumption might also contribute to increasing life-form diversity. Whilst adult trees are resistant to mechanical disturbance, trees at the sapling stage are susceptible to physical disturbance of medium and large-sized mammals by trampling and browsing (Rosin et al., 2017). In a tropical forest of South-East Asia, Luskin *et al.* (2019) found that the experimental exclusion of the Bornean bearded pigs *Sus barbatus* almost doubled tree populations while liana abundance increased in the presence of wild pigs. Interestingly, the most abundant species of LMH in our experiment belongs to the Tayassuidae family (the white-lipped peccary *Tayassu peccari),* which is functionally similar to wild pigs in Asia. According to such evidence, lianas appear to be more resilient to mechanical damage than trees. Additionally, the wide range of survival strategies in lianas might allow them to cope with high levels of mechanical disturbance (Andersen, 1997; Wright, 2002; Kilgore et al., 2010; Beck et al., 2013). The ability to regenerate from disturbances, such as trampling or leaf consumption, might also explain why bamboos were not affected by the experimental exclusion of LMH (Terborgh et al., 2008; Buckingham et al., 2011; Calderón-Sanou et al., 2019). Bamboos possibly have low attractiveness for herbivores, and their solid biomechanical structures, as well as vegetative regeneration and propagation, might additionally contribute to regeneration from LMH disturbance (Rother et al., 2013b).

A frequently overlooked mechanism that might also contribute to our results is the changes in soil physical properties derived from the impact of LMH trampling and the large amounts of soil overturned by LMH. Changes in palm abundance were mainly driven by the hyper-dominant palm *Euterpe edulis*, which represents 95% of the palms in our plots. Saplings of this palm have a superficial root system that is incapable of reaching the water in the deep wet soil layer during the dry season, so they are weak competitors for soil water availability (Matos et al., 1999). LMH have been shown to increase soil evapotranspiration on grassland ecosystems, shifting plant communities towards more drought-tolerant species (Veldhuis et al., 2014). If this mechanism also operates in tropical forests (as suggested by Villar et al., 2020), we expect that LMH might shift sapling communities towards more drought-tolerant life-forms, to the detriment of palms. Shrubs, whose relative abundance was favored by LMH presence, have an efficient below-ground root system that allows them to uptake water and nutrients in systems with variable soil water availability (Brown et al., 1998). Herbs, also favored by LMH presence, whilst being less competitive than shrubs in their below-ground ability to capture water under stress conditions, have a superior ability to tolerate variable microclimates and aboveground stress conditions, such as drought periods or light limitation (Brown et al., 1998; Whigham, 2004). Furthermore, whilst tree saplings might be more resilient to drought, palm saplings, which benefited the most from exclusion, are the most drought-sensitive amongst the life-forms studied (van der Sande et al., 2013). Thus, LMH impact on soil physical conditions may contribute to increased life-form diversity.

In addition to these mechanisms, it is likely that the on-going climate change and increasing drought conditions (Rifai et al., 2019), might have also played an important role in the population increment of some life-forms. For instance, during the course of our experiment, lianas and herbs increased in both treatments, whilst neither shrubs nor bamboos experienced any temporal change in any of the treatments. Lianas are more abundant in seasonally dry tropical forests and their abundance increases relative to trees with the increasing length and intensity of the dry season (Schnitzer, 2005; DeWalt et al., 2010). Thus, an increase in lianas across both treatments might be suggestive of a long-term increase in drought in our study region. This might also explain trends in the herbs, whose ability to tolerate drought periods might have contributed to their increase in both treatments. On the contrary, as a result of LMH exclusion palms experienced a demographic boom during the first three years of study, but soon afterward they joined the steady long-term decline evident on open plots. This decline is also consistent with the hypothesis of a long-term increase in drought conditions over the course of our experiment (Figure S3, Supplemental Material), which seemed to affect the balance between different life-forms across the study sites. Furthermore, shrubs, most likely the life-form least sensitive to belowground drought, experienced no net changes in absolute abundance throughout our experiment. Thus, we suspect that these patterns indicate the increasing influence of climate change in the background long-term trends of our experiment.

4.2. The impact of LMH on life-form diversity and coexistence

We argue that defaunation might also alter coexistence dynamics between and among life-forms. The increase of palm relative abundance on closed plots occurred with a concomitant increase in palm plant *evenness* diversity driven by a decrease in the dominance by *E. edulis* and an increase in the abundance of the other palm species, including *Geonoma elegans, G. gamiova, G. pauciflora, G. schottiana*, *Astrocaryum aculeatissimum,* and *Attalea dubia*. Tree *evenness* diversity also increased substantially on closed plots over the course of the experiment, with an abundance increase of a few abundant species. During the course of our experiment, 22% of the tree species in closed plots experienced an increase in abundance, against 13% in open plots. Exclusion also doubled the abundance of the medium and -large fruit tree species *Eugenia expansa* and *Garcinia gardneriana* over the course of the experiment. In open plots, *G. gardneriana* was more abundant in the first sampling but experienced a significant decrease over the course of the experiment, while in the closed plots its abundance increased up to 83% higher than in open plots by the end of the experiment. Thus, LMH exclusion led to an increase in the diversity *within* both life-forms that were also the most favored by this treatment. Simultaneously, diversity *among* life-forms increased on open plots. We suggest that this might indicate a trade-off between diversity *within* life-forms vs. *among* life-forms within the boundaries imposed by community size and competition for resources. In other words, LMH disturbances might favor a variety of alternative plant life-form strategies, subsequently preventing the many species within otherwise dominant life-forms to take over the resources available for the whole plant community.

Examination of pairwise abundance relationships also supports this view. Results clearly show that negative pairwise abundance correlations only occurred on closed plots, suggesting that the conditions for coexistence between different life-forms might be more constrained when defaunation occurs. Within such pairwise abundance relationships, trees were the least affected by the defaunation, whilst for other life-forms negative relationships of different magnitudes emerged, suggesting that defaunation triggers antagonistic dynamics amongst these “lesser” life-forms. In this scenario, shrubs, for which all pairwise relationships were negative on closed plots but positive on open plots, clearly underperformed compared to other life-forms as a result of experimental defaunation. In contrast, palms appeared to benefit from such competitive dynamics. It is important to bear in mind that our approach does not allow us discerning direct pairwise spatiotemporal competitive dynamics or the conditions for coexistence, yet it facilitates detecting shifts in the relative competitive abilities of different life-forms between open and closed plots. It is remarkable, though, that all pairwise abundance relationships on open plots had a positive or neutral sign, suggesting that disturbances from LMH might, at least partially, override competitive dynamics between life-forms.

As a cautionary note, our experiment focuses on the sapling stage and therefore our inferences only apply directly to sapling communities. Plant diversity in tropical forests may take decades to centuries to recover from anthropogenic disturbances (Rozendaal et al., 2019). However, the early stages is where mortality is highest and where environmental conditions strongly act as a filter to select the better survival traits that are critical to determining plant diversity and dominance in later stages of development (Peet and Christensen, 1987; Forrister et al., 2019). Thus, changes at the sapling stage might have a strong impact on the life-form composition of adult plant communities.

4.3. LMH impacts on life-form communities in face of global environmental change

Many grassland ecosystems worldwide are experiencing woody plant encroachment with the increasing dominance of woody plants such as trees and shrubs (65). This is alarming since this process has many unwanted outcomes on e.g., soil composition, soil structure, and climate regulation (Archer et al., 2017; Staal et al., 2020). In these ecosystems, LMH effects and interaction among plants are considered prominent factors that prevent woody plant encroachment (Staal et al., 2020), so that LMH defaunation benefits woody species (Levick and Rogers. 2008; Wigley et al., 2014). Accordingly, our results show that LMH prevents the proliferation of trees and palms in tropical forests and might modulate the competitive dynamics between life-forms.

Whilst studies from defaunated forests suggest that removal of LMH might benefit lianas (Wright et al., 2007; Kurten, 2013), our experimental results, and in agreement with Luskin *et al.* (2019), show that LMH appears to benefit herbs, shrubs, and especially lianas to the detriment of larger woody life-forms, such as trees and palms. In fact, lianas may form dense tangles in the canopy, harming the establishment and growth of shade-tolerant life-form species (Cai et al., 2009; Favreto et al., 2010; Schnitzer et al., 2014), and suppressing the growth of trees, shrubs (and palms) through light interception in the canopy (Stevens, 1987; Schnitzer et al., 2014; Luskin et al., 2019). Furthermore, lianas accumulate and store less carbon than trees (van der Sande et al., 2013). However, our analyses also show that LMH increases life-form diversity, and therefore it is possible that LMH might also curtail the proliferation of lianas as these become increasingly dominant. In addition, our study does not address the impacts of other functional groups of large herbivores affected by defaunation (such as arboreal primates and birds), which might or might not benefit other life-forms to the detriment of lianas.

Long-term changes in environmental stability, like precipitation or temperature, have been shown to affect plant composition and communities at the global scale (Feeley et al., 2020; Sala et al., 2020). Large mammals might have also an important role in buffering tropical forests against such changes. Our results show that the long-term shifts in life-form composition, possibly strongly influenced by climate change in the region, do not increase life-form diversity on closed plots but only on open plots. Lianas and herbs, whose absolute abundances increased on both treatments over the course of the experiment, also experienced a concomitant increase in species evenness, suggesting that a higher long-term gain in recruitment will also benefit diversity within these life-forms. Furthermore, large mammals might curtail the dominance of trees and palms but, as our results show, this does not lead to a net decline in their diversity over the course of the experiment. Such results strongly suggest that LMH might be a useful management tool to improve diversity (within and amongst) plant life-forms, and hence the dynamics and ecosystem functions, of tropical rainforests subjected to climate change. Whilst these considerations need further inspection, we conclude that, by decreasing life-form diversity, defaunation will likely lead to the vertical and horizontal structural simplification of tropical rainforests, reduce diversity in the understory, and erode the alternative functions carried out by different life-forms.

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6. SUPPLEMENTARY MATERIAL

Supplementary text

Generalized linear mixed model (GLMM) structures formulas

i. **Abundance (table 1):**
*life-form ~ Treatment * log(Time+1) + (1 |Site/Plot/Month)*

ii. **Abundance correlations (table S1):**
*life-form ~ Treatment * log(life-form relationship +1) + (1 |Site/Plot/Month)*

iii. **Relative abundance (table 1):**
*cbind(life-form,all the other life-forms) ~ Treatment * log(Time+1) + (1 |Site/Plot/Month)*

iv. **Evenness diversity within life-forms species (table 1):**
*Life-form Species Inverse Simpson Index ~ Treatment * log(Time+1) + (1 |Site/Plot/Month)*

v. **Evenness diversity among life-forms (text):**
*Life-form Inverse Simpson Index ~ Treatment * log(Time+1) + (1 |Site/Plot/Month)*

Table S1. Statistical results of life-form abundance relationships. of the table shows the GLMM results for the six life-forms abundance correlations. The “C” is for closed plots and “O” for open plots, and the model interactions term between life-forms are represented by the life-form first letter (Palms = “P”, Lianas = “L”, Shrubs = “S”, Herbs = “H”, and Bamboos = “B”). All the P-values below 0.001 were set as P< 0.001.

Life-forms	Palms		Lianas		Shrubs		Herbs		Bamboos	
	Estimate (SE)	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Trees	**Int:** 1.876 (0.12)	<0.01	**Int:** 1.876 (0.12)	<0.01	**Int:** 1.925 (0.11)	<0.01	**Int:** 1.739 (0.10)	<0.01	**Int:** 1.923 (0.11)	<0.01
	C: 0.4351 (0.04)	<0.01	**C:** 0.507 (0.02)	<0.01	**C:** 0.461 (0.02)	<0.01	**C:** 0.392 (0.04)	<0.01	**C:** 0.524 (0.01)	<0.01
	P*O: 0.052 (0.01)	0.005	**L*O:** 0.127 (0.02)	<0.01	**S*O:** 0.036 (0.01)	0.06	**H*O:** 0.131 (0.02)	<0.01	**B*O:** 0.077 (0.02)	0.01
	P*C: 0.015 (0.02)	0.47	**L*C:** -0.063 (0.02)	0.004	**S*C:** 0.021 (0.02)	0.38	**H*C:** 0.024 (0.01)	0.21	**B*C:** -0.093 (0.02)	<0.01
Palms	-	-	**Int:** 1.285 (0.17)	<0.01	**Int:** 1.336 (0.17)	<0.01	**Int:** 1.211 (0.17)	<0.01	**Int:** 1.139 (0.19)	<0.01
			C: 0.385 (0.02)	<0.01	**C:** 0.458 (0.03)	<0.01	**C:** 0.926 (0.05)	<0.01	**C:** 0.560 (0.02)	<0.01
			L*O: 0.177 (0.03)	<0.01	**S*O:** 0.064 (0.02)	0.01	**H*O:** 0.088 (0.03)	0.01	**B*O:** 0.526 (0.03)	<0.01
			L*C: -0.115 (0.03)	<0.01	**S*C:** -0.137 (0.03)	<0.01	**H*C:** -0.295 (0.02)	<0.01	**B*C:** -0.452 (0.02)	<0.01
Lianas	-	-	-	-	**Int:** -0.379 (0.28)	0.17	**Int:** -1.245 (0.34)	<0.01	**Int:** -0.691 (0.24)	0.004
					C: 0.768 (0.08)	<0.01	**C:** 0.996 (0.12)	<0.01	**C:** 0.605 (0.05)	<0.01
					S*O: -0.062 (0.06)	0.32	**H*O:** 0.454 (0.07)	<0.01	**B*O:** 0.499 (0.06)	<0.01
					S*C: -0.212 (0.08)	0.01	**H*C:** -0.260 (0.06)	<0.01	**B*C:** -0.017 (0.05)	0.767
Shrubs	-	-	-	-	-	-	**Int:** 0.092 (0.27)	0.73	**Int:** 0.145 (0.24)	0.54
							C: 0.769 (0.12)	<0.01	**C:** 0.347 (0.05)	<0.01
							H*O: 0.099 (0.06)	0.13	**B*O:** 0.310 (0.07)	<0.01
							H*C: -0.355 (0.06)	<0.01	**B*C:** -0.721 (0.07)	<0.01
Herbs	-	-	-	-	-	-	-	-	**Int:** 1.471 (0.29)	<0.01
									C: 0.109 (0.02)	<0.01
									B*O: 0.053 (0.03)	0.07
									B*C: 0.216 (0.02)	<0.01

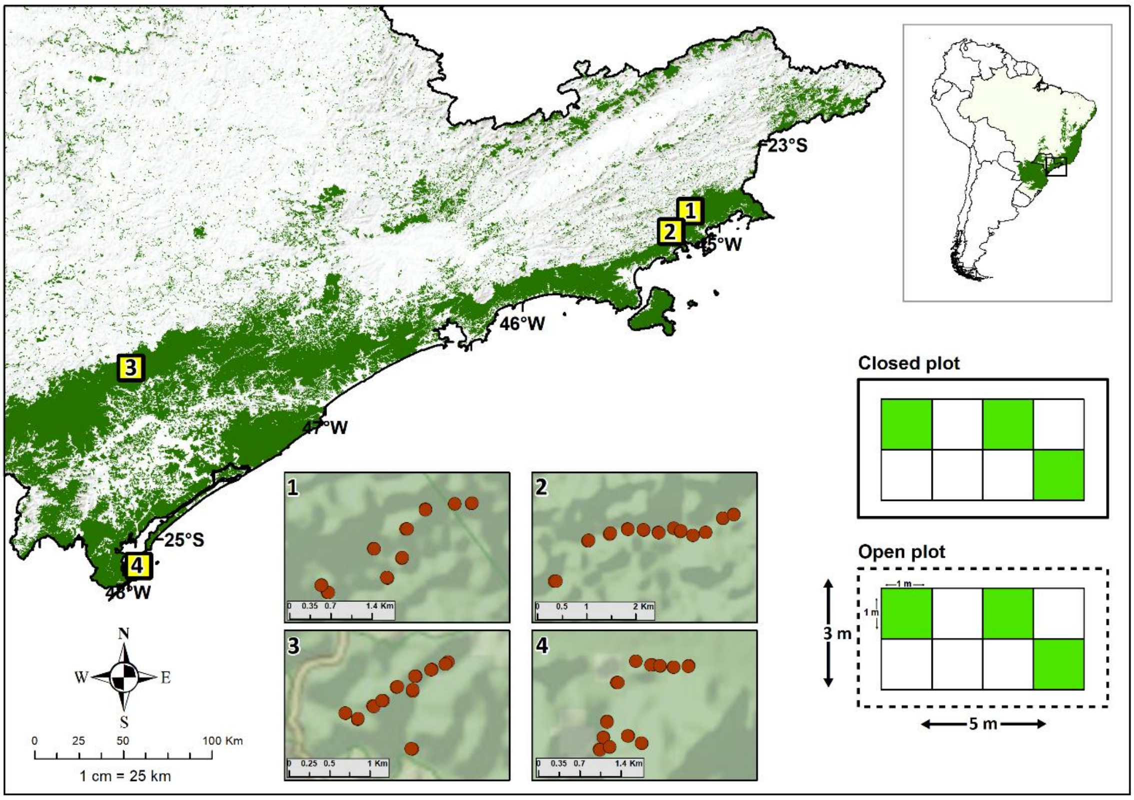

Figure S1. Study areas and plot locations in the Atlantic forest, Brazil (green area). The yellow squares represent the four sampled areas (1) ITA, (2) VGM, (3) CBO, and (4) CAR, and the brown dots in the minor panel represent the respective paired plots locations. Plot design is represented at the right bottom, in which green squares illustrate the sampled subplots where all early stage >10 cm and up to 1 m were marked and monitored for 10 years.

Figure S2. Early stages of plants at the DEFAU-BIOTA experiment in the Atlantic forest, Brazil. Examples for each life-form. A) *Eugenia expansa* (tree), B) *Euterpe edulis* (palm), C) *Paullinia seminuda* (liana), D) *Doliocarpus* sp. (shrub), E) *Ctenanthe lanceolata* (herb), and F) *Chusquea* sp. (bamboo). Photo credits: Rafael Souza.

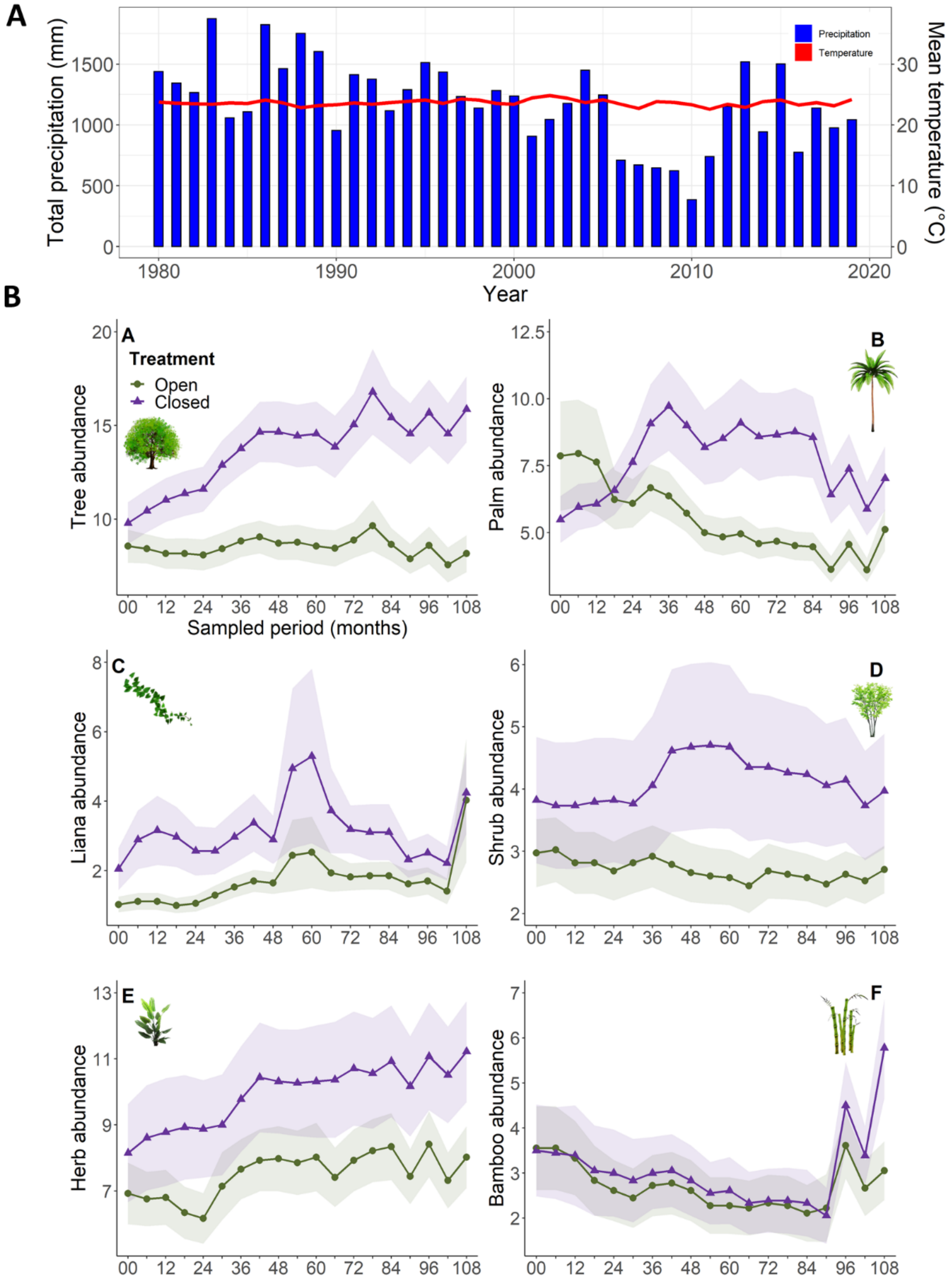

Figure S3. Temporal trajectories of species evenness among and within life-forms in the LMH exclusion experiment at the Atlantic forest (Brazil). (A) Inverse Simpson index among life-forms (dark green = open plots, dark purple = closed plots). (B) Inverse Simpson index within every life-form. In both figures, shaded areas show standard errors**.**