**Medium and large-sized terrestrial herbivores shape plant community spatiotemporal synchrony dynamics in a tropical Brazilian rainforest**

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**INTRODUCTION**

Tropical forests are hotspots and home to many organisms and species worldwide, many of which are endemic and rare to the boundaries of their ecosystems (Mittermeier et al., 2011). The ecological hyper-diversity aspect of these forests hides the magnitude of their species composition, which seems always to be a work in progress where new species, taxonomic groups, and taxa are recorded at a high rate (Leigh et al., 2004; Deikumah et al., 2014). This highlights that much is still left to be known and explored about these ecosystems (Lawton et al., 2018). Although the significance of tropical forests for the global maintenance and equilibrium of ecosystems is well-established on both small and large scales (through nutrient cycling, carbon sink, and the long-term carbon stock), they still remain vulnerable and a primary target of anthropogenic disturbances (Mittermeier et al., 2011; Barlow et al., 2016; Alroy, 2017; Belo et al., 2024).

As human development continues, natural areas are being converted into urban centers, artificial forests, or agricultural land. This irreversible conversion has dire consequences, including the loss of undiscovered species due to the over-exploitation of natural resources, thus raising serious concerns about the long-term sustainability of these natural habitats (Mittermeier et al., 2011; Alroy, 2017; Souza et al., 2019). In this sense, the Atlantic Forest biome is a prime example of the devastating effects of human activities, which mostely happened by deforestation. It lost 88% of its original cover from 1498 to 2007, resulting in a drastic habitat loss (Ribeiro et al., 2009). While a recovery to 22% of its original cover has been reported, most of these areas are scattered among isolated forest patches (Ribeiro et al., 2009; Vancini et al., 2020) that experience a loss in species and genetic diversity given the lack of ecological functions played by many animals, such as many frugivores and herbivores, a process known as defaunation (Galetti et al., 2013; Dirzo et al., 2014; Souza et al., 2019; Belo et al., 2024).

The loss of large frugivores due to habitat fragmentation is known to have a large impact on plants due to the loss of functional diversity (Galetti et al., 2017; Galetti et al., 2021; Belo et al., 2024). For example, in response to the functional extinction of large frugivores, plants may decrease their fruit and seed size as an adaptation to the remaining small body-sized frugivores, which are more resistant to changes in their natural habitat and hence able to disperse small seeds or even shift their selection to smaller seeds over the large ones (Galetti et al., 2013; Luskin et al., 2019). Moreover, long-term exclusion experiments worldwide have shown trophic cascade consequences of medium and large-sized herbivore extinction in shaping and determining plant community composition dynamics. These herbivores control hyper-dominant and invasive plant species that usually take over the place after an ecological disruption caused by an intense disturbance – such as defaunation (Villar et al., 2020; Souza et al., 2022). This may even lead to a shift from top-down control determined by herbivores to bottom-up driven by the foundation and dominant plant species, with consequences for both plant species and functional diversity led by intense competitive exclusion (Souza et al., 2021; Pringle et al., 2023). Once the abundant and dominant species are released from the herbivory, grazing, tramping, and other physical impacts caused by large-bodied animals, the remaining plant species lack the strategies to outcompete the dominant ones (Luskin et al., 2019; Souza et al., 2022).

Although many forest ecosystems can successfully recover through human intervention, such as reforestation and restoration practices (Crouzeilles et al., 2017; Shimamoto et al., 2018; Belo et al., 2024), the same is not true for medium and large-sized mammals and their irreplaceable roles. These animals are more susceptible and present low resistance against factors that disproportionately affect their population sizes, such as illegal hunting, poaching, and habitat loss (Souza et al., 2019; Galetti et al., 2021). Practices such as rewilding are alternative solutions to rescue endangered animal species and their ecological functions (Perino et al., 2019). However, these methods require a huge effort, and their success may only be seen in the long term (Perino et al., 2019). Even in a scenario in which the species’ reintroduction succeeds, it is possible that the community structure and composition would never recover its original state. In some cases, the ecosystem might have already shifted towards an alternative state, which could make its recovery efforts even more challenging (Malhi et al., 2014; Nogués-Bravo, et al., 2016).

Understanding the persistence and ecological stability of populations and communities over both temporal and spatial contexts is key to comprehending the consequences of species losses for their ecosystem’s maintenance and services. One way to unveil this information is by examining the metapopulation response to changes across time and space, as well as how species populations synchronize their response along with the drivers of disturbances (Wang et al., 2019). For instance, plant dispersal limitations can arise due to the functional extinction of their respective mutualist frugivores, which results in low community stability and decreases in spatial synchrony, led by asynchrony changes in plant species abundances (Souza et al., 2022). These responses that arise from changes in species population dynamics determine the stability of the metacommunities scale-wide (Wang et al., 2019). However, identifying which ecological factors shape synchrony changes across scales and their net contribution can be challenging.

Herbivory and frugivory interactions play an important role in shaping and maintaining tropical forests by controlling the growth and dominance of plant species, which is achieved by either feeding on the plant's tissues directly or by dispersing their seeds (Galetti et al., 2021). These interactions help to prevent a clumped distribution of plant species, providing space and chances for other species to grow and thrive, hence reducing competitive exclusion among different species and maintaining diversity in plant communities (Comita et al., 2014; Souza et al., 2022). Here, I used a long-term exclusion experiment data collection to disentangle the effects of terrestrial mammals, specifically medium and large-size herbivores, on the spatial and temporal synchrony of plants in the Brazilian Atlantic rainforest by addressing two questions: i) whether herbivores affect the overall plant abundance across four independent areas over time, and ii) how these changes in abundance, in turn, affect the species diversity across these areas. I hypothesize that changes in abundance would impact species diversity and predict that herbivores would drive abundance heterogeneity, hence leading to a more asynchronous pattern than in their absence. This, in turn, should affect species diversity by leading to high synchrony across space in the presence of herbivores.

**METHODS**

**Study sites**

This research is part of the long-term exclusion experiment DEFAU-BIOTA located in the Brazilian Atlantic Forest that has been carried out by a large research group over the last 15 years (for more information, please visit https://souzayuri.shinyapps.io/biota/). This experiment comprises four old-growth dense ombrophily evergreen moist forest regions in the Atlantic forest in Southeast Brazil located at the Serra do Mar State Park. Despite being within the same state park boundaries, these areas are geographically distant and share a similar vegetation composition, composed of large trees and a diverse understory. Even with a history of degradation, they are considered late-successional or mature forests and share a similar assemblage of mammal species, including herbivores, carnivores, and seed dispersers (Brocardo et al., 2012; Galetti et al., 2017; Souza et al., 2019; Villar et al., 2020; Souza et al., 2022). These areas comprise an annual temperature of 20-24°C and precipitation ranging from 1500 to 4000 mm within an elevation range from sea level to 975m, where tapirs *Tapirus terrestris* and white-lipped peccaries *Tayassu pecari* are the largest ground-dwelling LMHs (Galetti et al., 2017). Besides them, other large terrestrial vertebrates (>10kg) such as Agoutis (*Dasyprocta* spp.), pacas (*Cuniculus paca*), brocket deer (*Mazama* spp*.*)*,* and collared peccaries (*Pecari)* are also present at the sites (Villar et al., 2020).

**Experimental plots and plant sampling**

The sampling design consists of using open and closed plots of 5x3 m (15 m²) to simulate large mammalian herbivores' (LMH from here and on) functional extinctions on plant species sapling dynamics over time (such as recruitment, persistence, mortality, and composition). The control plots were open and delimited by a nylon wire and plastic piles set at 1m height and accessible by any animals or natural events. The closed plots consist of a fenced area (1.6 m high metal fence with 5 cm wire mesh) that physically prevents medium and large-sized terrestrial mammals from accessing them. The plots are paired and separated by 2-7m. A total of 60 paired plots were established at the beginning of the experiment and split among the four sites, each containing fifteen pairs. Each paired plot was at least 200m apart for the closest one. Within each plot, all the plant early-stage saplings were sampled (defined as young plants ranging between 0.1 to 1 meter in vertical height) as these are considered critical stages for the long-term dynamics and composition of tropical forests (Green et al., 2014). Each individual plant was identified using a unique aluminum tag containing a unique registered code, and the tags were securely fastened to the base of the plant with a wire that allowed for growth without constriction. This enabled us to monitor the progress of both old and new individuals during all visits and throughout the entire duration of the experiment (Villar et al., 2019; Souza et al., 2022).

These plots were deployed in 2009 and have been sampled until currently. Unfortunately, due to COVID-19, the years 2019 to 2022 were not sampled. To avoid the misinterpretation of the lack among these years, here I used the data available from 2009-2018, where the data was consistently collected semi-annually. Due to the natural falling of trees by natural uncontrolled causes, some plots were damaged and lost. In this work, I used data from the remaining 86 individual plots (43 pairs) that survived to October 2019. Over these 10 years, a total of 8,737 sapling individuals were sampled, comprising a total of 337 plants identified at the level of genus or species and five growth forms. A total of 1,629 individuals were removed from my analyses because their taxonomy could not be determined since saplings did not have floral structures or fruits during this stage that could facilitate their identification or yet if they were too uncommon to be included in our analyses (Table 1). The growth forms were determined according to the description present in a Brazilian tropical plant guide (Souza & Lorenzi, 2012) and the “Flora do Brasil” taxonomy platform (<http://floradobrasil.jbrj.gov.br/>) and includes five dominant groups, tree, palm, liana, shrub, and herb.

|  |  |  |  |
| --- | --- | --- | --- |
| **Sites** | **Open** | **Closed** | **Total** |
| Species/Abundance | Species/Abundance | Species/Abundance |
| Cardoso Island | 126 / 1287 | 111 / 1582 | 237 / 2869 |
| Carlos Botelho | 113 / 759 | 104 / 741 | 217 / 1500 |
| Vargem Grande | 118 / 1296 | 142 / 1445 | 260 / 2741 |
| Itamambuca | 96 / 697 | 100 / 930 | 196 / 1627 |
| **Total abundance** | 4039 | 4698 | 8,737 |

**Table 1.** Summary of plant species and abundance per site and treatment. A total of four sites were sampled over the 10 years.

**Statistical analyses**

I used a synchrony analysis approach to investigate the effects of LMH's exclusion on plant abundances, growth form composition, and species diversity. This analysis accounts for the incorporation of the coupled effect of LMH exclusion over the 10 years of exclusion, along with the estimation of spatial variability patterns across plots and sites, which is incorporated based on the Pearson correlation coefficient and a one-tailed *Monte Carlo* randomization test, thus accounting for spatiotemporal autocorrelation. This analysis generates a variogram profile by computing spatial patterns of variability (e.g., correlation, covariance, and semivariance) between pairs of locations, and the results are plotted as a function of the lag distance that separates them (Gouhier & Guichard, 2014).

The plant's dynamic response to spatiotemporal synchrony of LMH treatment among areas was accessed by fitting models for the plant’s absolute abundance, growth form composition, and plant species diversity as response variables. Given the model limitations for interannual measurements, I used only the last measurement taken for each year (July period), thus accounting for the net change in abundance and composition throughout the year. For each of the above models, both sampled year, plot coordinates, and treatment were set as predictors of spatiotemporal pattern changes and were randomized 500 times using the *Morte Carlo* approach within the model. The robustness of the model for predicting synchrony and the effect size between treatments were both interpreted by the root-mean-square deviation (RMSE) and the Akaike information criterion (AIC), respectively. The RMSE measures the difference between actual and predicted values to estimate model accuracy. I also perfomed a linear correlation analysis using the Pearson coefficient provided by the model to track the trend of the change.

In order to investigate the impact of how LMH affects plant growth form and species diversity, I used the *Inverse Simpson index*. This diversity index takes into account the evenness of the community and considers both community richness and proportions while emphasizing the importance of abundant species in relation to rare species (Chao et al., 2014). A suitable approach for testing hypotheses pivoting plants' dominance in tropical forests. All the analyses were performed in R using the “*synchrony*” package (Gouhier & Guichard, 2014) for the synchrony analyses and the “*hillR*” packages for the inver Simpson diversity index (Li, 2018). All the data and scripts can be found in this repository: <https://github.com/souzayuri/PCB_5443_YSS_exam_3_adv.ecos.eco>.

**RESULTS**

The synchrony analysis results highlight a difference driven by the exclusion treatment. In the presence of LMH, the plant abundance is synchronized only for two out of the four sites. In contrast, in their absence, the abundance is synchronized across the four sites with a higher and less negative effect size (Figure 1A, AIC = -15.81 and AIC = -13.98, respectively). In closed plots, it shows that synchrony is more likely to occur within a low lag distance range, where sites are within the 95% confidence interval, while in open plots the synchrony does not change with lag distance. Overall, this model predicts that plant abundance synchrony decreases more in open plots with lag distance and shows a better fit than in closed plots (RMSE: 0.08, RMSE: 0.10, respectively).

Regarding diversity, the synchrony model shows that plant growth forms diversity was not affected by the treatment over the spatiotemporal scale (Figure 1B, open plots—RMSE: 0.01, closed plots—RMSE: 0.02). Both treatments highlighted asynchronous patterns across the four sites, with a slight decrease in open plots compared to closed plots (AIC = -31.6 and AIC = -26.32, respectively). The closed treatment also shows a departure of one site from the mean.

On the other hand, LMH seems to have a higher and more positive effect on controlling plant species diversity than they do on growth forms. The model tested here shows high synchrony among three of the four areas driven by the herbivore's presence, which tends to increase with lag distance. Conversely, in closed plots, there is an asynchrony among areas with the exception of one area (Figure 1C). Both results seem consistent and do not show a significant departure from the mean, although closed plots are slightly negative (open plots—RMSE: 0.04 and AIC = -21.39; closed plots—RMSE: 0.04 and AIC = -21.63).

A screenshot of a computer game

Description automatically generated

**Figure 1.** Synchrony graph of plots with LHM presence (open) and exclusion (closed plots). The correlation effects among sites are represented by the Pearson Correlation on the y-axis and lag distance on the x-axis, showing whether the correlation is different or equal to the regional mean (dashed line).The Monte Carlo randomizations are shown by the 95% confidence interval in the gray region. Filled circles represent statistically significant levels of synchrony (α < 0.05; two-tailed test) based on 500 Monte Carlo randomizations computed via function *vario()*, while the statistic values represent the linear regression output from *vario.fit()* function.

**DISCUSSION**

The spatiotemporal synchrony of sites with and without LMH examined here portrays the importance of these animals for the maintenance and stability of tropical forests. My analyses showed that the first direct effect of herbivores on plant dynamic is likely to occur by their release from disturbances such as herbivory and predation, which aligns with my first hypothesis and first prediction. The plant’s abundance in closed plots synchronized more than in the open, showing that over time, those plots were moving towards the same ecological direction, even though they were spatially apart from each other. One intuitive mechanism that might explain this result is the plant release from the LMH. For example, adult plants are resistant to mechanical disturbance, such as many trees, due to their trunk and bark. However, at the sapling stage, they are vulnerable to trampling and browsing by medium and large-sized mammals (Rosin et al., 2017).

Beyond the explicit effects of herbivory, LMH has a preference for fruits and seeds, given their rich nutritional content (Wright et al., 2007). As a consequence, seed predation by LMH is thought to reduce plant recruitment and population densities strongly (Beck et al., 2013; Kurten et al., 2015; Theimer et al., 2011). Moreover, plants with large fruits are considered late successional plants and good competitors in primary forests because they can rely upon their seeds rich in water content and nutrients required to grow (Beck et al., 2013; Kurten et al., 2015). This adaptation provides them advantages over other species, especially during the sapling stage, where competition is more intense (Wright et al., 2007). Some taxonomic groups, such as palms and lianas, have higher fecundity and relatively high germination rates and are hyper-dominant in the Atlantic forest (Pizo et al., 2006; Wright et al., 2007; Staggemeier et al., 2017). Other morphological adaptations, such as thin and flexible stems, may help many species to persist in the presence of LMH and to thrive in their absence (Beck et al., 2013; Luskin et al., 2019). The combined effects of herbivory and seed predation release from LMH result in homogeneous synchrony or uniform response of closed plots. Conversely, my findings show that the net effects of LMH positively contribute to a spatial heterogeneous response composed of synchronous and asynchronous areas. This variability may be due to the turnover of plant abundance, which is influenced by species richness and dominance.

In regards to plant growth form composition, the model results show no difference in synchrony caused by the LMH. This lack of difference may be attributed to the high diversity of growth forms in tropical forests and the high number of species that belong to these groups (Souza et al., 2022). Even if the proportion of dominant groups changes, it is likely that these groups will still be represented by at least a few species or the dominant one. (Kurten & Carson, 2015; Souza et al., 2022). On the opposite, species diversity seems to respond to LMH strongly. In the presence of herbivores, the plant species diversity synchronizes with lag distance, while the opposite is true in their absence whereas the sites tend to be asynchronous. This is particularly interesting if compared to the plant abundance, as they are both moving towards a diffent direction. For instance, in open plots, plant abundance was more asynchronous, given the heterogeneous effect of LMH on their dynamic. The joint effect of abundance and species diversity analyses suggests that these two variables are negatively correlated in regarding synchrony. The variability in plant abundance determined by LMH functions controls the population fluctuation, which in turn open space and opportunities for young plant species to emerge and shortly occupy the available niche. However, it is likely that these plants do not get permanently established, thus starting the cycle again. In summary, it shows that LMH controls for plant abundance, which determines their spatial species diversity turnover. On the opposite, LMH exclusion leads to asynchrony among sites given the low stability of plant species population size. These same patterns have been reported previously by studies using the same long-term dataset (Villar et al., 2019; Souza et al., 2022).

The results depicted here indicate that LMH defaunation holds the potential to change the stability of the plant community over time and space. The herbivores' effect alone was strong enough to change background temporal trends already present in the plots prior to the experiment, thus highlighting the weight of their effects on sapling communities in both treatments in this experiment. This is likely to happen due to the functional extinction of herbivory and seed predation, an important antagonistic interaction that controls plants' abundance and dominance, and the lack of physical damage caused by LMH, which can be caused by trampling on young or small plants (Pizo et al., 2006; Rosin et al., 2017; Souza et a., 2022). Along with antagonistic interactions, herbivores also play a key role in facilitating seed dispersal, which contributes to plant dispersal and spatial distribution (Beck et al., 2013; Comita et al., 2014). Here, I found less synchronized patterns among sites regarding plant abundance in the presence of LMH than in their absence. I discussed that in the exclosure plots, plants may recruit and take over more rapidly than in their presence (open plots), which shows us the community ability to synchronize plant population abundances in response to defaunation. This also shows us that LMH have a heterogenous effect on plant abundance even across scales.

These findings support the predictions that the loss of LMH can reduce plant species diversity and turnover but not plant growth form composition, which can have unwanted long-term outcomes for the structure and diversity of tropical forests (Kurten & Carson, 2015; Villar et al., 2019; Souza et al., 2022). To better disentangle and comprehend the consequences of LMH extinction for tropical forest maintenance, I suggested incorporating other aspects into the model, such as the plants' life history and ontogeny within plant growth form diversity, as well as changes in environmental stability, such as temperature and precipitation. This way, we can advance in understanding the role of these animals in contributing to the carrying capacity of tropical forests and the ecological spatiotemporal thresholds at which plant communities might shift to an alternative state.

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