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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA,  
EVOLUÇÃO E BIODIVERSIDADE

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**DIVERSIDADE FUNCIONAL DE PLANTAS DISPERSAS POR ANIMAIS EM UMA  
CRONOSSEQUÊNCIA DE FLORESTAS SECUNDÁRIAS DA MATA ATLÂNTICA**

**WILLIAN BARBOSA SIMIONI**

**Rio Claro – SP  
2024**

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**WILLIAN BARBOSA SIMIONI**

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, Evolução e Biodiversidade.

Orientadora: Prof.<sup>a</sup>. Dra. Marina Corrêa Côrtes

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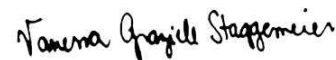
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*Dedico esta dissertação aos meus pais Dirce e Antonio,  
às minhas irmãs Daniele e Juliana, e aos meus sobrinhos  
Victor, Pedro, Isac, Matheus e Gabriel.*

*Dedico especialmente à memória de minha querida Tia Neide.*

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## RESUMO

Frutos zoocóricos apresentam grande variedade de atributos funcionais que são importantes para as interações mutualísticas de dispersão de sementes, sobretudo para o processo de regeneração passiva de florestas secundárias. À medida que a composição de espécies vegetais varia em resposta ao processo de sucessão ecológica e às variáveis ambientais e bióticas, é esperado que os atributos funcionais também variem ao longo da (re-)organização das novas comunidades. Nesse estudo, nós caracterizamos o espaço funcional de atributos de frutos em comunidades de plantas dispersas por animais ao longo de uma cronosequência de florestas de regeneração natural da Mata Atlântica Semidecídua. Nós também investigamos a influência da idade, cobertura vegetal e distância geográfica entre manchas de florestas sobre a diversidade funcional alfa e beta. Nós utilizamos inventários florísticos de espécies zoocóricas em 55 parcelas de 20 x 45m localizadas em fragmentos de floresta secundária na região da Bacia Hidrográfica do Rio Corumbataí – SP, e os atributos das 130 espécies zoocóricas registradas foram obtidos a partir de uma extensa compilação de bases de dados, estudos científicos publicados e de amostras coletadas em campo. Os dados faltantes foram obtidos utilizando um algoritmo de imputação de dados com base na filogenia das espécies. Nossa análise de coordenadas principais foi capaz de capturar ao todo 71.35% da variação dos atributos para os primeiros cinco eixos, e 39.48% para os primeiros dois eixos. A primeira dimensão (PCoA1) representou 24.17% da variação dos atributos. Encontramos evidências de que a idade de restauração e a distância entre as comunidades contribuem para aumentar a diversidade funcional de características de frutos e sementes em comunidades de espécies zoocóricas, o que está alinhado com nossas hipóteses anteriores. Embora não tenhamos encontrado efeito significativo da idade e da distância nos índices de diversidade alfa FRic e na FEve, os índices FMPD e FDis mostraram uma tendência a aumentar à medida que as comunidades envelhecem e com distância entre elas. Da mesma forma, a diversidade funcional beta foi influenciada positivamente pela diferença de idade e distância geográfica entre as comunidades. A dissimilaridade de Jaccard e o turnover foram maiores entre comunidades maior diferença de idade e distância. Uma maior diversidade funcional na dispersão de sementes pode contribuir para a manutenção da biodiversidade e de processos ecossistêmicos essenciais em florestas secundárias em regeneração.

**Palavras-chaves:** Ecologia de comunidades, ecologia funcional, diversidade funcional alfa e beta, atributos funcionais, frugivoria, restauração.

## ABSTRACT

Zoochorous fruits exhibit a wide range of functional attributes that are important for mutualistic seed dispersal interactions, especially for the passive regeneration process of secondary forests. As the composition of plant species varies in response to ecological succession and environmental and biotic variables, it is expected that functional attributes will also vary throughout the (re-)organization of new communities. In this study, we characterized the functional space of fruit traits in animal-dispersed plant communities along a natural regeneration chronosequence of Semideciduous Atlantic Forest. We also investigated the influence of forest age, forest cover, and geographic distance between forest patches on alpha and beta functional diversity. We used floristic inventories of zoochorous species in 55 plots of 20 x 45m located in secondary forest fragments in the Corumbataí River Watershed – SP region, and the attributes of the 130 recorded zoochorous species were obtained from an extensive compilation of databases, published scientific studies, and field-collected samples. Missing data were obtained using a data imputation algorithm based on species phylogeny. Our principal coordinate analysis was able to capture in total 71.35% of trait variation for the first five axes, and 39.48% for the first two axes. The first dimension (PCoA1) represented 24.17% of trait variation. We found evidence that restoration age and distance between communities contribute to increased functional diversity of fruit and seed characteristics in zoochorous species communities, aligning with our previous hypotheses. Although we did not find a significant effect of age and distance on the alpha diversity indices FRic and FEve, the indices FMPD and FDis showed a tendency to increase as the communities age and with greater distance between them. Similarly, beta functional diversity was positively influenced by the difference in age and geographical distance between communities. Jaccard dissimilarity and turnover were higher between communities with greater differences in age and distance. Greater functional diversity in seed dispersal may contribute to the maintenance of biodiversity and essential ecosystem processes in regenerating secondary forests.

**Keywords:** Community ecology, functional ecology, alpha and beta functional diversity, functional traits, frugivory, restoration.

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## 1 INTRODUCTION

Frugivory and seed dispersal represent key processes in terrestrial ecosystem ecology (Herrera, 1985). Through frugivory, plants have their seeds dispersed by animals, allowing them to be deposited in different locations as animals move through the landscape, contributing to seedling recruitment and consequently, to the colonization and establishment of both primary and secondary forests (Kitamura, 2011; Rozendaal et al., 2019). Several factors determine the mutualistic interactions of frugivory and seed dispersal (Jordano, 2000). The occurrence of interaction depends not only on the co-occurrence of interacting species in space and time but also on the correspondence between fruit and frugivore characteristics (Dehling et al., 2016; González-Castro et al., 2015).

On one hand, the optimal diet theory postulates that foraging, ingesting, and digesting food resources incur energetic costs for the consumer. On the other hand, the seed dispersal syndrome hypothesis suggests that fruit-bearing plants offset the energetic expenditure of frugivores by enhancing fruit attractiveness through investment in nutritive compounds (Debussche et al., 1987; Van der Pijl, 1982) in response to the dietary needs and sensory capacities of dispersers (Lei et al., 2021). However, plants dispersed by animals face an evolutionary dilemma between producing excessively attractive fruits (Cazetta et al., 2008), susceptible to herbivore and pathogen attacks, and investing in physical and chemical defenses against predation, which might hinder frugivory and seed dispersal (Cipollini et al., 2004; Cipollini & Levey, 1997; Schaefer et al., 2003). Secondary compounds, for instance, serve as chemical defenses against microorganisms and predators, making interaction with frugivores more challenging (Whitehead & Bowers, 2014).

Angiosperm fruits have evolved a wide array of attractive features that constitute the fruit-frugivore syndromes (Valenta et al., 2017; Van der Pijl, 1982), known as functional or phenotypic traits (Violle et al., 2007). Fleshy fruits or those with nutritious seeds generally exhibit detectable traits for dispersing frugivores, such as fruit color and size (Jordano et al., 2011; Valido et al., 2011). Fruit shape, the presence of secondary structures (Burns et al., 2009; Galetti et al., 2003; Valido et al., 2011), nutritional composition, and fruit energy content (Jordano, 2000; Nevo et al., 2019) are other important traits for frugivory. For example, fruits dispersed by birds must fit the opening of the bird's beak, and after ingestion, the bird must be able to digest it and discard viable seeds in favorable microsites (Jordano, 2000).

The functional diversity of plants dispersed by animals encompasses a spectrum of traits associated with fruit morphology, nutritional composition, and adaptation to frugivore preferences. These traits play a crucial role in determining the interactions between plants and their dispersers, influencing seed dispersal effectiveness, and ultimately shaping the structure and dynamics of regenerating communities (Knapp et al., 2016). Variations in fruit traits, such as size, color, pulp-to-seed ratio, and nutritional content, contribute to the establishment of diverse frugivore-plant networks, where specific traits attract different frugivore species (Ordano et al., 2017). This functional diversity not only enhances the chances of successful seed dispersal but also promotes the establishment of a wide range of plant species, fostering biodiversity in regenerating ecosystems (Hawes et al., 2020).

The environmental variables present in naturally regenerating communities exert significant influence on the functional diversity of plants dispersed by animals. Factors such as habitat structure, successional stage, and landscape connectivity impact the availability and diversity of resources for frugivores, consequently affecting the selection pressure on plant traits (Monteiro et al., 2022; Stevenson et al., 2023). For instance, in early successional stages characterized by open habitats, fruit traits favoring visibility and attraction may predominate to entice dispersers (Cote et al., 2017). Conversely, in more mature stages with denser vegetation, i.e. high connectivity, fruit traits may evolve towards adaptations, like large fruits with big seeds and attractive colors, that aid in long-distance dispersal or appeal to specific frugivore guilds (Valenta & Nevo, 2020). These environmental variables contribute to shaping the functional diversity of zoochorous plants by driving selective pressures on fruit traits, thereby influencing the composition and interactions within the frugivore-plant network during community regeneration (Poorter et al., 2019; Zuñe-da-Silva et al., 2022).

Neotropical forests naturally exhibit spatial variation in plant species composition (Myers et al., 2013) and functional diversity (Aslan et al., 2019). This variation can be further accentuated in ecological communities facing the impacts of deforestation, forest fragmentation (Haddad et al., 2015), and natural or assisted forest regeneration processes (Lohbeck et al., 2012). In this context, considering the use of functional diversity metrics in community studies is crucial to understand how these species establish themselves in communities and their role in providing ecosystem services (Lohbeck et al., 2013). Furthermore, evaluating functional diversity metrics can provide valuable insights into the effectiveness of the regeneration process and can guide future restoration strategies (Poorter et al., 2019).

Approximately half of the world's tropical forests are in a secondary stage of ecological succession (Wright & Muller-Landau, 2006). This implies an opportunity for the establishment of new taxonomic and functional configurations during the ecological succession process, where variables such as the land history prior to the restoration process, connectivity, and forest age are crucial in shaping these communities and their functional traits (Poorter et al., 2019; Zuñe-da-Silva et al., 2022).

The restoration process favors the spontaneous regeneration of forests, enabling ecological succession and consequently affecting the diversity and composition of the species present (Rozendaal et al., 2019). The presence and behavior of seed-dispersing animals play a crucial role in reintroducing seeds and re-establishing ecological interactions, directly influencing trait (dis)similarity of plants that colonize these restored environments. Variation in food preferences and movement patterns of dispersing animals results in different seed dispersal strategies, thus shaping the diversity and composition of plant communities (Almeida et al., 2022). Around 75% of tree species in the Atlantic Forest are animal-dispersed (Almeida-Neto et al., 2008), with birds and mammal groups standing out as crucial for seed dispersal due to their ability to move between fragments and use degraded areas and regenerating vegetation (Kitamura, 2011; Tiffney, 2004).

In this scenario, knowledge of how environmental factors shape the diversity of fruit traits and the associated frugivore-plant interactions informs restoration strategies aimed at enhancing seed dispersal and promoting species diversity. In this study, we characterized the functional space of fruit traits in animal-dispersed plant communities along a natural regeneration chronosequence of Semideciduous Atlantic Forest. We also investigated the influence of forest age, forest cover, and geographic distance between forest patches on alpha and beta functional diversity. We hypothesized that the oldest plant communities in terms of regeneration have higher functional diversity of traits and, therefore, greater heterogeneity of traits, and that the geographic distance between plant communities increases the functional dissimilarities between them due to seed dispersal distance limitation.

## 5 CONCLUSION

Our study sheds light on the intricate relationships between zoochorous fruit traits and the dynamics of seed dispersal in regenerating Semideciduous Atlantic Forests. The investigation unveiled how these functional attributes vary across communities undergoing ecological succession, showing congruent responses to factors like restoration age and geographic distance between forest fragments. Our findings highlight the significance of considering fruit and seed traits as key elements shaping the assembly and persistence of plant communities reliant on animal-mediated seed dispersal. We found that alpha and beta functional diversity indices demonstrated noticeable trends towards increased variation with the aging of communities and greater geographic isolation between them. These outcomes underscore the importance of preserving a diverse array of functional traits in seed dispersal mechanisms for long-term resilience and biodiversity conservation within secondary forest ecosystems. Ultimately, recognizing and preserving the multifaceted functional diversity of seed dispersal mechanisms can prove crucial for fostering the resilience and vitality of regenerating secondary forests, thereby ensuring the sustainability of essential ecosystem processes and the conservation of biodiversity in these ecosystems.

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