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"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

SEED DISPERSAL AND PLANT DIET OF FRUIT-EATING BIRDS IN SECONDARY FOREST FRAGMENTS

CARINA ISABELLA MOTTA

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RESUMO

A mobilidade das aves frugívoras as torna dispersoras chave de sementes na paisagem fragmentada atual, impulsionando o estabelecimento e sucessão de novas florestas. Distúrbios antropogênicos circundantes moldam essas florestas em estágio inicial, resultando em comunidades florestais secundárias novas. Para entender melhor em quais condições a dispersão de sementes é mais eficaz, assim como as espécies de plantas na dieta das aves dessas comunidades, trabalhamos em dez parcelas de floresta em estágio inicial na bacia do rio Corumbataí no estado de São Paulo. Estabelecemos redes de neblina em cada parcela uma vez por mês ao longo de um ano para coletar fezes de indivíduos capturados. As sementes encontradas nas fezes foram usadas para testar o componente quantitativo da efetividade da dispersão de sementes (SDE) entre as parcelas e espécies de aves. Características do habitat tais como idade da floresta, cobertura florestal e comunidade de espécies de plantas lenhosas zoocóricas não explicaram as variações no componente quantitativo da SDE entre as parcelas. A espécie *Antilophia galeata* se destacou como a dispersora mais efetiva, seguida de *Turdus leucomelas*, *Ramphocelus carbo* e *Tachyphonus coronatus*. O grau de frugivoria das aves se relacionou positivamente com a SDE enquanto que a massa corporal não teve efeito. O sequenciamento de um mini-barcode de *rbcL* (Ribulose-1,5-Bifosfato Carboxilase), foi aplicado em DNA isolado das fezes de dez espécies de aves dispersoras de sementes. Dos gêneros de plantas detectados, quatro são exóticas e, embora a maioria tenha sido classificada como árvore ou arbusto, pelo menos dois são de hábito herbáceo. Embora tenhamos detectado variação na dispersão de sementes entre fragmentos, indicando heterogeneidade espacial de processos ecológicos em florestas jovens, essa variação não é explicada pelas características analisadas. Nossa análise da dieta indica que algumas espécies de aves quantitativamente eficientes na dispersão de sementes provavelmente forrageiam fora das florestas. Se por um lado a movimentação para além da floresta potencialmente aumenta a conectividade entre os fragmentos, também pode aumentar a introdução de espécies exóticas, contribuindo para a organização de novos ecossistemas na Mata Atlântica.

Palavras-chave: Restauração florestal; Frugivoria; Metabarcoding; Interação animal-planta; Fezes

ABSTRACT

The mobility of fruit-eating birds makes them key seed dispersers in today's fragmented landscape, ultimately driving the establishment and succession of new forests. Surrounding anthropogenic disturbances shape these early successional forests, favoring habitat generalist bird species and introducing exotic plants, resulting in novel, secondary forest communities. To better understand under which conditions seed dispersal is most effective, as well as the plant species important to bird diet within these new communities, we worked in ten plots of early successional forest throughout the Corumbataí river basin in the state of São Paulo. We mist netted in each plot once a month over the course of a year to collect droppings from captured individuals. Seeds found in droppings were used to calculate and test the quantitative component of seed dispersal effectiveness (SDE) among plots and bird species. Habitat feature differences in age, forest cover, and the zoochorous woody plant species community were not found to explain changes in the quantitative component of SDE among plots. We identified *Antilophia galeata* to be the most quantitatively effective seed disperser, followed by *Turdus leucomelas*, *Ramphocelus carbo*, and *Tachyphonus coronatus*. Bird species-level SDE was found to be explained by the degree of bird frugivory, but not bird body mass. Using metabarcoding sequencing of *rbcL* (Ribulose-1,5-Bisphosphate Carboxylase), a locus used to identify plants in the diet, we analyzed droppings from ten key, seed dispersing bird species to detect diet items beyond seeds present in droppings. Of the plant genera detected, four are exotic, and, while a majority were classified as trees or shrubs, at least two are herbaceous. Although we detected variation in seed dispersal among fragments, indicating heterogeneity in ecological functions, this variation is not explained by analyzed characteristics. Additionally, our diet analysis indicates that bird species we found to be highly efficient at dispersing seeds are foraging outside of forests and, while potentially increasing connectivity among fragments, can also increase the introduction of exotic species.

Key-words: Forest restoration; Frugivory; Metabarcoding; Plant-animal interaction; Feces

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1 INTRODUCTION

Mutualistic relationships between plants and their animal seed dispersers are keystone interactions that form the foundation of forest ecosystem structure (BASCOMPTE; JORDANO, 2007; CARLO *et al.*, 2011). The movement of seeds by animals is essential to the maintenance and formation of forests, with a majority of woody plants being dispersed by frugivores and granivores (HERRERA, 2002). Meanwhile, many animal dispersers depend on plants as an integral part of their diet, especially in the tropics, where the consumption of fruit by vertebrate species is proportionally higher than in other regions (FLEMING *et al.*, 1987; JORDANO, 2000). The increase of fruit in animal diet in the tropics is matched by an increase in animal-mediated seed dispersal, principally by birds (ESCRIBANO-AVILA *et al.*, 2018; WHEELWRIGHT, 1988). In Brazil's Atlantic Forest, 51% of animal-dispersed woody plant species are dispersed by birds (ALMEIDA-NETO *et al.*, 2008). Birds and plants depend on and benefit from one another for services and resources, especially in Atlantic Forest.

Today, less than 15% of the Atlantic Forest remains, with more than 80% of remaining forest consisting of scattered fragments (REZENDE *et al.*, 2018). The aggressive deforestation of this incredibly biodiverse ecosystem has created an urgency to not only conserve the forest that is left, but also to restore areas that were once forested (MELO *et al.*, 2013; ZWIENER *et al.*, 2017). A Brazilian law created in 1934 and amended in 2012 established incentives and obligations for private landowners to allocate a portion of their land as natural reserves (Law 12.651/2012, Brancalion et al. 2016). This law, in combination with other social and economic factors, led to the abandonment of areas previously deforested to make pasture lands, allowing the forest to naturally regenerate (CALABONI *et al.*, 2018; GOMES *et al.*, 2013). However, the forests that establish in these abandoned pasture lands are not the same as the forests that once occupied the space (CÉSAR *et al.*, 2021; ROZENDAAL *et al.*, 2019). Aside from being young, these forests are novel in the sense that they contain species that previously did not occur in the region, such as plant species introduced by humans for agricultural cultivation or unintentionally (PETRI *et al.*, 2018; SUGANUMA *et al.*, 2014). The exotic species within these reconstructed forests can establish interactions with seed dispersing bird species, creating new mutualisms.

The fragmented nature of these secondary forest fragments has not only resulted in a novel suite of species interactions, but has also further exaggerated the importance of, as well as modified, plant-bird mutualisms (EMER *et al.*, 2020). The surrounding matrix of these forests, as well as habitat features of the fragment itself, such as forest age, connectivity, and plant community, can determine habitat accessibility and quality for frugivores, impacting seed dispersal dynamics (GONZÁLEZ-VARO *et al.*, 2017; RIBEIRO DA SILVA *et al.*, 2015). The mobility of bird species has always made birds key players in long-distance seed dispersal, transporting seeds further away from the maternal plant and facilitating gene flow among plant populations (DICK *et al.*, 2008; JORDANO, 2017). Today's fragmented landscape, with urban areas and open pastures separating forests, has made habitat generalist bird species essential in the establishment of new forests (HAGEN *et al.*, 2012). The tolerance of these bird species to anthropogenic disturbance and dynamic environments allows them to move between fragments, consequently dispersing seeds in the open areas that separate the forests (CARLO; MORALES, 2016; HARRIS; PIMM, 2004). Simultaneously, these secondary forests are critical in providing food to fruit-eating species in a resource-limited landscape (QUITIÁN *et al.*, 2019; VLEUT *et al.*, 2013). Although fruit availability in secondary forests is known to be lower than that available in primary forest, the early successional forests are often the only refuge from the surrounding, human-impacted areas (BARLOW *et al.*, 2007; CHAZDON *et al.*, 2009). Therefore, just as birds are necessary for the establishment and maintenance of new forests, these forests provide essential resources for the remaining bird populations.

Insights can be gained into plant-bird mutualisms, especially how to facilitate and preserve these interactions in the context of active restoration efforts, by evaluating the plant perspective of seed dispersal. The function of plant species within seed dispersal networks can be measured both quantitatively and qualitatively using the seed dispersal effectiveness (SDE) framework (SCHUPP, 1993; SCHUPP *et al.*, 2010, 2017). Traditionally, the quantitative component of the SDE provides a standardized measure of seed dispersal effectiveness by frugivorous species by distilling the data collected into comparative metrics, like the frequency of visits and number of seeds dispersed (e.g., Godinez-Alvarez and Jordano 2007, Rother et al. 2016). While focal observations of disperser activity and feeding behavior are most

often used to assess the quantitative component of SDE, bird capture rate from mist netting sampling serves as a proxy of bird activity and can be used to evaluate visitation frequency (MONTAÑO-CENTELLAS, 2013). Similarly, seeds found in droppings collected from captured birds allows for the quantification of seeds being dispersed (NOGALES *et al.*, 2017). The quantitative component of SDE can be used to explore differences in seed dispersal effectiveness among habitat types, as well as bird species (BLENDINGER, 2017; HOHMANN *et al.*, 2023). Among bird species, characteristics such as body size and diet can heavily influence seed dispersal effectiveness (GODÍNEZ-ALVAREZ *et al.*, 2020). While the quantitative component of SDE is key in evaluating the plant perspective of bird-plant interactions, the equally important bird perspective, assessed through the resource-provisioning effectiveness (RPE), has only recently begun to be explored (QUINTERO *et al.*, 2020, 2023). The assessment of both plant and bird perspectives can deepen our understanding of plant-bird mutualisms essential to forest regeneration.

By complementing the quantitative component of SDE with knowledge of all plant species that comprise bird diet, a more comprehensive image of plant-bird mutualisms can be created (GONZÁLEZ-CASTRO *et al.*, 2022; QUINTERO *et al.*, 2020). Evaluating the effectiveness of plants as resources not only provides critical insights as to which plants may be dispersed, but can also indicate the quality of available resources, as well as foraging habits of species, both of which further determine seed dispersal potential (FONTÚRBEL *et al.*, 2017; MILESI *et al.*, 2008). While seeds found in bird droppings provide direct evidence of plant species consumption, in the case of large, pulpy fruits with small seeds, such as exotic *Psidium guajava* (Myrtaceae), birds may ingest the pulp while avoiding swallowing the seeds (FOSTER, 2016; LOPES *et al.*, 2016). In recent years, molecular techniques have begun to be developed in order to identify the diet items present in droppings of which seeds were not ingested (ANDO *et al.*, 2020; SHUTT *et al.*, 2021). While challenging to apply in tropical areas due to high plant diversity, the development of universal, mini-barcodes enable the identification of plant family and genera from bird droppings, even in the absence of a robust reference library (ROSEMARY *et al.*, 2018; VASCONCELOS *et al.*, 2021). The characterization of bird diet in conjunction with the quantification of SDE provides a more robust understanding of the plant-bird mutualisms that are so critical for future forests.

In this study, we explore both the plant community and bird perspective of bird-mediated seed dispersal in secondary Atlantic Forest fragments. We quantify SDE from the plant perspective to investigate differences in seed dispersal effectiveness across areas that vary in forest age, cover, and zoochorous woody tree species communities, as well among bird species and their species traits. Using molecular techniques, we evaluated the bird perspective of seed dispersal by identifying plant genera present in the diet of principal seed dispersers. We predicted an increase in the quantitative component of SDE with an increase in forest age, cover, and zoochorous woody plant species abundance, as well as richness. Additionally, we predicted an increase in SDE with an increase in bird body size and the percent of diet composed of frugivory. Due to the heavy anthropogenic impact on these secondary forests, we expected to detect exotic and weedy plant species in bird diets.

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