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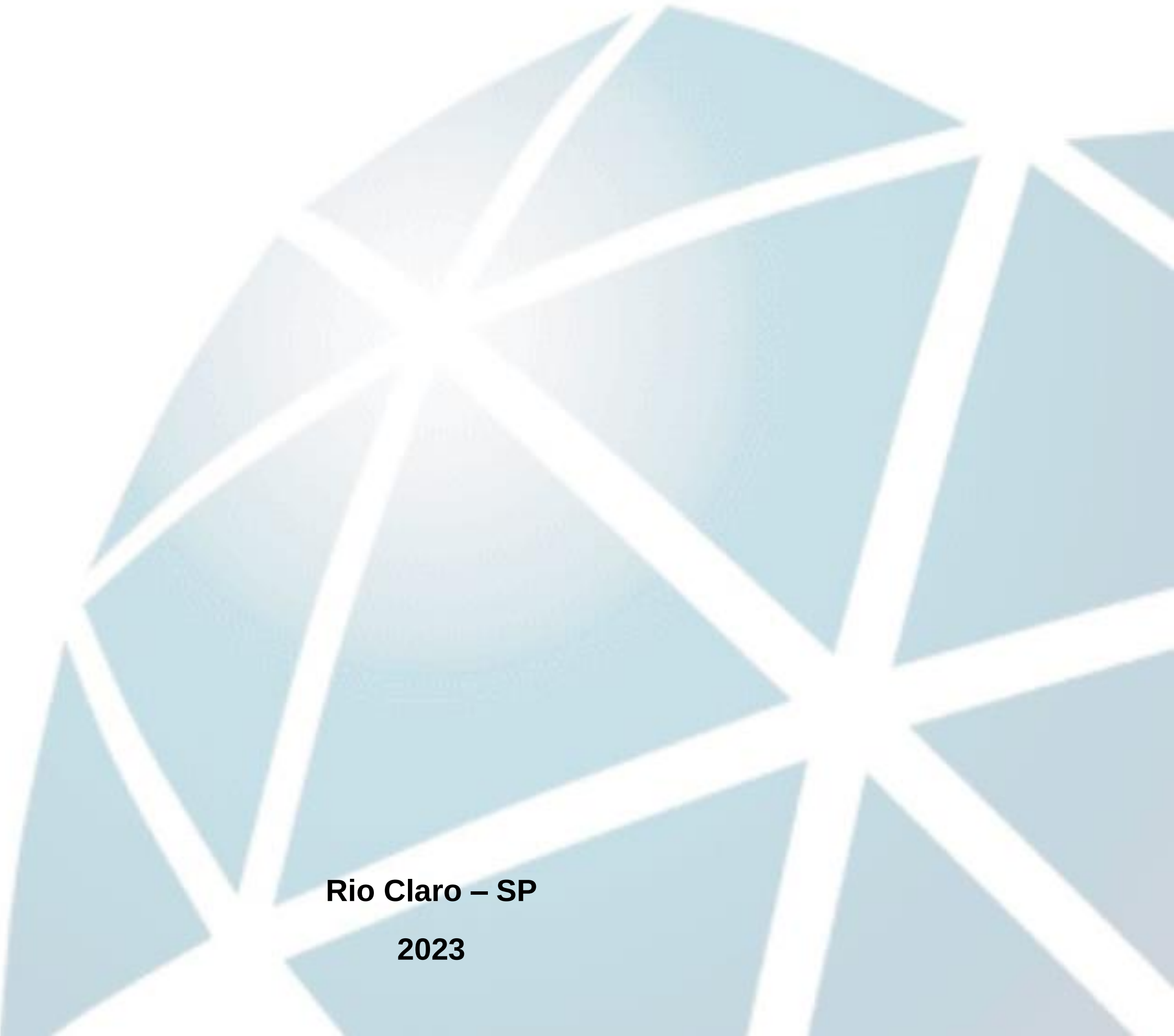
UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

PREDIZENDO SOMBRAS DE SEMENTES EM DIFERENTES CONTEXTOS AMBIENTAIS: UMA ABORDAGEM DA MODELAGEM PARA UM FRUGÍVORO ARBORÍCOLA

EDUARDO MIGUEL ZANETTE



Rio Claro – SP

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

Orientadora: Dra. Laurence Culot

Coorientadores: Ronald Bialozyt e Eckhard W. Heymann

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TÍTULO DA DISSERTAÇÃO: PREDIZENDO SOMBRAS DE SEMENTES EM DIFERENTES CONTEXTOS AMBIENTAIS: UMA ABORDAGEM DA MODELAGEM PARA UM FRUGÍVORO ARBORÍCOLA

AUTOR: EDUARDO MIGUEL ZANETTE CORREIA

ORIENTADORA: LAURENCE MARIANNE VINCIANNE CULOT

Aprovado como parte das exigências para obtenção do Título de Mestre em Ciências Biológicas, área: Biodiversidade pela Comissão Examinadora:

Profa. Dra. LAURENCE MARIANNE VINCIANNE CULOT (Participaçao Presencial)
Departamento de Biodiversidade / Unesp - IB Rio Claro

Profa. Dra. ÉRIKA GARCEZ DA ROCHA (Participaçao Presencial)
Departamento de Ecologia / UFRJ

Carla Cristina Gestich
Profa. Dra. CARLA CRISTINA GESTICH (Participaçao Presencial)
Departamento de Genética e Evolução / Universidade Federal de São Carlos

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“[…] Science is the search for neat, predictable curves, compact ways of summarizing the data. But there is always the danger that the curves we see are illusory, like pictures of animals in the clouds. As we draw our self-propelling arcs, some points will inevitably lie outside the line—those that must be dismissed as random error or noise. So we are left with a gnawing dissatisfaction: Are we missing something?”

George Johnson – Fire in the Mind (1995)

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Quem me conhece sabe que eu deixo a notícia boa por último. Durante este período, tive duas infecções por covid (uma com internação, uso de VMI e 10 kg a menos; e outra simples, mas impedindo minha ida pra Alemanha na data programada e me rendendo muitos meses de burocracia). Uma clavícula quebrada. Uma alergia insistente aos carrapatos da estação seca da Floresta Estadual Semidecídua no Pontal do Paranapanema. E por fim, oito mudanças (baldeando entre Rio Claro, Curitiba e Göttingen), no meio da indecisão pandêmica.

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RESUMO

A dispersão endozoocórica de sementes mantem a estrutura e dinâmica de florestas, sendo um processo central na manutenção da biodiversidade de florestas tropicais. Neste cenário, primatas Neotropicais tem papel central ao dispersar sementes ao longo de suas áreas de vida. Entretanto, os altos níveis de degradação e fragmentação do hábitat destes primatas resultaram em fragmentos florestais de diferentes tamanhos e formas e com diferentes distribuições de recursos, levando à uma possível alteração do papel funcional deles como dispersores de sementes. Apesar do aumento do número de estudos sobre dispersão de sementes por primatas durante as últimas décadas, ainda é incerto como o serviço de dispersão de sementes será afetado por características locais dos fragmentos. Recentemente, no entanto, o desenvolvimento de modelos baseados em agente (ABMs) capazes de predizer o movimento dos primatas e as sombras de sementes resultantes abriram novas perspectivas. O mico-leão-preto, (*Leontopithecus chrysopygus* ou “mico”), é um efetivo dispersor de sementes endêmico da Mata Atlântica. Seu hábitat está entre os mais fragmentados entre as espécies de primatas Neotropicais. Nesse estudo, eu desenvolvi e validei um ABM para predizer os padrões de dispersão de sementes pelo mico-leão-preto. No primeiro capítulo, eu explorei os padrões de movimento de quatro grupos habitando quatro fragmentos florestais. Eu concluí que os padrões de movimento diferem extensivamente e que esses padrões podem ser modulados pelas propriedades do fragmento (tamanho e forma), muito provavelmente afetando a dispersão de sementes (especialmente a distância média). A partir destas análises, eu derivei “regras” para implementação do ABM desenvolvido no Capítulo 2, onde eu adaptei um modelo previamente desenvolvido para uma espécie de calitriquídeo amazônico para o mico-leão-preto. A maioria dos padrões (isso é, as variáveis que emergem do modelo), especialmente a distância de dispersão (SDD), tamanho da área de vida e deslocamento diário (DPL), foram bastante similares ao observado na natureza. Além disso, o modelo foi capaz de reproduzir outros padrões não inicialmente considerados durante o desenvolvimento do modelo, como a taxa de movimento (MR) e tortuosidade da rota (PT), portanto destacando o potencial do modelo em predizer a sombra de sementes em diferentes fragmentos florestais. O único problema evidente do modelo foi que ele não reproduziu tão bem o tamanho da área de vida na floresta contínua, onde os micos têm a maior área de vida registrada para a espécie. Além disso, eu discuti as implementações do modelo e os processos que talvez não estejam nele representados, como a territorialidade e interações com conspecíficos, em relação à mais recente literatura sobre movimento e ABMs. No Capítulo 3, eu gerei fragmentos teóricos com formas, tamanhos e distribuição de recursos variáveis. Eu fiz isso por meio de um gerador de florestas e utilizo o tamanho da área de vida previsto por um modelo estatístico com base no tamanho do fragmento e na densidade populacional dos micos. Por fim, gerei a distribuição de recursos a partir de um processo de ponto de Thomas. Resultados preliminares apontam a densidade de micos como o principal fator afetando a SDD, seguido pelo DPL e MR, enquanto a distância entre arvores frutíferas (agregação dos recursos) se mostrou pouco influente. A simples parametrização do modelo com velocidades empíricas e estimativas de tempo de consumo (*feeding bouts*) e tempo de passagem pelo trato digestório, em conjunto com um submodelo energético, são suficientes para predizer grande parte da variação nos padrões de sombra de sementes. Apesar das análises sugerirem ser necessário implementações de alguns processos não inclusos no modelo, esses quais diminuem a capacidade preditiva do modelo (como a territorialidade), destaco que o ciclo de modelagem deve continuar, com enfoque especial em implementar regras mais mecanísticas – isto é, aquelas que dependam menos de parameterizações e conhecimentos *ad hoc* -, retirando a necessidade de estimar uma velocidade média de deslocamento para cada grupo. Eu espero que essa dissertação contribua para um maior entendimento dos padrões de movimento e de dispersão de sementes dos mico-leões-pretos, e que estimule futuros esforços de modelagem e amostragem.

PALAVRAS-CHAVE: Sombra de sementes; *Kernel* de dispersão de sementes; Modelagem baseada em agentes; Ecologia do movimento, Comportamento e uso do espaço.

ABSTRACT

Endozoochorous seed dispersal maintains forest community structure and dynamics, thus being an underpinning process for tropical forest biodiversity. In this scenario, Neotropical primates play a major role by dispersing seeds throughout their home ranges. However, high levels of forest degradation and fragmentation have modified their habitat into fragments of distinct sizes, shapes, and resource distributions, leading to a possible alteration of their functional role as seed dispersers. Despite the huge increase of primate seed dispersal studies during the last decades, it is still unknown how the seed dispersal service will be affected by local forest fragment characteristics. More recently, the development of agent-based models (ABMs) able to predict primate movement and the associated seed shadows opened new perspectives. The black lion tamarin (*Leontopithecus chrysopygus* or simply "tamarin") is a seed disperser, endemic to the Atlantic Forest whose habitat is among the most fragmented among Neotropical primate species. Here, I developed an ABM to predict black lion tamarin seed dispersal patterns. In the first chapter, I explored the movement patterns of four tamarin groups inhabiting four forest fragments. I concluded that tamarins differ extensively in movement patterns, and this might be modulated by the fragment properties (size and shape), thus likely affecting seed dispersal distances. From this chapter, I derived "rules" for the ABM implementation in Chapter 2, where I adapted a previously developed model to the black lion tamarin. Most of the patterns (i.e., variables that emerge from the model), namely seed dispersal distance (SDD), home range size, and daily path length (DPL) were very similar to the observed. I further showed the model was able to reproduce other patterns not initially aimed, like the movement rate (MR) and path twisting (PT), therefore highlighting its potential to predict seed shadows in distinct forest fragments. The only drawback of the model was that it did not predict well home range sizes in continuous forest, where tamarins reach the largest observed home range sizes for the species. I then discussed the model implementation and processes that might be lacking, such as territoriality and conspecific interactions, in face of the recent ABM movement literature. In Chapter 3, I generated theoretical forest fragments with varying sizes, shapes, and resources distributions. I did this by creating a forest fragment generator, by predicting home range sizes for each of these fragments based on tamarin density and fragment size with statistical modeling, and I finally generate resource distributions based on a Thomas (point)-process. Preliminary results show a great effect of tamarin density on the SDD, followed by DPL and MR, but a small effect of the distance between fruiting trees (resource aggregation). The simple parameterization of the model with empirical velocities plus the estimates of feeding bouts and gut transit times, altogether linked with an energetic sub model, are enough do predict most of the variation in seed shadow. Although most patterns of interest were successfully predicted, further implementations of non-included processes in the model (such as territoriality) should continue through the modeling cycle, possibly enhancing the model predictability of movement and seed dispersal patterns in distinct environments. This might be attained by implementing more mechanistic rules – i.e., rules that rely less on parameterization and *ad-hoc* knowledge – further making the parameterization of the model with empirical velocities unnecessary. I highlight that the model structure captures the essence of movement and seed dispersal by tamarins. I hope this thesis has contributed to a greater understanding of black lion tamarin movement patterns and seed dispersal services and stimulates further modeling and sampling endeavors.

KEYWORDS: Seed shadow; Seed dispersal kernel; Agent-based modeling; Movement ecology; Ranging behavior.

TABLE OF CONTENTS

1. GENERAL INTRODUCTION

The search for general principles has been one of the most outstanding attributes of science, and has struggled ecology as an emerging discipline, especially because of its inherent variant subject: individuals and populations in relation to their environments. This debate grew strongly in the 50’s, where the search for mere “rules of thumb” was deemed insufficient (JUDSON, 1994). With the development of computational power, though, a huge field emerged in the main form of simulation models. But it was just around the 90’s that the agent (or individual)-based modeling emerged as a discipline (JUDSON, 1994). These models, unlike mathematical and statistical models (although some of those could), were able to include individual-level variation in autonomous entities (“agents”), especially in those situations where biological discontinuities, rare events and randomness were dooming predictability of natural systems (JUDSON, 1994). Thus, these models enable to study and test mechanisms working in the smaller levels of complexity that might be generating the patterns at the higher, aggregated level.

The dispersal of seeds from (mainly) Angiosperms and its dispersers is a very interesting biological process that can directly benefit from simulation-based studies. Although historically having received less attention (SNOW, 1970; VAN DER PIJL, 1969) in comparison to other more directly observed and tenured processes, such as population dynamics and predation, host-parasites, etc., the seed dispersal process is still urging for generality and predictability. This is demonstrated by recent research yet struggling to understand the major drivers of animal movement and what are the consequences of this on the seed dispersal effectiveness (BORAH; BECKMAN, 2021; CÔRTES; URIARTE, 2013; KARUBIAN; DURÃES, 2009; LEVEY et al., 2005; NIELD et al., 2020; PEGMAN; PERRY; CLOUT, 2017). In this line, an urge for more mechanistic models of seed dispersal (i.e., models that emerge from unitary rules – movement decisions, energy levels, predator avoidance, etc.) has sprouted in the last decade (COUSENS et al., 2010; MORALES; MORÁN LÓPEZ, 2022), with the understanding of animal ecology in different scales pointed out as a major drawback in these seed dispersal simulation studies (CÔRTES; URIARTE, 2013).

Simulation models emerge as an important tool for understanding seed dispersal patterns, albeit it is recognized as no trivial task (CÔRTES; URIARTE, 2013; MORALES; MORÁN LÓPEZ, 2022).

Black lion tamarins (*Leontopithecus chrysopygus*, hereafter "tamarins") are endangered frugivorous-insectivorous, arboreal and territorial primates that inhabit the highly fragmented Atlantic Forest hotspot in the state of São Paulo, southeast Brazil. By having usually large home ranges (REZENDE et al., 2020 and references therein) that they frequently cross in a single day, tamarins are known to disperse seeds effectively (BUFALO; GALETTI; CULOT, 2016; COIMBRA-FILHO; MITTERMEIER, 1973; PASSOS, 1997), especially medium-sized seeds (DE ALMEIDA E SILVA, 2022). Tamarins inhabit the seasonal Atlantic Forest of São Paulo State (also known as semideciduous forest; VALLADARES-PÁDUA; CULLEN JR, 1994). Although recent populations have been discovered in the Carlos Botelho State Park (ombrophilous forest or Atlantic Forest *strictu sensu*), we restrict our study to the groups and populations inhabiting the semideciduous forest in the interior of São Paulo State. As they inhabit very distinct environmental contexts throughout their highly anthropized geographical range, from riparian forests to continuous protected forest in State Parks, I selected this species as a model to study seed dispersal in relation to local level responses to fragment size, shape, and resource distributions.

Previous work managed to develop a model that successfully predicted the seed dispersal of two Amazonian tamarin species, *Leontocebus nigrifons* and *Saguinus mystax*, in a continuous forest context, based on behavioral rules guided by energy levels. This agent-based model (ABM) of seed dispersal from Bialozyt et al. (2014), originally implemented in Java, was adapted by M. Mulato in NetLogo (WILENSKY, 1999) to fit the environmental context that black lion tamarin (*Leontopithecus chrysopygus*, hereafter "tamarin") inhabit in the heavily fragmented Atlantic Forest. These adaptations included: a) the inclusion of tamarin specific data for parameterization (travel speed, gut retention time, main activities, duration of feeding and foraging events); b) the modification of the energy gain per foraging (on insects); and c) the removal of scent marking of trees (SANTOS, 2020). However, these implementations were still not sufficient to reproduce satisfactorily tamarin movement and seed dispersal patterns. Specifically, the simulated trajectories only reached almost half of the daily distances expected for tamarins in a small (100 ha) forest fragment. Thus, the agent goal of homeostasis (keeping energy levels positive), as implemented in the model, was not enough to reproduce an important pattern (daily distances and therefore its resulting seed shadow). Therefore, a revision of the parameters previously included in the model was needed as well as the inclusion of additional factors to develop a model able to predict tamarin seed shadows in different environmental contexts, which is the main goals of this thesis.

Although this thesis title starts with ‘predicting’, a point should be made about its meaning. I will start with an example from the literature on statistical modelling, which is likely the most frequently known modeling literature for ecologists. According to Shmueli (2010), statistical modelling can be both causal and predictive. While explanatory modelling is commonly done with the application of statistical models (often associative, e.g., regression) with a theoretical construct supporting the association, predictive modeling refers to the application of statistical models for the purpose of predicting values of output Y based on input X. Thus, predictive modeling is any method that produces predictions (point, interval, distributions, or rankings of new observations) regardless of its underlying approach (Bayesian or frequentist, parametric or non-parametric, data mining or statistical modeling, etc.). Where does ABMs fit into these definitions, one could ask. Well, in my humble opinion – and as far as I am concerned -, it does not. Instead, ABMs allow us to make predictions based on the underlying unitary assumptions (the interactions between agents and the rules that guide them). That is, ABMs, through the pattern-oriented modeling (POM, GRIMM et al. 2014) provide predictions if the mechanisms and processes involved in the model structure are correct (GALLAGHER et al., 2021), avoiding the black box of correlational models.

In this thesis, I explore the movement and seed dispersal patterns of the black lion tamarins, an arboreal frugivore, later developing an ABM general enough for understanding forest fragment level differences in size, shape, and resources. I further explore how these characteristics affect the spatial pattern of seed dispersal, namely, the seed shadow, which is the emerging pattern of my interest. In Chapter 1, I first explore their movement patterns, searching for “rules” that can be implemented in an ABM, which, in turn, I develop in Chapter 2. In the second chapter, I show that it is possible to predict seed shadows (and most movement patterns) of tamarins with relatively simple (independent of estimates of resource availability) foraging rules coupled with an energy model. Finally, I preliminarily explore the consequences of increasing habitat availability (forest fragment size) and changing shape and resource distribution on the seed shadow generated by black lion tamarins.

6. GENERAL CONCLUSIONS

Here, I explore the application of agent-based simulation models to understand the generated seed shadows by a tropical, endangered, and exclusively arboreal frugivore. In Chapter 1 I show black lion tamarin movement patterns as pervasively variable, even though I was able to derive some simple rules from quantitative and qualitative patterns. After extending a previously developed ABM to the black lion tamarin and implementing these rules on it, we saw how generable the model is in predicting both movement and seed dispersal patterns. In a preliminary analysis, we apply this model to theoretical forest fragments to explore the long-debated effect of “resource aggregation” - a historically assigned but rarely assessed factor affecting on movement patterns of primates -, as well as the effect of forest fragment size and shape on the seed shadow.

Although I have struggled to understand the rules guiding black lion tamarin to move, our knowledge and data are still limited, thus impeding me to develop a more mechanistic model. However, even with simple rules (i.e., decide whether to move to the closest or to a random tree) and with known issues (*e.g.* the lack of a territorial process), the model here developed has shown potential in predicting seed shadows, especially in smaller and medium sized (100-505 ha), isolated fragments. Movement ecology research has developed in faster than ever (JOO et al., 2020), and it is certain that newer methods will allow us to infer deeply about the movement process in light of the movement ecology paradigm (NATHAN et al. 2008). Specifically, I hope that the social behavior between groups of tamarins (territoriality, border patrol, home range overlap) receive further attention, rendering enough understanding to derive rules for simulations.

As research with the movement and cognition of this elusive species develops, including energy expenditure and nutritional ecology, we will be able to take for granted the incredible power and versatility of ABMs to understand the natural systems (MALISHEV et al. 2021), and further apply it to the modeling of seed shadows (MORALES; MORÁN LÓPEZ, 2022). It is evident, therefore, that the modeling cycle will loop a few more times, through a few primatologists and ecologists, in order to understand the simple rules (maybe not as simple as in the classic Flocking Model) that guide the movement ecology of the black lion tamarin and other arboreal vertebrates. While they travel, thriving to survive, escape predators, feed and mate, the seed shadow unfold in a curious loose mutualism.

7. REFERENCES

AGOSTINELLI, C.; LUND, U. **R package {circular}: Circular Statistics (version 0.4-93)**. CA: Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University, Venice, Italy. UL: Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA, 2017. Disponível em: <https://r-forge.r-project.org/projects/circular/>

ALMEIDA, P. J. A. L. et al. Indices of movement behaviour: Conceptual background, effects of scale and location errors. **Zoologia**, v. 27, n. 5, p. 674–680, 2010.

ANDRESEN, E.; ARROYO-RODRÍGUEZ, V.; RAMOS-ROBLES, M. Primate seed dispersal: old and new challenges. **International Journal of Primatology**, v. 39, n. 3, p. 443–465, 2018.

ARISTIZABAL, J. F. et al. Spatial aggregation of fruits explains food selection in a neotropical primate (Alouatta pigra). **Scientific Reports**, v. 9, n. 1, 1 dez. 2019.

ARROYO-RODRÍGUEZ, V. et al. Assessing Habitat Fragmentation Effects on Primates: The Importance of Evaluating Questions at the Correct Scale. Em: MARSH, L. K.; CHAPMAN, C. A. (Eds.). **Primates in Fragments: Complexity and Resilience**. 2. ed. New York: Springer, 2013. p. 13–31.

ARROYO-RODRÍGUEZ, V.; MANDUJANO, S. Forest fragmentation modifies habitat quality for Alouatta palliata. **International Journal of Primatology**, v. 27, n. 4, p. 1079–1096, 2006.

AUGUSIAK, J.; VAN DEN BRINK, P. J.; GRIMM, V. Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. **Ecological Modelling**, v. 280, p. 117–128, 24 maio 2014.

BADDELEY, A.; TURNER, R. {spatstat}: An {R} Package for Analyzing Spatial Point Patterns. **Journal of Statistical Software**, v. 12, n. 6, p. 1–42, 2005.

BARTOŃ, K. **MuMIn: Multi-Model Inference**. , 2022.

BATES, D. et al. Fitting Linear Mixed-Effects Models Using **lme4**. **Journal of Statistical Software**, v. 67, n. 1, 2015.

BENTLAGE, A. A. **Do Differences In Fruit Abundance Explain Patterns Of Grouping And Intersexual Dominance In Artificial Chimpanzees And Bonobos?** [s.l: s.n.].

BIALOZYT, R. et al. Predicting the seed shadows of a Neotropical tree species dispersed by primates using an agent-based model with internal decision making for movements. **Ecological Modelling**, v. 278, p. 74–84, 2014.

BONNELL, T. R. et al. Emergent Group Level Navigation: An Agent-Based Evaluation of Movement Patterns in a Folivorous Primate. **PLoS ONE**, v. 8, n. 10, p. 1–11, 2013.

BORAH, B.; BECKMAN, N. G. Studying seed dispersal through the lens of movement ecology. **Oikos**, p. 1–13, 5 jul. 2021.

BÖRGER, L.; DALZIEL, B. D.; FRYXELL, J. M. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. **Ecology Letters**, v. 11, n. 6, p. 637–650, 2008.

BOYER, D. et al. Scale-free foraging by primates emerges from their interaction with a complex environment. **Proceedings of the Royal Society B: Biological Sciences**, v. 273, n. 1595, p. 1743–1750, 2006.

BOYER, D.; WALSH, P. D. Modelling the mobility of living organisms in heterogeneous landscapes: Does memory improve foraging success? **Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences**, v. 368, n. 1933, p. 5645–5659, 2010.

BOYLE, S. A. et al. Travel and spatial patterns change when Chiropotes satanas chiropotes inhabit forest fragments. **International Journal of Primatology**, v. 30, n. 4, p. 515–531, 2009.

BRACIS, C.; BILDSTEIN, K. L.; MUELLER, T. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. **Ecography**, v. 41, n. 11, p. 1801–1811, 1 nov. 2018.

BRAVO, S. P. Implications of Behavior and Gut Passage for Seed Dispersal Quality: The Case of Black and Gold Howler Monkeys. **Biotropica**, v. 41, n. 6, p. 751–758, nov. 2009.

BUCHMANN, C. M. et al. An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. **Oikos**, v. 120, n. 1, p. 106–118, 1 jan. 2011.

BUENO, R. S. et al. Functional Redundancy and Complementarities of Seed Dispersal by the Last Neotropical Megafrugivores. **PLoS ONE**, v. 8, n. 2, p. e56252, 2013.

BUFALO, F. et al. **Route planning process by the endangered black lion tamarin (Leontopithecus chrysopygus) is influenced by resource distribution and spatial limitations**. Virtual Meeting of the Association for Tropical Biology and Conservation. **Anais**...2021.

BUFALO, F. S.; GALETTI, M.; CULOT, L. Seed Dispersal by Primates and Implications for the Conservation of a Biodiversity Hotspot, the Atlantic Forest of South America. **International Journal of Primatology**, v. 37, n. 3, p. 333–349, 2016.

BURY, A. **Mécanismes des interactions intergroupes d'un primate néotropical, le tamarin lion à croupe dorée (Leontopithecus chrysopygus), dans la forêt atlantique brésilienne**. [s.l: s.n.].

CALDANO, L. T. P.; MONTICELLI, C.; GALETTI JR., P. M. Demography of the black lion tamarins (*Leontopithecus chrysopygus*, Mikan) in Capão Bonito National Forest (State of São Paulo). **Neotropical Primates**, v. 1, p. 40–41, 2016.

CALENGE, C. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. **Ecological Modelling**, v. 197, p. 1035, 2006.

CAMPOS, F. A. et al. Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, Cebus capucinus. **Animal Behaviour**, v. 91, p. 93–109, 2014.

CANTOR, M. et al. Individual variation in resource use by opossums leading to nested fruit consumption. **Oikos**, v. 122, n. 7, p. 1085–1093, jul. 2013.

CARRETERO-PINZÓN, X. et al. What do we know about the effect of patch size on primate species across life history traits? **Biodiversity and Conservation**, v. 25, n. 1, p. 37–66, 2016.

CHAPMAN, C. A. Primate seed dispersal: Coevolution and conservation implications. **Evolutionary Anthropology: Issues, News, and Reviews**, v. 4, n. 3, p. 74–82, 1995.

CHAPMAN, C. A. et al. Are Primates Ecosystem Engineers? **International Journal of Primatology**, v. 34, n. 1, p. 1–14, 2013.

CHAPMAN, C.; RUSSO, S. E. Primate seed dispersal: Linking behavioral ecology with forest community structure. Em: CAMPBELL, J. ; et al. (Eds.). **Primates in Perspective**. 1. ed. New York: Oxford University Press, 2007. p. 510–525.

CHAVES, O. M. et al. Primate extirpation from rainforest fragments does not appear to influence seedling recruitment. **American Journal of Primatology**, v. 77, n. 4, p. 468–478, 1 abr. 2015.

CHAVES, Ó. M.; BICCA-MARQUES, J. C.; CHAPMAN, C. A. Quantity and quality of seed dispersal by a large arboreal frugivore in small and large Atlantic forest fragments. **PLoS ONE**, v. 13, n. 3, p. 4–6, 2018.

CIBIM, C. F. D. C. **Avaliação da qualidade do habitat para micos-leões-pretos (*Leontopithecus chrysopygus*) em fragmentos florestais de distribuição atual e potencial.** Rio Claro: UNESP, 2022.

COIMBRA-FILHO, A. F.; MITTERMEIER, R. A. Distribution and Ecology of the Genus Leontopithecus.pdf. **Primates**, v. 14, n. 1, p. 47–66, 1973.

COMITA, L. S. et al. Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. **Journal of Ecology**, v. 102, n. 4, p. 845–856, 2014.

CÔRTES, M. C.; URIARTE, M. Integrating frugivory and animal movement: A review of the evidence and implications for scaling seed dispersal. **Biological Reviews**, v. 88, n. 2, p. 255–272, 2013.

COSTA, T. DA S. O. et al. Relationships between food shortages, endoparasite loads and health status of golden-headed lion tamarins (Leontopithecus chrysomelas). **Biota Neotropica**, v. 22, n. 4, 2022.

COUSENS, R. D. et al. Towards better prediction of seed dispersal by animals. **Functional Ecology**, v. 24, n. 6, p. 1163–1170, 2010.

CROUSE, K. N. et al. Larger territories reduce mortality risk for chimpanzees, wolves, and agents: Multiple lines of evidence in a model validation framework. **Ecological Modelling**, v. 471, p. 110063, 1 set. 2022.

CULOT, L. et al. New Records , Reconfirmed Sites and Proposals for the Conservation of Black Lion Tamarin (Leontopithecus Chrysopygus) in the Middle and Upper. **Neotropical Primates**, v. 22, n. 1, p. 32–39, 2015.

CULOT, L. et al. Synergistic effects of seed disperser and predator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. **Scientific Reports**, v. 7, n. 1, p. 1–8, 2017.

DE ALMEIDA E SILVA, A. S. **Efetividade do mico-leão-preto (*Leontopithecus chrysopygus*) como dispersor de sementes e seu papel na regeneração florestal**. Dissertation—Rio Claro: Universidade Estadual Paulista “Júlio Mesquita Filho”, 2022.

DE GUINEA, M. et al. Disentangling the importance of social and ecological information in goal-directed movements in a wild primate. **Animal Behaviour**, v. 173, p. 41–51, 2021a.

DE GUINEA, M. et al. Cognitive maps in the wild: Revealing the use of metric information in black howler monkey route navigation. **Journal of Experimental Biology**, v. 224, n. 15, 1 ago. 2021b.

DEANGELIS, D. L.; DIAZ, S. G. Decision-Making in Agent-Based Modeling: A Current Review and Future Prospectus. **Frontiers in Ecology and Evolution | www.frontiersin.org**, v. 1, p. 237, 2019.

DELIGNETTE-MULLER, M. L.; DUTANG, C. fitdistrplus: An R Package for Fitting Distributions. **Journal of Statistical Software**, v. 64, n. 4, p. 1–34, 2015.

DI BITETTI, M. S. Home-range use by the tufted capuchin monkey (Cebus apella nigritus) in a subtropical rainforest of Argentina. **Journal of Zoology**, v. 253, n. 1, p. 33–45, 2001.

DUNN, J. C.; CRISTÓBAL-AZKARATE, J.; VEÁ, J. J. Differences in diet and activity pattern between two groups of Alouatta palliate Associated with the availability of big trees and fruit of top food taxa. **American Journal of Primatology**, v. 71, n. 8, p. 654–662, 2009.

ELLIS, K.; DI FIORE, A. Variation in space use and social cohesion within and between four groups of woolly monkeys (Lagothrix lagotricha poeppigii) in relation to fruit availability and mating opportunities at the Tiputini Biodiversity Station, Ecuador. Em: **Movement ecology of Neotropical forest mammals**. [s.l: s.n.]. p. 141–171.

ESTRADA, A. et al. Impending extinction crisis of the world's primates: Why primates matter. **Science Advances**, v. 3, n. 1, p. e1600946, 2017.

EVANS, D. M. et al. Habitat patch shape, not corridors, determines herbivory and fruit production of an annual plant. v. 93, n. 5, p. 1016–1025, 2015.

EVERAARS, J.; SETTELE, J.; DORMANN, C. F. Fragmentation of nest and foraging habitat affects time budgets of solitary bees, their fitness and pollination services, depending on traits: Results from an individual-based model. **PLoS ONE**, v. 13, n. 2, 1 fev. 2018.

FERNANDO SANCHO CAPARRINI. **A General A* Solver in NetLogo**.

FRANKLIN, S. P. et al. Golden Lion Tamarin sleeping-site use and pre-retirement behavior during intense predation. **American Journal of Primatology**, v. 69, n. 3, p. 325–335, mar. 2007.

FUZESSY, L. F. et al. How do primates affect seed germination? A meta-analysis of gut passage effects on neotropical plants. **Oikos**, v. 125, n. 8, p. 1069–1080, ago. 2016.

FUZESSY, L. F.; JANSON, C. H.; SILVEIRA, F. A. O. How far do Neotropical primates disperse seeds? **American Journal of Primatology**, v. 79, n. 7, p. e22659, jul. 2017.

FUZESSY, L. F.; JANSON, C.; SILVEIRA, F. A. O. Effects of seed size and frugivory degree on dispersal by Neotropical frugivores. **Acta Oecologica**, v. 93, n. September, p. 41–47, 2018.

FUZESSY, L.; SOBRAL, G.; CULOT, L. Linking howler monkey ranging and defecation patterns to primary and secondary seed dispersal. **American Jornal of Primatology**, n. October, p. 1–11, 2021.

GARBER, P. A.; PORTER, L. M. Navigating in small-scale space: The role of landmarks and resource monitoring in understanding saddleback tamarin travel. **American Journal of Primatology**, v. 76, n. 5, p. 447–459, 2014.

GARDNER, C. J. et al. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. **Nature Communications**, v. 10, n. 1, p. 1–7, 2019.

GAVRILITCHENKO, N. et al. CoFee-L: A model of animal displacement in large groups combining Cohesion maintenance, Feeding area search and transient Leadership. 2022.

GAZAGNE, E. et al. Seed Shadows of Northern Pigtailed Macaques within a Degraded Forest Fragment, Thailand. **Forests**, v. 11, n. 11, p. 1184, 10 nov. 2020.

GELMI-CANDUSSO, T. A. et al. Estimating seed dispersal distance: A comparison of methods using animal movement and plant genetic data on two primate-dispersed Neotropical plant species. **Ecology and Evolution**, v. 9, n. 16, p. 8965–8977, 2019.

GÓMEZ-POSADA, C.; REY-GOYENECHE, J.; TENORIO, E. A. Ranging Responses to fruit and arthropod availability by a tufted capuchin group (Sapajus apella) in the Colombian Amazon. Em: REYNA-HURTADO, R.; CHAPMAN, C. A. (Eds.). **Movement Ecology of Neotropical Forest Mammals: Focus on Social Animals**. [s.l: s.n.]. p. 195–215.

GONZÁLEZ-ZAMORA, A. et al. Sleeping Sites and Latrines of Spider Monkeys in Continuous and Fragmented Rainforests: Implications for Seed Dispersal and Forest Regeneration. **PLoS ONE**, v. 7, n. 10, p. 1–11, 2012.

GONZÁLEZ-ZAMORA, A. et al. Contagious deposition of seeds in spider monkeys' sleeping trees limits effective seed dispersal in fragmented landscapes. **PLoS ONE**, v. 9, n. 2, 2014.

GOULD, L.; MCLENNAN, M.; DONATI, G. Surviving in fragmented landscapes: Identifying variables that influence primate population viability and persistence in forest fragments and a summary of the included papers. **American Journal of Primatology**, v. 82, n. 4, p. 1–4, 2020.

GRIMM, V.; RAILSBACK, S. F. Pattern-oriented modelling: A “multi-scope” for predictive systems ecology. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 367, n. 1586, p. 298–310, 2012.

HANKERSON, S. J.; FRANKLIN, S. P.; DIETZ, J. M. Tree and forest characteristics influence sleeping site choice by golden lion tamarins. **American Journal of Primatology**, v. 69, n. 9, p. 976–988, 1 set. 2007.

HAWES, J. E.; PERES, C. A. Ecological correlates of trophic status and frugivory in neotropical primates. **Oikos**, v. 123, n. 3, p. 365–377, 2014a.

HAWES, J. E.; PERES, C. A. Ecological correlates of trophic status and frugivory in neotropical primates. **Oikos**, v. 123, n. 3, p. 365–377, 2014b.

HESS, B. et al. PioLaG: a piosphere landscape generator for savanna rangeland modelling. **Landscape Ecology**, v. 35, n. 9, p. 2061–2082, 1 set. 2020.

HEYMANN, E. W. et al. DNA fingerprinting validates seed dispersal curves from observational studies in the neotropical legume Parkia. **PLoS ONE**, v. 7, n. 4, p. 1–7, 2012.

HEYMANN, E. W. New sniffing at New World primates: recent advances in the study of platyrrhine olfactory communication. **https://doi.org/10.1080/03949370.2021.2015454**, v. 34, n. 3, p. 260–273, 2022.

HOFMEISTER, J. et al. Species-rich plant communities in interior habitats of small forest fragments: the role of seed dispersal and edge effect. **Journal of Vegetation Science**, p. e13152, 12 set. 2022.

HOPKINS, M. E. Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. **Animal Cognition**, v. 19, n. 2, p. 387–403, 23 mar. 2016.

HURFORD, A. GPS Measurement Error Gives Rise to Spurious 180° Turning Angles and Strong Directional Biases in Animal Movement Data. **PLOS ONE**, v. 4, n. 5, p. e5632, 20 maio 2009.

JANG, H. et al. Do Javan gibbons (Hylobates moloch) use fruiting synchrony as a foraging strategy? **American Journal of Primatology**, v. 83, n. 10, p. e23319, 1 out. 2021.

JANSON, C. H.; BYRNE, R. What wild primates know about resources: opening up the black box. **Anim Cogn**, v. 10, p. 357–367, 2007.

JONES, L. R. et al. Closing the gaps for animal seed dispersal: Separating the effects of habitat loss on dispersal distances and seed aggregation. **Ecology and Evolution**, v. 7, n. 14, p. 5410–5425, 2017.

JUDSON, O. P. The rise of the individual-based model in ecology. **Trends in Ecology and Evolution**, v. 9, n. 1, p. 9–14, 1994.

KAISIN, O. **Stressed-out primates?** [s.l: s.n.].

KARUBIAN, J.; DURÃES, R. Effects of seed disperser social behavior on patterns of seed movement and deposition. **Oecologia Brasiliensis**, v. 13, n. 1, p. 45–57, 2009.

KUHN, M. **caret: Classification and Regression Training**. , 2022.

LAURANCE, W. F.; FERREIRA, L. V.; LAURANCE, J. M. R. M. S. G. Rain forest fragmentation and the dynamis of Amazonin tree communities. **Ecology**, v. 79, n. 6, p. 2032–2040, 1998.

LEVEY, D. J. et al. Effects of landscape corridors on seed dispersal by birds. **Science**, v. 309, p. 146–148, 2005.

LIU, C. et al. Linking pesticide exposure and spatial dynamics: An individual-based model of wood mouse (Apodemus sylvaticus) populations in agricultural landscapes. **Ecological Modelling**, v. 248, p. 92–102, 2013.

LUCAS, P. DA S. et al. Spatial response to linear infrastructures by the endangered golden lion tamarin. **Diversity**, v. 11, n. 7, p. 1–12, 2019.

MALISHEV, M.; KRAMER-SCHADT, S. Movement, models, and metabolism: Individual-based energy budget models as next-generation extensions for predicting animal movement outcomes across scales. **Ecological Modelling**, v. 441, n. December 2020, p. 109413, 2021.

MAMEDE-COSTA, A. C.; GOBBI, N. The black lion tamarin Leontopithecus chrysopygus - Its conservation and management. **ORYX**, v. 32, n. 4, p. 295–300, 1998.

MARSHALL, B. M.; DUTHIE, A. B. abmAnimalMovement: An R package for simulating animal movement using an agent-based model [version 1; peer review: awaiting peer review]. 2022.

MAZEROLLE, M. J.; VILLARD, M.-A. Patch characteristics and landscape context as predictors of species presence and abundance: A review. **Ecoscience**, v. 6, n. 1, p. 117–124, 1999.

MCLEAN, K. A. et al. Movement patterns of three arboreal primates in a Neotropical moist forest explained by LiDAR-estimated canopy structure. **Landscape Ecology**, v. 31, n. 8, p. 1849–1862, 2016.

MCLENNAN, M. R.; SPAGNOLETTI, N.; HOCKINGS, K. J. **The Implications of Primate Behavioral Flexibility for Sustainable Human–Primate Coexistence in Anthropogenic Habitats**. **International Journal of Primatology**Springer New York LLC, , 1 abr. 2017.

MORALES, J. M. et al. Frugivore Behavioural Details Matter for Seed Dispersal: A Multi-Species Model for Cantabrian Thrushes and Trees. **PLoS ONE**, v. 8, n. 6, p. e65216, 11 jun. 2013.

MORALES, J. M.; CARLO, T. A. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. **Ecology**, v. 87, n. 6, p. 1489–1496, 2006.

MUÑOZ LAZO, F. J. J. et al. Effect of Resting Patterns of Tamarins (Saguinus fuscicollis and Saguinus mystax) on the Spatial Distribution of Seeds and Seedling Recruitment. **International Journal of Primatology**, v. 32, n. 1, p. 223–237, 1 fev. 2011.

NATHAN, R. An emerging movement ecology paradigm. **Proceedings of the National Academy of Sciences of the United States of America**, v. 105, n. 49, p. 19050–19051, 2008.

NATHAN, R. et al. Dispersal kernels: review. Em: CLOBERT, J. et al. (Eds.). **Dispersal Ecology and Evolution**. 1. ed. [s.l.] Oxford University Press, 2012. p. 186–210.

NIELD, A. P. et al. The spatial complexity of seed movement: Animal-generated seed dispersal patterns in fragmented landscapes revealed by animal movement models. **Journal of Ecology**, v. 108, n. 2, p. 687–701, 2020.

O’SULLIVAN, D.; PERRY, G. L. **Spatial Simulation**. [s.l.] John Wiley & Sons., 2013.

PASSOS, F. Seed dispersal by black lion tamarin, *Leontopithecus chrysopygus* (Primates, Callitrichidae), in southeastern Brazil. **Mammalia**, v. 61, n. 1, p. 109–111, 1997.

PEARCE, F. et al. Space-use scaling and home range overlap in primates. **Proceedings of the Royal Society B: Biological Sciences**, v. 280, n. 1751, 22 jan. 2013.

PEGMAN, A. P. M. K.; PERRY, G. L. W.; CLOUT, M. N. Exploring the interaction of avian frugivory and plant spatial heterogeneity and its effect on seed dispersal kernels using a simulation model. **Ecography**, v. 40, n. 9, p. 1098–1109, 2017.

PERES, C. A. Costs and benefits of territorial defense in wild golden lion tamarins, Leontopithecus rosalia. **Behavioral Ecology and Sociobiology 1989 25:3**, v. 25, n. 3, p. 227–233, set. 1989.

PESSOA, M. S. et al. Deforestation drives functional diversity and fruit quality changes in a tropical tree assemblage. **Perspectives in Plant Ecology, Evolution and Systematics**, v. 28, p. 78–86, 1 out. 2017.

PETRERE, M. The variance of the index (R) of aggregation of Clark and Evans. **Oecologia**, v. 68, p. 158–159, 1985.

POTTS, J. R.; BÖRGER, L. How to scale up from animal movement decisions to spatiotemporal patterns: An approach via step selection. **Journal of Animal Ecology**, 14 nov. 2022.

R CORE TEAM. **R: A Language and Environment for Statistical Computing**. Vienna, AustriaThe R Foundation for Statistical Computing, , 2022. Disponível em: <https://www.r-project.org/>

RABOY, B. E.; DIETZ, J. M. Diet, foraging, and use of space in wild golden-headed lion tamarins. **American Journal of Primatology**, v. 63, n. 1, p. 1–15, 2004.

RAGHUNATHAN, N. et al. Deterministic modelling of seed dispersal based on observed behaviours of an endemic primate in Brazil. **PLoS ONE**, v. 15, n. 12 December, 1 dez. 2020.

RAILSBACK, S. F.; GRIMM, V. **Agent-Based and Individual-Based Modeling: A pratical introduction**. [s.l.] Princeton University Press, 2012.

RAMSAY, M. S. et al. Consequences of Habitat Loss and Fragmentation for Primate Behavioral Ecology. Em: **Primate Conservation in Shared Landscapes**. [s.l.] Springer, Cham, 2023. p. 9–28.

RANC, N.; CAGNACCI, F.; MOORCROFT, P. R. Memory drives the formation of animal home ranges: Evidence from a reintroduction. **Ecology Letters**, n. May 2021, p. 1–13, 2022.

REYNA-HURTADO, R. et al. Primates adjust movement strategies due to changing food availability. **Behavioral Ecology**, v. 29, n. 2, p. 368–376, 2018.

REZENDE, G. C. et al. **Leontopithecus chrysopygusThe IUCN Red List of Threatened Species 2020**. [s.l: s.n.]. Disponível em: <https://www.iucnredlist.org/species/11505/17935400>.

REZENDE, G. C. et al. **Black lion tamarins do not change daily distance in small forest fragments but reduce and share their home ranges**. Virtual Meeting of the Association for Tropical Biology and Conservation. **Anais**...2021.

ROHWÄDER, M. S.; JELTSCH, F. Foraging personalities modify effects of habitat fragmentation on biodiversity. **Oikos**, 1 dez. 2022.

RUSSELL, E.; WILENSKY, U. **Consuming spatial data in NetLogo using the GIS Extension**. The annual meeting of the Swarm Development Group, , 2008.

RUSSO, S. E.; AUGSPURGER, C. K. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in Virola calophylla. **Ecology Letters**, v. 7, n. 11, p. 1058–1067, 2004.

SALECKER, J. et al. The nlrx r package: A next-generation framework for reproducible NetLogo model analyses. **Methods in Ecology and Evolution**, v. 10, n. 11, p. 1854–1863, 2019.

SAN-JOSÉ, M. et al. The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. **Landscape Ecology**, v. 34, n. 5, p. 1069–1080, 2019.

SAUNDERS, D. A.; HOBBS, R. J.; MARGULES, C. R. Biological Consequences of Ecosystem Fragmentation: A Review. **Conservation Biology**, v. 5, n. 1, p. 18–32, 1991.

SCHUPP, E. W. et al. Intrinsic and extrinsic drivers of intraspecific variation in seed dispersal are diverse and pervasive. **AoB PLANTS**, v. 11, n. 6, 1 nov. 2019.

SCHUPP, E. W.; JORDANO, P.; GÓMEZ, J. M. Seed dispersal effectiveness revisited: A conceptual review. **New Phytologist**, v. 188, n. 2, p. 333–353, 2010.

SENGUPTA, R. et al. Automated extraction of movement rationales for building agent-based models: Example of a Red Colobus monkey group. **Advances in Geographic Information Science**, n. 201509, p. 59–71, 2018.

SERIO-SILVA, J. C.; RICO-GRAY, V. Interacting effects of forest fragmentation and howler monkey foraging on germination and disperal of fig seeds. **Oryx**, v. 36, n. 3, p. 266–271, 2002.

SIGNER, J.; FIEBERG, J.; AVGAR, T. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. **Ecology and Evolution**, v. 9, n. 2, p. 880–890, 1 jan. 2019.

SIGNER, J.; FIEBERG, J. R. A fresh look at an old concept: Home-range estimation in a tidy world. **PeerJ**, v. 9, p. e11031, 19 mar. 2021.

SNOW, D. W. Evolutionary aspects of fruit-eating by birds. **Ibis**, v. 113, p. 194–202, 1970.

STARK, D. J. **Habitat use and movement of proboscis monkeys (Nasalis larvatus) in a degraded and human-modified forest landscape**. [s.l: s.n.].

STEVENSON, P. R. et al. Frugivory in canopy plants in a western Amazonian forest: Dispersal systems, phylogenetic ensembles and keystone plants. **PLoS ONE**, v. 10, n. 10, p. 1–22, 2015.

TOCHIGI, K. et al. Differentiation and seasonality in suitable microsites of seed dispersal by an assemblage of omnivorous mammals. **Global Ecology and Conservation**, v. 40, p. e02335, dez. 2022.

TONOS, J. et al. Individual-based networks reveal the highly skewed interactions of a frugivore mutualist with individual plants in a diverse community. **Oikos**, p. 1–13, 2021.

TSUJI, Y. et al. Intraspecific differences in seed dispersal caused by differences in social rank and mediated by food availability. **Scientific Reports**, v. 10, n. 1, p. 1–9, 2020.

TUCKER, M. A. et al. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. **Science**, v. 359, n. 6374, p. 466–469, 26 jan. 2018.

TUCKER, M. A. et al. Human-induced reduction in mammalian movements impacts seed dispersal in the tropics. **Ecography**, v. 44, n. 6, p. 897–906, 1 jun. 2021.

URIARTE, M. et al. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. **Ecology**, v. 92, n. 4, p. 924–37, 2011.

VAN DER PIJL, L. **Principles of Dispersal in Higher Plants**. Berlin, Heidelberg: Springer Berlin Heidelberg, 1969.

WANG, B.; SMITH, T. Closing the Seed Loop. **Trends in Ecology & Evolution**, v. 17, n. 8, p. 379–386, 2002.

WICKHAM, H. et al. Welcome to the Tidyverse. **Journal of Open Source Software**, v. 4, n. 43, p. 1686, 21 nov. 2019.

WILENSKY, U. **NetLogo**. Evanston, IL, USA, 1999.

WILLIGHAGEN, E.; BALLINGS, M. **genalg: R Based Genetic Algorithm**. , 2022.

ZWOLAK, R. How intraspecific variation in seed-dispersing animals matters for plants. **Biological Reviews**, v. 93, n. 2, p. 897–913, 2018.