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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

2023

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EDUARDO MIGUEL ZANETTE

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.

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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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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.

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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.

2. CHAPTER 1 - UNDERSTANDING DRIVERS OF PRIMATE MOVEMENTS IN FRAGMENTS: EXPLORATIONS FOR AN AGENT-BASED SIMULATION MODEL

Eduardo M. Zanette, Anne Sophie de Almeida & Silva, Felipe Bufalo, Yness Messaoudi, Bernardo Niebuhr, Laurence Culot

2.1 ABSTRACT

The understanding of primate responses to fragment size and shape has been impaired by huge costs of following multiple groups with true replication design. While previous reviews have shown a contingent (i.e., variable and site-specific) response of primate behavior and movement to fragment size, no study has investigated the effect of fragment shape. Moreover, these two factors (size and shape) have been assigned to affect resource distribution, but most study do not explicitly test for this effect. Thus, how primates respond to fragment characteristics is still under debate. The development of mechanistic models such as the agent-based models (ABMs) provides an opportunity to answer this question with reduced field work and in controlled conditions. A previous developed model to predict seed dispersal of an Amazonian arboreal primate, was recently adapted to the black lion tamarin (*Leontopithecus chrysopygus*, hereafter “tamarin”), but it performed badly in predicting both movement patterns and seed dispersal. Yet, such models are known to be “data hungry” and are built with bottom-up approaches, namely through the creation of (mainly behavioral) rules. **In this chapter**, we compare tamarin movement patterns of four groups in four distinct contexts: continuous primary forest, 500-ha fragment, 100-ha fragment, and narrow riparian forest. We aimed at identifying patterns of movement and resource revisitation to derive such behavioral rules and further implementing it in the model. We used previously collected data of group locations every 5 min from studies of 4 to 12 months. Using complete trajectories, we calculated the step lengths and turning angles for each group. Then, we filtered the movement patterns by behavior, selecting foraging, traveling to fruiting trees (three and six steps before feeding) and traveling to sleeping sites (three and six steps before the end of activity period). Overall, we found that movement patterns vary extensively between forest fragments and sometimes in a monthly basis. Step length and turning angles (a proxy of velocity and directionality, respectively) differed between all four areas. The tamarin group inhabiting the continuous forest presented longer step lengths (23.9 m) and more directed routes, while the one living in the smallest fragment presented less directed routes. Step lengths were the smallest in the riparian forest (8.9 m). Velocity of tamarins in the continuous forest was frequently two or three-fold longer (up to 60 m) than in the other groups. Directionality of behaviors varied in the other areas but was usually less directed in the smallest fragment and riparian forest. As expected, tamarins moved faster and with high directionality to feeding trees, except in the smaller fragment. Foraging also showed some directionality in all areas, except in the smallest fragment. We concluded that tamarins move faster and with more directed trajectories in larger areas, and slower and less directionally in smaller fragments, suggesting that movement patterns are modulated by forest patch size and shape. Revisitation to resources inherently varied, echoing similarities with other lion tamarin species, such as high fidelity (inferred from high revisitation rates) to sleeping sites, but visits to multiple feeding trees (20 to 80) per timeframe. These results are a first step towards a better understanding of how the environmental context, such as patch size and shape can affect the movement patterns of forest restricted vertebrates, such as Neotropical primates and guided the implementation of the ABM described in **Chapter 2**.

KEYWORDS: Ranging patterns; Movement ecology; Resource monitoring; Revisitation; Recursion; Movement trajectory; Spatial cognition.

2.2 INTRODUCTION

Primates are a representative part of the dispersers in tropical forests, composing up to 40% of frugivore biomass (CHAPMAN, 1995; STEVENSON et al., 2015) and providing irreplaceable seed dispersal services (ANDRESEN; ARROYO-RODRÍGUEZ; RAMOS-ROBLES, 2018; GARDNER et al., 2019). Particularly to frugivorous Neotropical primates, this important functional role emerges mainly due to their high degree of frugivory (BUFALO; GALETTI; CULOT, 2016; HAWES; PERES, 2014a) and movement patterns (BORAH; BECKMAN, 2021; CHAPMAN; RUSSO, 2007; CÔRTES; URIARTE, 2013). Specifically, some Neotropical primates travel long distances daily and establish large home ranges, which may result in highly spread deposition of seeds and, therefore, important dispersal services to the plant community (FUZESSY; JANSON; SILVEIRA, 2017, 2018).

However, anthropogenic activities, including fragmentation and habitat loss, have impaired the movement patterns of these highly forest dependent species (TUCKER et al., 2018) by creating edges and altering resource distribution and abundance within the remaining forest patches (ARROYO-RODRÍGUEZ; MANDUJANO, 2006) or even changing the whole forest community dynamics (*e.g.*, (CHAVES; BICCA-MARQUES; CHAPMAN, 2018; GONZÁLEZ-ZAMORA et al., 2012). These changes mainly result in shorter seed dispersal distances (SDD) and clumped seed dispersal, which are predictors of lower seed dispersal effectiveness (**SDE**, SCHUPP; JORDANO; GÓMEZ, 2010) because of diminishing probability of seed and seedling survival by means of density-dependent (Janzen-Connell) processes, such as pathogen attacks and granivores (JANZEN 1970; CONNEL 1971; COMITA et al., 2014). For instance, linear structures have been demonstrated to affect golden lion tamarins' movement patterns: they reduce their home range size to avoid some types of linear structures and avoid moving towards it in specific situations, especially when these linear structures are highways or forest edges (unhabitable matrix) (LUCAS et al., 2019). Overall, these landscape changes induced by anthropic activities probably affect the spatial distribution patterns of seeds dispersed by primates, but we still lack a clear understanding of the underlying mechanism that leads to such changes through the analysis of primate movement.

Black lion tamarins (*Leontopithecus chrysopygus*, hereafter “tamarins”) are arboreal, territorial, and frugivorous-insectivorous primates. They inhabit the highly fragmented Atlantic Forest and are classified as endangered by the IUCN. Despite their small size, tamarins can have large home ranges and travel more than 2 km a day even in small and isolated forest fragments, dispersing seeds throughout it. However, while their home range sizes vary largely throughout their geographic distribution (from 35 to 400 ha), it is still unknown how much the environmental context, for instance patch size and shape, affects their movement patterns, such as the daily traveled distances, home range size, movement speed and directionality, as well as their pattern of revisitation to fruiting trees and sleeping sites. Understanding the effect of these factors on primate movement patterns and their consequences on seed dispersal is a challenging task, especially when considering the efforts needed in the field and the numerous confounding factors, restricting further generalizations and conclusions about the seed dispersal process.

The development of agent-based models (hereon “ABMs”) capable of predicting primate movement and their associated seed shadows opened new perspectives (BORAH; BECKMAN, 2021; CÔRTES; URIARTE, 2013; PEGMAN; PERRY; CLOUT, 2017). ABMs are models that simulate individuals (“agents”) as unique and autonomous entities that interact with their environment locally, thereby allowing our understanding of collective effects of individuals on the modeled system and vice-versa (COUSENS et al., 2010; RAILSBACK; GRIMM, 2012). These features strengthen the use of ABMs to predict ecological patterns in other environmental contexts, lessening the required effort to modeling primate seed shadows.

As explained in the introduction of this thesis, the implementation of an ABM able to predict seed dispersal of Amazonian tamarins were not sufficient to reproduce satisfactorily black lion 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 simulate tamarin seed shadows in theoretical contexts.

As a first step, **in this chapter**, I summarize some of the main findings of the analysis of tamarin movement patterns in four environmental contexts: small-sized, medium-sized, large (continuous forest) and a narrow (up to 400 m width) riparian forest. If tamarins' movement patterns respond strongly in these different contexts, we could consider them a strong predictor of movement variation (i.e*.,* a strong pattern) and implement it as a model rule or parameterization. I further discuss how these analyses have grounded the implementation of rules for the ABM model **in Chapter 2**.

2.3 METHODS

Data was collected from four groups of tamarins in distinct regions of the species distribution range: Guareí (small fragment, 100 ha), Santa Maria (medium fragment, 500 ha), Suzano (riparian forest) and Taquara (continuous forest – Morro do Diabo State Park, 33,800 ha) groups. Groups were followed *in situ* with GPS and had their locations recorded with a handled GPS and main activity (behavior) assessed every five minutes. Although these groups inhabit distinct forest fragments in terms of size and shape, all of them inhabit the seasonal forest of São Paulo State (semi-deciduous forest) (IBGE, 2012; VALLADARES-PÁDUA; CULLEN JR, 1994; VELOSO H. P.; RANGEL-FILHO A. L. R.; LIMA J. C. A., 1991), which goes through a warmer and humid period (summer) and cold and dry period (winter) (ROLIM et al., 2007). Data was collected by a different team of researchers in different months and years (**Table 1**).

We used complete (from one sleeping site to the next) and incomplete days of following. When the groups were out of sight for more than 5 minutes, a new trajectory was defined. Trajectories were created with adehabitatLT (CALENGE,

2006) and manipulated with *tidyverse* collection of packages in R 4.2.1 (R CORE TEAM, 2022; WICKHAM et al., 2019). We corrected incorrect GPS locations with the GAL (Grab Absurd Location) filter to remove GPS errors that produced unrealistically long displacements. This function is implemented in R and checks if the animal made a very large displacement and then came back almost to the same place, considering it a spurious large displacement according to a threshold (Niebuhr, B. *unpublished*).

Table 1 - Data collection of four black lion tamarin groups in four distinct forest fragments.

Fragment	**Type**	**Group size (individuals)**	**Time span (months)**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Guareí	Small fragment (100 ha)	5	5				x	x	x	x	x				
Santa Maria	Medium fragment (500 ha)	2	4		x	x	x	x							
Taquara	Continuous fragment (33.800 ha)	4	12	x	x	x	x	x	x	x	x	x	x	x	x
Suzano	Riparian forest	4-6	4		x		x					x			x

We analyzed overall step lengths and turning angles of all groups and behaviors, distinguishing between events of frugivory, foraging and traveling. We also analyzed five specific behaviors: foraging (FOR), three and six steps before feeding (BFEED3 and BFEED6) and three and six steps before traveling to sleeping sites (BSLEEP3 and BLEEP6), since we expected they could present specific movement patterns. For example, more frugivorous primates are expected to have more directed behavior, and this might be linked to planned routes

(Trapanese et al. 2018; de Guinea et al. 2021b). Similarly, entering a sleeping site might present specific movement patterns due to predation avoidance (FRANKLIN et al., 2007). We used step length as a proxy of velocity and turning angles as a proxy of directionally, as the later represents how directional the movements are in relation to the previous relocation.

We compared mean step lengths among groups with Shapiro-Wilk tests of normality, since none of the groups (or behaviors) presented normally distributed step lengths (Shapiro-Wilks test, $p \leq 0.01$). Post-hoc tests were done using a pairwise Wilcoxon test with Bonferroni correction. We applied circular statistics tests of the *circular* package (AGOSTINELLI; LUND, 2017) to the turning angles data. We tested if turning angles were uniformly distributed in every direction with Rayleigh tests (rayleigh.test function) and compared mean directions among groups with Watson-Wheeler non-parametric test (watson.wheeler.test function). We did not run post-hoc comparisons. All analysis were run considering significance level $\alpha = 0.05$.

We explored the revisitation patterns to fruiting trees and sleeping sites of the four groups by drawing a circle with a radius of 12.5 m around each resource location and counting the number of times the tamarins stepped into and went out of it. An event was counted as revisitation if the timespan between two visits were longer than 30 minutes. We did this for every time frame, which was defined as any time window of 2 to 10 sequential days which had no more than 3 continuous days without sampling. This is roughly equivalent to each sampling month. In the smallest fragment, where tree diameter data was available, we tested the relationship between tree diameter and revisits using a GLM with Poisson distribution and log link function. We estimated de R^2 (*pseudo* R^2) by diminishing the deviance of the fitted model from the deviance of null model from one (1 – (Residual Deviance/Null Deviance)).

2.4 RESULTS

Black-lion tamarins' groups showed distinct movement patterns (**Fig. 1**). Mean step length differed between areas, increasing from small to continuous forests (15.75±19.32 to 23.24±30.83 m, respectively) but were the smallest in the riparian forests (8.93±10.67 m). None of the groups had uniform directionality (Rayleigh test, $p < 0.\ 0001$). Directionality increased from small to continuous forests but were more directional in the riparian forest than in the small patch (Fig. 1, Table 2).

When looking at the behaviors of our interest (traveling to fruits, foraging, and traveling to sleeping sites; **Figure 2, Table 2**), all behaviors were directional in the continuous forest, with step length frequently two-fold longer than the small and medium sized patches and three-folder in relation to the riparian forest. Post-hoc tests can be found in **Figure A1**.

Directionality of behaviors varied but was usually less directed in the smallest forest fragment. Overall, as expected, tamarins moved faster to sleeping sites and with high directionality to feeding trees, except in the smaller fragment. The low number of observations regarding the directionality to sleeping sites hampers further comparisons. Foraging also showed some directionality in all areas, except in the smallest fragment. Notably, most specific behaviors exhibited similar movement patterns between the small and the medium sized fragment.

Tamarins spend different proportion of times in different fragments (**Figure 3**). The most striking difference was in the small fragment, where tamarins basically did not stay in stationary activities (resting and idle) during the study period. Furthermore, the group inhabiting the medium sized fragment travelled the least. However, this lower proportion of traveling might be due to the high proportion of NAs (when tamarins were lost), which is far more likely to occur during fast travel behavior.

We found that the number of revisits significantly, but moderately, increases with tree diameter (AIC = 872.4, *pseudo* $R^2 = 0.1346$, $p = 0.0021$). Generally, the most revisited resources were sleeping sites (**Figure 4**).

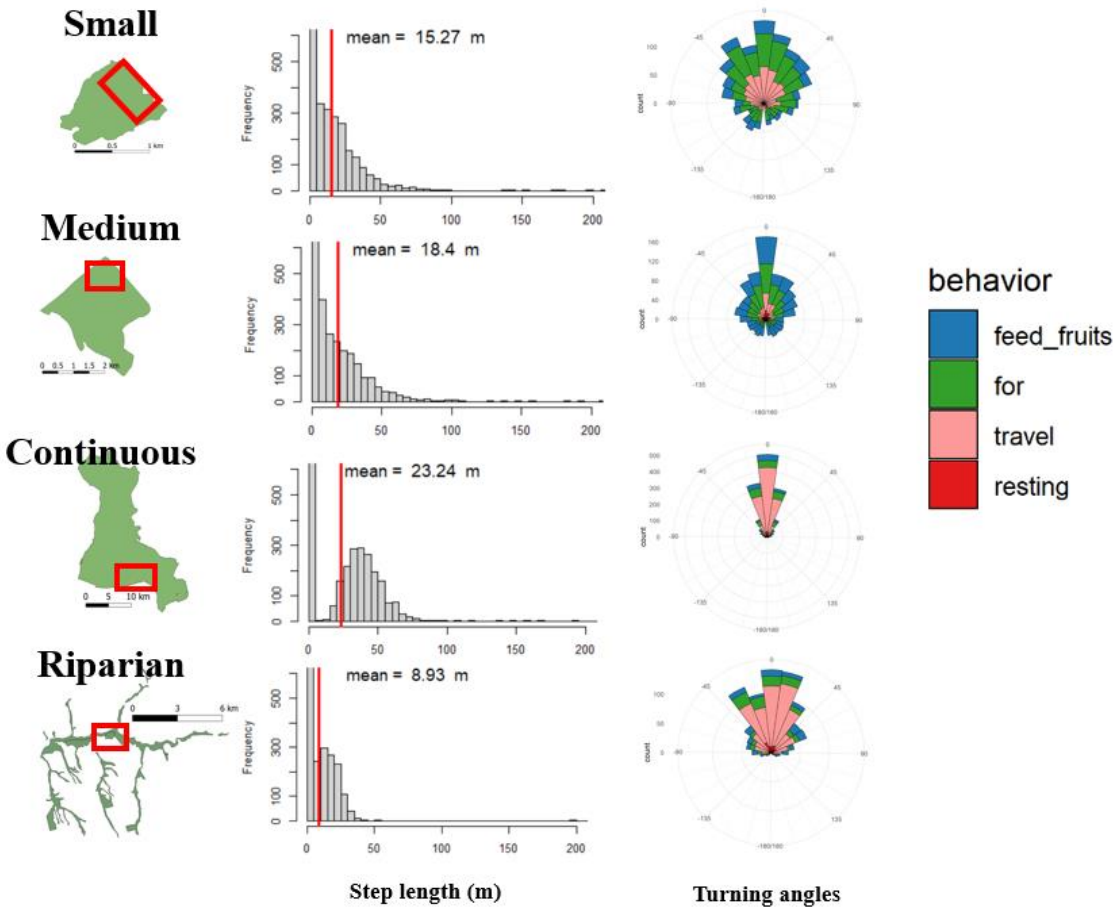

Figure 1 - Black lion tamarin movement patterns in four distinct forest fragments varying in size and shape. Left: Patch characteristics. Middle: Step length distribution (proxy of velocity) and mean step length shown by vertical red line. Right: Turning angles distribution (or relative angles, representing directionality in relation to the previous point). Data derived from 5-minute interval points gathered by on-ground following with GPS. Behavior: “feed_fruits” = events of frugivory; “for” = events of foraging (usually by insects); “travel” = events of group traveling; “resting” = events of resting. Patch silhouettes are out of scale.

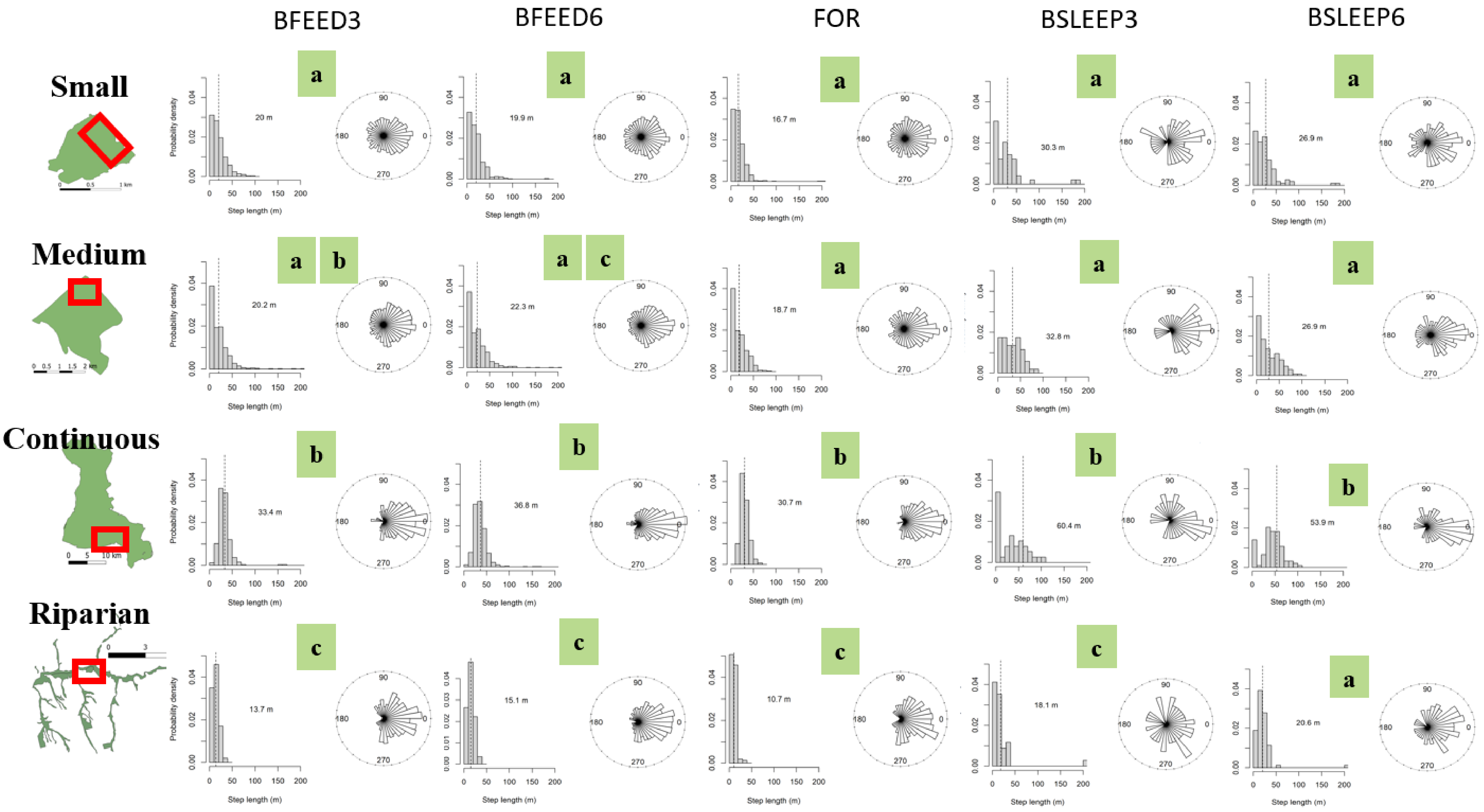
BFEED3
BFEED6
FOR
BSLEEP3
BSLEEP6
Small
Medium
Continuous
Riparian
0
0.5
1 km
0
0.5
1
1.5
2 km
0
5
10 km
0
3
a
20 m
a
19.9 m
a
16.7 m
a
30.3 m
a
26.9 m
a
b
20.2 m
a
c
22.3 m
a
18.7 m
a
32.8 m
a
26.9 m
b
33.4 m
b
36.8 m
b
30.7 m
b
60.4 m
b
53.9 m
c
13.7 m
c
15.1 m
c
10.7 m
c
18.1 m
a
20.6 m
Probability density
0.00
0.01
0.02
0.03
0.04
Step length (m)
0
50
100
150
200
90
180
270
0

Figure 2 - Black lion tamarin movement patterns of specific behaviors in four distinct forest fragments varying in size and shape. Left: Patch characteristics. For each specific behavior, the middle inset shows: Step length distribution (proxy of velocity) and mean step length shown by vertical dashed line and Turning angles distribution (or relative angles, representing directionality in relation to the previous point). Data derived from 5-minute interval points gathered by on-ground following with GPS. Specific behaviors: “BFEED3” = three steps before feeding on fruits; “BFEED6” = six steps before feeding on fruits; “for” = events of foraging (usually insects); “BSLEEP3” = events of group traveling. Letters in green represent similarities (same letter) and differences (different letters) in step length inferred from post-hoc tests (available in Anexo 1). Patch silhouettes are out of scale.

Table 2 - Step length and turning angles comparisons specific behaviors between four groups inhabiting four forest fragments. Post-hoc tests are shown in Anexo 1. BFEED3 = Three steps before feeding; BFEED6 = Six steps before feeding; FOR = foraging behavior; BSLEEP3 = Three steps before arriving at sleeping site; BSLEEP6 = Six steps before arriving at sleeping site. Step lengths were tested with Kruskall-Wallis and turning angles with Whatson-Wheeler tests.

Behavior	**Small**	**Medium**	**Continuous**	**Riparian**	**Step length**	**Turning angles**
All specific behaviors	19.9 ± 18	21.3 ± 20.9	36.6 ± 43.8	14.7 ± 11.8	χ2 = 617.92, df = 3, **p < 0.0001**	W = 1190.7, df = 6, **p < 0.0001**
BFEED3	20 ± 16.2	20.2 ± 21.3	33.4 ± 20.4	13.7 ± 6.8	χ2 = 247.61, df = 3, **p < 0.0001**	W = 121.16, df = 6, **p < 0.0001**
BFEED6	21 ± 17	22.3 ± 22.6	36.8 ± 24.3	15.1 ± 7.1	χ2= 509.76, df = 3, **p < 0.0001**	W = 262.32, df = 6, **p < 0.0001**
FOR	16.7 ± 15.7	18.7 ± 16.5	30.7 ± 9.2	10.7 ± 4.9	χ2 = 351.67, df = 3, **p < 0.0001**	W = 111.57, df = 6, **p < 0.0001**
BSLEEP3	30.3 ± 35.5	32.8 ± 20.4	60.4 ± 160.3	18.1 ± 33.8	χ2 = 21.623, df = 3, **p = 0.0017**	W = 9.5501, df = 6, p = 0.1449
BSLEEP6	26.9 ± 27.2	26.9 ± 22.2	53.9 ± 102.4	20.6 ± 22.9	χ2 = 59.667, df = 3, **p < 0.0001**	W = 30.249, df = 6, **p < 0.0001**

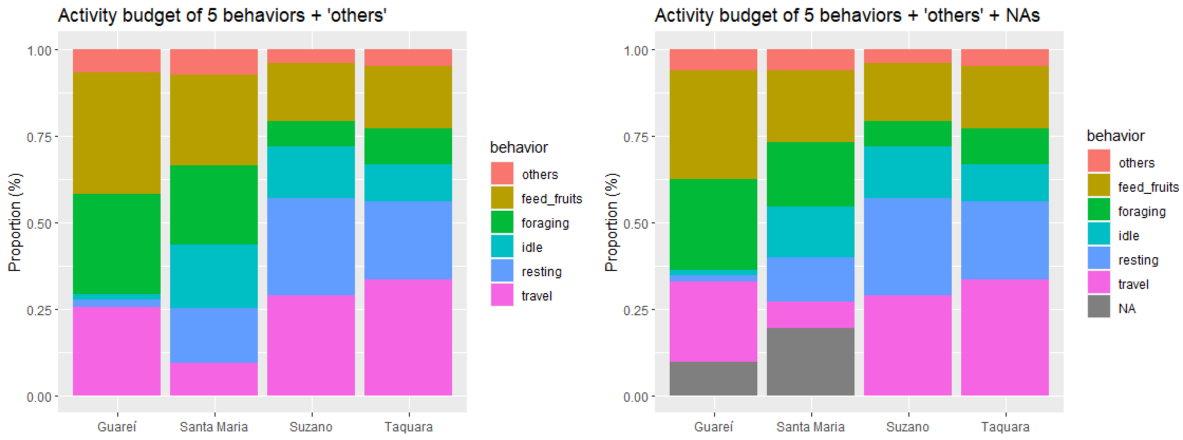

Figure 3 - Activity budget of black lion tamarins in four distinct forest fragments varying in size and shape. “Others” include less frequent behaviors such as feeding on exudates, social interactions (agonistic and antagonistic behaviors between groups and between individuals in the group), and fur-rubbing. NAs are points where tamarins were lost.

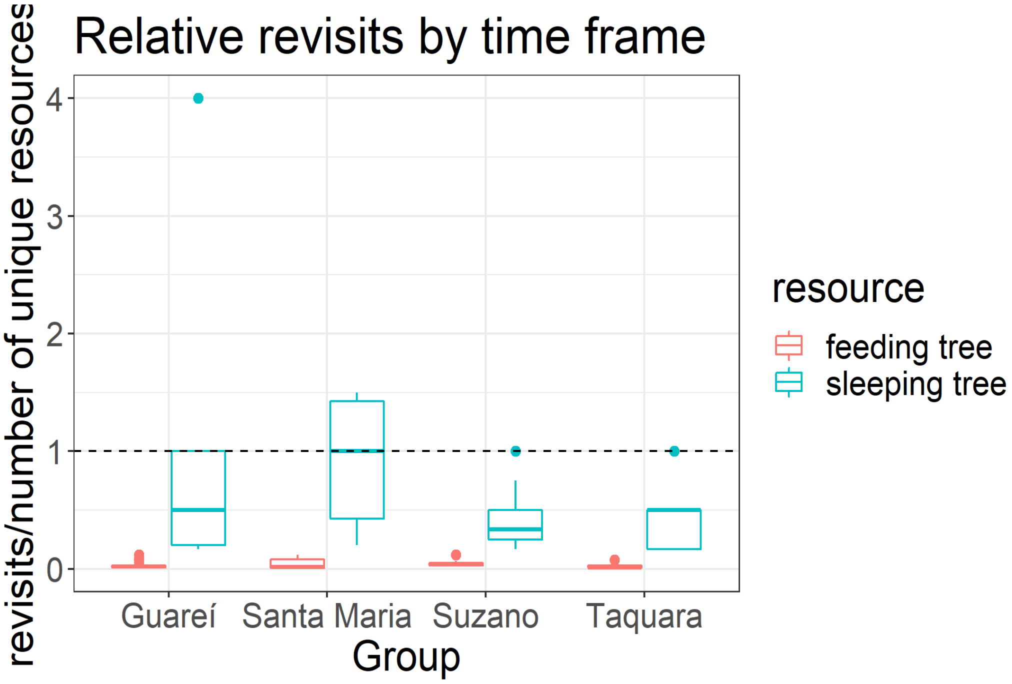

Figure 4 - Relative revisits of four groups of tamarins to resources (fruiting trees and sleeping sites) estimated from GPS routes in four forest fragments varying in size and shape. Revisits were accounted if the animals passed by close to the tree in a radius of 12.5 m, therefore representing actual revisits or resource monitoring. See *Methods* for details on the assessed timescale.

2.5 DISCUSSION

2.5.1 Movement patterns

Here, we showed that black lion tamarin movement patterns have a scaling relationship of movement patterns and fragment size. Tamarins were faster and highly directional in continuous forest, but both velocity and directionality diminished in medium sized and small sized patches to the point that there was no directionality in the small fragment. Furthermore, tamarins in the riparian forest showed a contrasting pattern of movement: they moved slowly but with high directionality, probably constrained by the narrow width of the forest along the river. In this sense, tamarin movement patterns seem more dependent on fragment size and shape than on behavior (e.g., frugivory, foraging, traveling).

In relation to specific behaviors, we show some consistent patterns between all areas: traveling to fruiting trees (BFEED3 and BFEED6) is highly directional, suggesting that tamarins do know resource locations, but is not faster than all specific behaviors of each area (Table 2). However, when tamarins are foraging, they usually move in a slower pace. This is expected, as foraging usually involves searching for insects in leaves, twigs, and bromeliads. Contrary to the expected, we saw no evidence of random movement while foraging, which is frequently described as a Brownian motion-like movement (REYNA-HURTADO et al., 2018). Instead, even foraging behavior was directional (except in the small patch), once more suggesting the strong effect of patch size. The lower velocity in foraging might also be linked to resource availability and primary food item spatial distribution. For example, Gómez-Posada et al. (2019) found strong responses of movement directionality (turning angles) of *Sapajus apella* to insect abundance. Thus, we might also expect seasonal differences in movement patterns related to more insect consumption in black lion tamarins. Furthermore, Reyna-Hurtado et al. (2018) showed a seasonal shift from Brownian-like to Levy-like movement patterns in six primate species, presumably in response to the shift from fruit (more patchily distributed) to leaves and/or insects (more randomly distributed) as the primary food item.

In contrast, travel to the sleeping site had the fastest observed velocities. Mean step lengths were 2 to 3 times larger when compared to all specific behaviors. Thus, tamarins cover great distances very briefly before entering the sleeping site, presumably in predator avoidance, as described for other lion tamarin species (FRANKLIN et al., 2007; HANKERSON; FRANKLIN; DIETZ, 2007).

The scaling of movement pattern variables with patch size has been seldom tested on primates, usually because replicating data collection with various groups is difficult (ANDRESEN; ARROYO-RODRÍGUEZ; RAMOS-ROBLES, 2018; HEYMANN; ZINNER; GANZHORN, 2013). For example, in a study with black bearded-sakis (*Chiropotes satanas*) with qualitative comparisons (four fragments, as in this study), movements were more circular (as well as revisitation of resources more frequent) as the patch size diminished (BOYLE et al., 2009). However, this might not occur for other primates. Proboscis monkeys daily path length, speed, route straightness and turning angles do not correlate to forest fragment size (STARK, 2018), although these proboscis monkey groups inhabited very similar regions.

The observed differences of movement patterns between areas might be attributed to different factors. First, the size and shape of the forest fragment may restrict tamarin movements. For instance, golden-lion tamarins (*Leontopithecus rosalia*, GLT) avoid moving towards the edges where there are non-suitable matrix or paved roads (LUCAS et al., 2019). Secondly, tamarin density might be extremely low in continuous forests, where tamarins usually have large home ranges (PARANHOS, 2006). This is also true for GLTs, that tend to have larger home ranges in continuous and protected forests compared to smaller fragments (LUCAS et al. 2019). Thus, as home ranges are larger, step lengths are larger, and movement is more directional. We suggest that the need to defend their territories from neighbors compels lion-tamarins to cross great part of their home range in a daily basis. Indeed, most of tamarins’ daily routes in the continuous forest covered great part of the home range, usually circumventing the home range borders (*pers. observation*). For golden lion tamarins, longer step lengths has been attributed to active defense from more abundant neighbors in protected forests, and larger home ranges has been attributed to low resource availability (LUCAS et al. 2019). Accordingly, later we show that space use seems to depend on the scaling of forest size and conspecific density (**Text A3** in Anexos), but with longer step lengths probably attributed to larger home sizes emerging from low conspecific density. Therefore, one would expect the same scaling to happen with the movement patterns (such as step lengths and turning angles), as suggested by our results. Which process reflects on step length and turning angles scaling, however, is uncertain. We maintain our statement that patch size (and shape) are important factors determining step lengths and directionality.

2.5.2 Revisitations

We found increased number of revisitations to resources in smaller fragments, a pattern reported in other primate ecological studies (BOYLE et al. 2009). Generally, the most revisited resources were sleeping sites. Given that the sleeping sites are only visited overnight, their small number compared to the number of feeding trees might lead to this pattern. However, as we do not have a full inventory of all sleeping sites, we cannot rule out that other processes such as sleeping site preference (*e.g.,* sites granting better predator avoidance or better temperatures) might be guiding these patterns (FRANKLIN et al. 2006). Furthermore, the revisitation of the same sleeping site was not expected given the increase in changes of parasite infection (HAUSFATER; MEADE, 1982). Other factors guiding revisitation (or recursion) is territoriality and border patrol (BERGER-TAL; BAR-DAVID, 2015; WATTS; MITANI, 2001) (BERGER-TAL; BAR-DAVID, 2015), but our data on this process is limited.

Among fruiting trees, *Syagrus romanzoffiana* was consumed throughout the year by all groups and was present in all fragments but was more revisited in the smaller fragment. The generalized linear model showed a weak relationship of DBH and revisitation to fruiting trees. However, most of the consumed fruits from the period and area were lianas, for which we used the DBH of the support tree as predictor. As the relationship between liana height and fruit set (but see Tonos et al. 2021) is more straightforward than fruit set and DBH, we think this analysis should be first replicated for other groups where such data is available before we draw any conclusions from it. Other recent studies of our team might support the idea of tamarins guiding their daily routes according to fruits. For instance, Bufalo et al. (2021) showed that 24 to 42% of points where tamarins significantly changed direction resulted in arriving in a fruiting tree, with the higher value for the smallest fragment, suggesting tamarins direct their routes mainly by frugivory. A complementary aspect of resource revisitation which we could not assess is the temporal patterns of resource revisitations (BRACIS; BILDSTEIN; MUELLER, 2018). As the overall results here presented suggest that there might be a general pattern deriving from resource distributions, we should first confirm this trend as more analysis on the temporal patterns of revisitations unfolds.

One aspect that might be driving movement patterns of tamarins and cannot be considered in this study because we lack data is social behavior and conspecific avoidance in relation to other groups in the same forest fragment. Recent research has shown that tamarins inhabiting a small fragment travel similar daily distances but overlap more than a third of their home ranges in relation to a group in a large sized fragment (REZENDE et al., 2021). This suggests that tamarins are constrained by their inhabiting fragment size, and that in smaller fragments they are going to be in high pressure to defend their overlapping territories. In small fragments they walk in less directed ways and occupy a smaller area, with small step lengths, while they occupy large territories with unknown degrees of overlapping in continuous forests. Together with our results, we conclude that fragment size and shape modulate tamarin ranging patterns. Therefore, if seed dispersal distances are a direct consequence of movement patterns (SPIEGEL & NATHAN 2007; FUZESSY et al. 2017), the seed dispersal distance might be consistently smaller in small fragments and longer in continuous forests and we might be able to predict it by modeling the movement of tamarins.

2.6 CONCLUSIONS

We show that black lion tamarins' groups differ extensively in movement patterns, and this might be modulated by the fragment properties (size and shape), meaning that a general movement model of this species will need parameterization depending on these properties. More importantly, we derive specific rules for the model in Chapter 2, either quantitative or qualitative. For example, we saw that those specific behaviors (specially foraging and traveling to the sleeping sites) have specific patterns distinguishable from the overall movement. Much more, the lack of some general patterns (such as revisitation to resources) informs that our model should not be based on these. Because of the inherently variance observed between groups, we conclude that a broader understanding of the movement patterns and its upscaling with habitat availability are still needed. Further studies should address the relationship between movement patterns and home range formation. We encourage studies assessing movement patterns in replicated forest fragments with varying sizes, such as those of Boyce et al. (2009), and we hope the present study shed light on the movement pattern scaling of forest restricted species.

3. CHAPTER 2 - PREDICTING SEED SHADOWS IN DIFFERENT ENVIRONMENTAL CONTEXTS: A MODELING APPROACH APPLIED TO AN ARBOREAL FRUGIVORE

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3.1 ABSTRACT

In tropical forests, a domain heavily used and historically destroyed by the human population, frugivorous primates make an important contribution to its regeneration by defecating viable seeds. Their role as seed dispersers is inherently dependent on their movement patterns that directly affect the spatial distribution of dispersed seeds. Due to their high contingent behavioral and ranging responses to local forest fragment characteristics, simulation models can help to better understand these responses and their consequences on tamarins seed dispersal service.

Here, we extend a previously developed agent-based model (ABM) implemented in Netlogo, to reproduce, *in silico*, the spatially explicit seed dispersal pattern (the *seed shadow*) of an endangered Neotropical primate, the black lion tamarin, in four forest fragments with varying characteristics (size, shape and resource distributions): one small sized (100 ha), one medium sized (515 ha), one continuous forest (34000 ha) and one riparian. The model focuses on behavioral modes guided by homeostasis, thus integrating responses to resources (fruiting trees) with movement capacity and internal energy state.

The model slightly overestimated daily path length and seed dispersal distances. This might be linked to longer time spent traveling in the model. Simulated home range sizes were similar to the observed, with the exception of the continuous forest which was consistently smaller, being territorial behavior and border monitoring one of the possible factors explaining this discrepancy. Simulated and observed movement rates and path twisting were similar, except in the riparian forest where simulated tamarins had less directed routes (higher path twisting) and slightly higher movement rates. The pattern of seed deposition (through feces) was usually aggregated (R index < 1) or random (never ordered/uniform), and the model generated R indexes slightly higher than observed, but still congruent with empirical observations.

The model runs on a set of parameters that can be estimated within few days of behavioral and feeding ecology data collection (feeding and sleeping tree coordinates and group behavior sampling) and has potential to predict seed shadows from multiple groups of tamarins, from riparian to small and medium fragments, thus highlighting its usefulness in predictive studies on fragmentation and habitat loss effects on ecosystem services. We encourage replication of such modeling efforts to other primate or non-primate forest dependent species so that an evaluation of the total seed dispersal service at a community-level and in different forest fragments be possible. Further developments should be conducted to reproduce realistic home range sizes in continuous forests. Integrating response to neighboring groups could be a solution.

KEYWORDS: Dispersal kernel; Frugivory; Plant-animal interactions; Primate seed dispersal; Movement ecology.

3.2 INTRODUCTION

The seed dispersal process by endozoochory is inherently dependent on the movement of dispersers. At fine spatial-temporal scales, numerous interactions (seed predation, competition of seedlings) are dependent on the plant local population and community dynamics resulting from seed dispersal (BORAH & BECKMAN, 2021). The **seed shadow** is the spatially explicit result of seed dispersal, emerging from animal's handling behavior and ranging patterns, thus being a function of interaction with environment such as plant spatial distributions and a set of trade-offs that the organisms are restricted to (CHAPMAN; RUSSO, 2007; NATHAN, 2008; NATHAN et al., 2012). However, such ranging patterns are known to be affected by habitat fragmentation and other anthropic impacts, as well as resources distributions (BOYLE et al., 2009; CARRETERO-PINZÓN et al., 2016; SERIO-SILVA; RICO-GRAY, 2002) in not so predictable manners (BORAH; BECKMAN, 2021; CHAVES et al., 2015; CHAVES; BICCA-MARQUES; CHAPMAN, 2018; HOFMEISTER et al., 2022; TUCKER et al., 2021). In this context, modeling emerges as a promising tool for untangling these confounding factors which trouble the thorough understanding of the effects of primate movement patterns on seed dispersal services.

Fragmentation and habitat loss have drastically impaired the movement patterns of forest dependent species by creating edges (TUCKER et al., 2018) and altering resource distribution and abundance within the remaining forest fragments (e.g., ARROYO-RODRÍGUEZ & MANDUJANO, 2006) or even changing the whole forest community dynamics (e.g., CHAVES et al., 2018; GONZÁLEZ-ZAMORA et al., 2012). These changes mainly result in shorter seed dispersal distances (SDD) and clumped seed dispersal, which are predictors of lower seed dispersal effectiveness (**SDE**, SCHUPP; JORDANO; GÓMEZ, 2010) because of diminishing probability of seed and seedling survival by means of density-dependent (Janzen-Connell) processes, such as pathogen attacks and granivores (JANZEN 1970; CONNEL 1971; COMITA et al., 2014). Indeed, fragment size has been shown to indirectly affect Neotropical primate ranging behavior, thus resulting in shorter SDD (FUZESSY et al., 2017).

Primate movements are constrained primarily by their diet, but also by seasonality, according to food availability and distribution. For instance, their primary food resource may be evenly (leaves) or patchily distributed (fruits, flowers, seeds, etc.), driving primarily folivore primates to show Brownian-like movements (or random searches), while primarily frugivorous ones tend to show non-Brownian or Lévy-walk movement patterns (REYNA-HURTADO et al., 2018). However, primate trajectories within their home ranges are not adequately modeled by random movements. Instead, they move according to intrinsic (physiology) and extrinsic (environmental) factors, intergroup competition, and predation pressure, which determine how they forage and consequently disperse seeds over space and time (CÔRTES & URIARTE, 2013; COUSENS ET AL., 2010; KARUBIAN & DURÃES, 2009; NATHAN, 2008; REYNA-HURTADO ET AL., 2018). Furthermore, primates do not respond consistently to fragmentation and anthropogenic disturbance (CARRETERO-PINZÓN et al., 2016; GOULD; MCLENNAN; DONATI, 2020; MCLENNAN; SPAGNOLETTI; HOCKINGS, 2017). Thus, developing a general model of movement and seed dispersal in different forest fragments becomes a non-trivial task.

Progress in understanding animal mediated seed shadow has been supported recently by an increasing number of simulation and modeling studies. In one of the first studies with empirical evidence linking edge effects on simulated movement behavior and thus on seed dispersal (by birds), Levey et al. (2005) first suggested that this effect depends on the propensity of animals to respond to the edges. Similar conclusions were drawn by a simulation study by Uriarte et al. (2011), who found movement and foraging behavior changes according to matrix/habitat type (primary vs. secondary forest) and edges, but these differences in movement did not alter seed dispersal distances. However, far less attention has been drawn to forest specialists such as Neotropical primates, which require a more specific approach at the forest fragment level instead of the landscape level as some processes are most predicted by patch-scale variables (MAZEROLLE; VILLARD, 1999), including seed dispersal (SAN-JOSÉ et al., 2019).

While a handful of models have been developed to estimate primate seed shadows, each one with advantages and disadvantages (CHAPMAN & RUSSO, 2007), all of them are context-dependent because their parameters have been quantified under a particular set of conditions (COUSENS et al., 2010), limiting the generalization of seed dispersal patterns (ANDRESEN et al., 2018). Models are intended to expand our knowledge on a specific subject, giving us predictive power and a deeper understanding of the system under investigation (RAILSBACK; GRIMM, 2012; RUSSO; PORTNOY; AUGSPURGER, 2006). It is thus important that, while modeling seed shadows, the model be capable of attaining generality, i.e., it should be able to adapt to new conditions (for example, being able to predict the movement and seed dispersal patterns of multiple groups). Agent-based (or Individual-based) models (**ABM**s), however, can handle these context-dependent particularities. ABMs are models that simulate individuals or agents as unique and autonomous entities that interact with their environment locally thereby allowing our understanding of collective effects of individuals and agents on the modeled system and vice-versa (Railsback & Grimm, 2012). Hence, the general advantage of ABMs is to rely on bottom-up approaches. For instance, through modeling behavioral responses and the agent's internal decision or "rules" (i.e., the movement capacity of animals *sensu* Nathan et al. 2008), which are more likely to remain constant than the outer environmental parameters, one may understand the bottom processes leading to the aggregate patterns (such as seed shadow) (DEANGELIS; DIAZ, 2019; MALISHEV; KRAMER-SCHADT, 2021). Indeed, this approach has proven beneficial for reproducing seed shadows *in silico* (BIALOZYT et al., 2014; GAZAGNE et al., 2020; NIELD et al., 2020; PEGMAN; PERRY; CLOUT, 2017).

Recent ABMs have adopted multiple approaches to model animal movement behavior, with some applications to seed dispersal models. Hopkins (2016) interfaced several movement models for howler monkeys feeding bouts in Barro Colorado Island, where resources were fully mapped. The author concluded that the best model reproducing observed movement bouts of this howler monkey species was Janson's Geometric model, which assumes travelling to a random direction until finding a resource patch, while other models such as random walk, correlated random walk or **step models** (models that drawn random values of step length and turning angle distributions) performed badly. Accordingly, Gavrilitchenko et al. (2022) have criticized step model approaches such as those used in Raghunathan et al. (2020), which simulates seed shadows of a very closely related species of our study, *Leontopithecus chrysomelas*. This model has also been replicated to reproduce seed shadows of *Macaca leonina* with a Hidden-Markov model (HMM). These models have in common that they depend strictly on data of one group/troop, thus they lack interfacing with the processes behind the movement decision and therefore lack predictive power for other groups. The main challenge, thus, is to link the emergence of movement and seed dispersal while avoiding producing *ad-hoc* models (in this case, highly site-dependent models, as pointed out by Malishev & Kramer-Schadt, 2021).

Here, we extend a previously developed ABM (BIALOZYT et al. 2014) to reproduce, *in silico*, the seed shadow of four distinct groups of an endangered primate, the black lion tamarin (*Leontopithecus chrysopygus*, hereafter “tamarins”), inhabiting four distinct patches of forests with varying characteristics (size, shape and resource distribution). These tamarins are small-sized, arboreal, endangered frugivorous-insectivorous and territorial primates that inhabit the highly fragmented Atlantic Forest hotspot of the state of Sao Paulo, in southeast Brazil. Previous analyses have shown that their movement patterns vary deeply in terms of ranging (daily path length, home range size, step length and turning angles), foraging patterns (revisitation to known fruiting trees, duration of feeding bout), among others (*cf*. Chapter 1 of this thesis). Furthermore, they show some flexibility in terms of habitat usage since they can be found in continuous forests to small fragments and riparian forests (Culot et al. 2015, Garbino et al. 2016). By having quite large home ranges in relation to their body size, which they frequently cross in a single day, tamarins are known to disperse viable seeds of more than 40 plant species at quite long distances (mean SDD of 150 to 280 m), especially medium-sized seeds (de ALMEIDA e SILVA, 2022).

We therefore explore if the same movement rules are sufficient for predicting seed dispersal patterns in different forest fragments. Our ultimate aim is to develop a model with enough power to predict seed shadows in forest fragments we still lack data on. First, we explore how energetic and behavior parameters (energy levels, feeding bout duration, etc.) affect the emerging patterns of tamarin movement, such as daily path length (DPL), home range size, activity budget and seed shadows (SDD and seed aggregation). We do this by means of a sensitivity analysis. Secondly, we explore how accurately the model predicts tamarin movement and seed shadows. We find a good predictability of movement and seed dispersal of four groups of tamarins inhabiting different forest fragments, while further discussing its generality in face of the ecological processes at hand.

3.3 METHODS

3.3.1. Study species and sites

We modeled the movement and assessed the seed dispersal patterns of the black lion tamarin (*Leontopithecus chrysopygus*) (see Chapter 1). Four groups of four different areas were studied during varying years and months (**Figure 1**). The groups varied in terms of size and composition (**Table 1**). Data from each group was collected by different researchers.

3.3.2. Model design

Our model investigates the seed shadows emerging from the interactions between frugivore behavior governed by its internal state (NATHAN et al. 2008) and their environment (resources and forest fragment borders). The model is spatially explicit and individual-based. As primates exhibit high behavioral flexibility and no consistent response to fragment size (CARRETERO-PINZÓN et al. 2016), having a model for forest specialists with behavioral flexibility presents a new opportunity for understanding the processes linked to the patch level responses of frugivores. We built this model for first validating such variable emerging phenomena (seed dispersal) and its causal process: the movement.

One main assumption is that, as forest specialists, tamarins will not trespass forest fragment borders. Although forest border avoidance has been reported for golden lion tamarins (*Leontopithecus rosalia*) (Lucas et al. 2019), black lion tamarins are known to occupy and use resources in isolated fragment borders. Below, we briefly describe the model, but a complete and detailed description of the model in the ODD format (Overview, Design concepts and Details) is available in **Text A2** in Anexos. The model is implemented in NetLogo 6.2 (WILENSKY, 1999). All simulations were run through the *nlrx* package (SALECKER et al., 2019). We used the R and GIS extension for NetLogo (RUSSELL; WILENSKY, 2008; SALECKER et al., 2019). The used parameters are available in **Table 2.**

The model runs for *n days*, matching the temporal scale of empirical data collection for the number of days collected in each time window. The length of each day is defined by the *simulation_time* parameter, which represent 90% of the empirical mean activity length of tamarins (in timesteps of five minutes) for each time window (Fig. 1 Text A2 in Anexos).

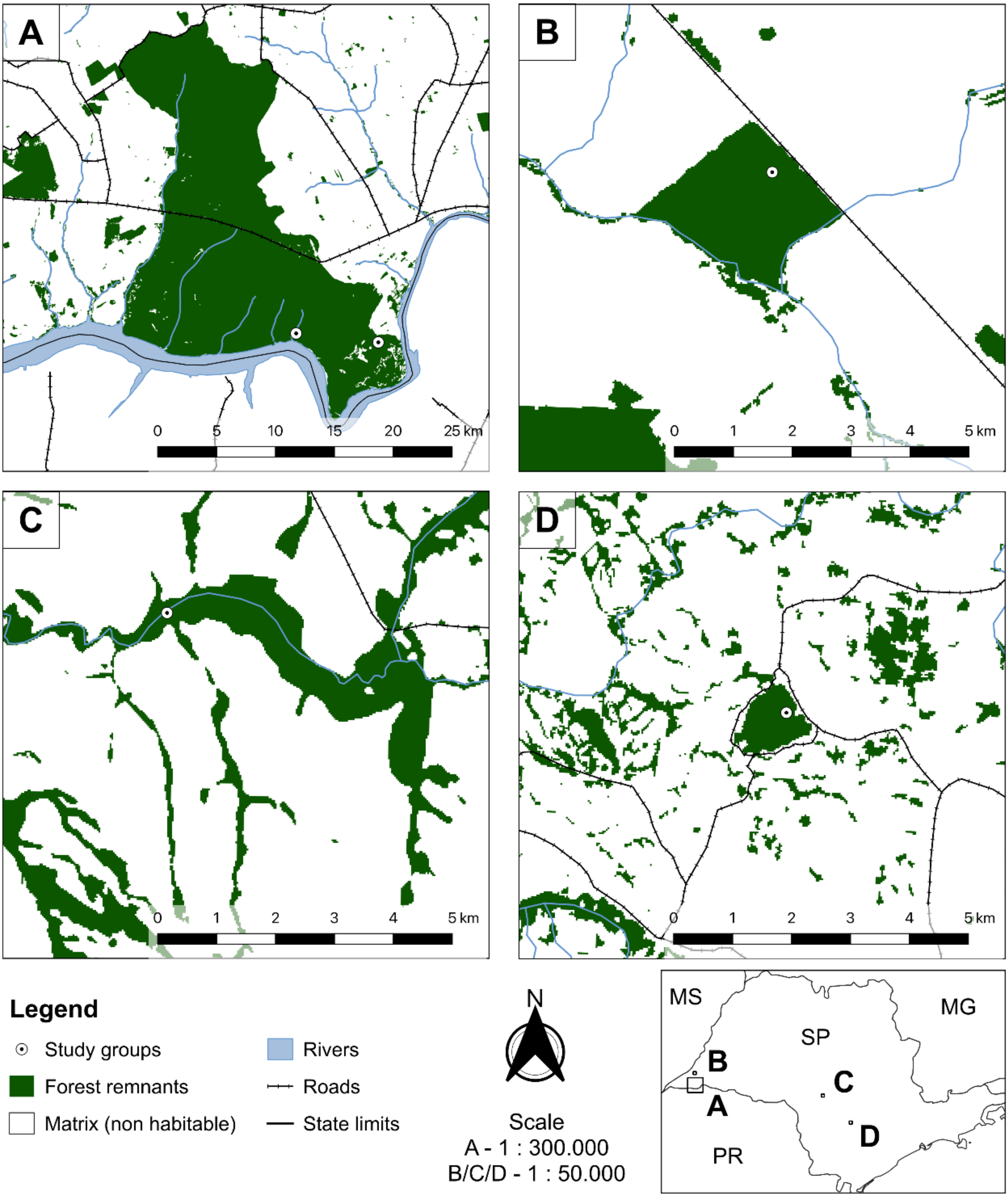
Agents start the day at a random sleeping tree. Based on its energy level and time of the day (Fig. 1 Text A2 in Anexos) the agents will, at each timestep, either a) travel, b) consume fruits, c) forage for insects, d) rest or e) search for a sleeping tree. While traveling to known resources to maintain homeostasis, tamarins defecate seeds of the consumed trees and lianas species based on empirical gut transit times.

During activity time (107 to 142 timesteps, corresponding to 8.91 to 11.83 hours, which are, respectively, the short and longest activity period registered in the field and with low energy (energy < energy-level-1), the agent travels (a) to the closest feeding tree (short-distance target-tree) and consumes its fruits (c) when in proximity (representing the frugivory process) for a period in timesteps (defined by feeding-species-time). At each traveling step, tamarins have the possibility of foraging (b) while traveling defined by the slider p_foraging_while_traveling (empirically estimate by p_foraging/(p_foraging + p_traveling) from empirical data) (Fig. 1 Text A2 in Anexos).

When energy > energy-level-2, tamarins either rest (d) if it is midday (48 > timestep > 68) or travel (a) to a long-distance target-tree, also with the possibility of foraging (b). When daytime reaches the 90% of the estimated day duration (107 to 142 timesteps), tamarins select the closest sleeping tree and travel (a) to it for the number of necessary steps (Fig. 1 Text A2 in Anexos).

At the end of each timestep (Fig. 1 Text A2 in Anexos), two sub models are executed: 1) the agents will defecate seeds according to the *gut-transit-time* parameter (*Seed dispersal sub model*) and 2) they will take out the visited feeding tree from the subset of trees that they have visited (memory-list) and include it again in the list of potential feeding trees according to the *step_revisit* parameter (*forget-trees* procedure). Furthermore, a secondary function does the same for the trees in the vicinity of the consumed fruiting tree (defined by the visual parameter). This process represents resource monitoring and memory (*Memory sub model*).

Throughout model development, we used *face validation* for data evaluation and model output corroboration (AUGUSIAK; VAN DEN BRINK; GRIMM, 2014). This means that we visually compared mean, median and variation of output variables (home range, DPL, activity budget and SDD) to determine if they were similar enough to the empirically observed values. If not, we proceeded through the modeling cycle, refining the model. During model development, other patterns emerged as candidates for validation, following the pattern-oriented modeling (GRIMM; RAILSBACK, 2012). These variables were: movement rate (MR), path twisting (PT) and seed dispersal aggregation, other movement metrics that are tightly linked to SDD according to previous studies (FUZESSY et al. 2017). We describe the Model adequacy assessment/evaludation process below.


A
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15
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25 km
B
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1
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4
5 km
C
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4
5 km
D
0
1
2
3
4
5 km
Legend
Study groups
Forest remnants
Matrix (non habitable)
Rivers
Roads
State limits
N
Scale
A - 1 : 300.000
B/C/D - 1 : 50.000
MS
MG
SP
B
C
A
D
PR

Figure 1 - Study sites and black lion tamarin groups (approximate group locations) throughout the species distribution. A) Taquara group in the continuous forest of Parque Estadual Morro do Diabo (PEMD), where one group has almost 300 hectares of monthly area used. The Sede group is represented as the easternmost white dot, and its data will be used for true validation (see *Methods*). B) Santa Maria fragment, a 515-ha forest where one group has 70 ha of monthly area used. C) Suzano group in the riparian forests of Fazenda Rio Claro, where one of the groups with the smallest home ranges area recorded (40 ha throughout a year). D) Guareí group in the small (100 ha) privately owned forest fragment, where a single group is known to occupy the whole northeast and east portion of the fragment (around 40 ha in a monthly basis). Outset: São Paulo State, Brazil, with inset locations of A, B, C and D. Notice the different scale in A. Elaboration: Gabriela C. Rezende.

Table 1 - Group size and composition of black lion tamarins inhabiting four distinct environmental contexts.

Group	Fragment size (ha)	month	Group size	Composition
Guareí	105 (small)	May	5	two adult males three adult females
		Jun	5	
		Jul	5	
		Aug	5	
Santa Maria	515 (medium)	Mar	2	one adult male one adult female
		Apr	2	
Suzano	Undefined (riparian)	Sep	4	two adult males two adult females
		Dec	6	two adult males two adult females two infants
Taquara	33800 (continuous)	Jan	4	one adult male three adult females

3.3.3 Data evaluation

We used movement and seed dispersal data of four groups of tamarins (Fig. 1). Empirical data was restricted to those months with at least three full consecutive and complete (sleeping site to sleeping site) days of data collection / monitoring. Two consecutive coordinates with a distance inferior to the estimated GPS error (8-12 m) were unified in cases the group behavioral scan was in a stationary phase (such as resting state), as these spurious steps can lead into extreme relative angles (HURFORD, 2009). From the movement data, we derived mean step length (meters traveled in 5 minutes, which is roughly the same as velocity), and maximum random angle values for the specific behavior of traveling and foraging (searching for fruits and insects). We used the observed mean step length and 75th quantile of turning angles as the maximum angle turned during these behaviors to parameterize the movement model (Table 2) corresponding to each simulation scenario (roughly equivalent to a specific month). From the seed dispersal data, we derived gut transit times for each seed species. These values were used to parameterize model runs (Table 2; see SM1 for details).

Movement patterns were estimated through the *amt* package (SIGNER; FIEBERG; AVGAR, 2019; SIGNER; FIEBERG, 2021). We estimated monthly areas used (95% and 50% Kernel density estimator - KDE), which we refer to as monthly area used and monthly core area, respectively, as our estimates were done on a monthly basis/time window and are not representative of the home range concept (BÖRGER; DALZIEL; FRYXELL, 2008). We also characterized step length and turning angles for each behavior (frugivory, foraging, resting and traveling). From this, we derived daily path length (DPL) as the sum of distances between all steps of each day, movement rate (DPL/activity time in hours) and path twisting (DPL^2/monthly area used in square meters), as it has been shown to predict SDD of primates (FUZESSY et al., 2017) and it does not depend on path analysis (ALMEIDA et al., 2010).

Seed dispersal events were monitored in the field by observation but discarded when another individual of the same tree or liana species were consumed prior to defecation (Heymann et al., 2012). Seed dispersal distances (SDD) were estimated by the linear distance of the defecation point to the mother tree/liana. Seed dispersal aggregation was assessed with the R index based on the Clark-Evans test (*clark.evans* function in *spatstat* package in R, BADDELEY; TURNER, 2005). Using $p \leq 0.05$ (bicaudal test), when $R < 1$, the seed shadow was considered clumped (aggregated), while it was considered ordered when $R > 1$. When $p \geq 0.05$ (bicaudal test) and R was close to 1, the seed shadow was considered random. All analyses were done in R 4.2.1 (R CORE TEAM, 2022).

3.3.4 Conceptual model evaluation

One of the main assumptions of the model is that tamarins structure their routine according to their level of energy (homeostasis) and that they are able to direct their paths exclusively to feeding trees. Although some evidence points to an effect of intergroup encounters on route direction and space use (BURY, 2022), an analysis of changing points showed that the most important driver of route directionality in tamarins was feeding tree locations, representing 24-46% of the change points (BUFALO et al. 2022) in the studied groups.

In the model, tamarins have two modes of moving: one when energy is low (below level 1), representing a “hungry” state when they travel to the closest feeding tree; and a second one when tamarins are satiated (above level 2), when they travel randomly to any known feeding tree in the landscape. Both moving modes are parameterized with empirical velocities (meters moved in one timestep, Table 2). Thus, the process generating movement is based on the energetic needs (internal state) and targets of the agents. This differs from a common step model which draws random step lengths and turning angles for each step, thus lacking a movement ‘why’ to move (Nathan et al. 2008). There are no fruit abundance estimates for each feeding tree. Instead, we use the empirical feeding bout durations to specify how much time tamarins will spend on each tree. After approaching a feeding tree, tamarins will stop feeding on it either when 1) the empirical feeding bout is reached or 2) when the day duration is reached, forcing them to immediately go to the closest sleeping site. Each timestep feeding on fruiting trees, the tamarins receive an amount of energy, which is constant. This rationale is a workaround the scarce energy intake estimates of fruits in nature, which might be captured in the feeding bout duration. With this approach, we can model frugivore attraction without explicitly measuring fruit availability in resource patches (LEVEY et al., 2005; MORALES et al., 2013; MORALES; CARLO, 2006; PEGMAN; PERRY; CLOUT, 2017). Empirical feeding bouts are available in **Figure A2.2**.

The emerging pattern of seed dispersal happens not only through movement, but also through a seed dispersal sub model. In short, each timestep the tamarins feed on a fruiting tree, one seed is consumed, and each seed receives a gut transit time value based on a poisson distribution with mean empirical values for each seed species (as the seed species characteristics may vary, leading to distinct gut transit times). Every timestep after, this attributed gut transit time is diminished by one, up to the point it gets to 0. Then, the seed is defecated. Multiple seeds might get defecated at the same time. Empirical gut transit times for each tamarin group is available in **Figure A2.3**.

Finally, we also include the sleeping sites (either tree hollows or liana crowns in the canopy) in the model. The number of sleeping sites varied from 1 to 7 for each time frame (month).

Table 2 - Model input parameters.

Parameter	Description	Guareí	Santa Maria	Suzano	Taquara	Source
start_energy	Initial level of energy at the start of each day		900			educated guess
energy_level_1	Level of energy which below it the tamarin is considered "hungry"		999			educated guess
energy_level_2	Level of energy which above it the tamarin is considered "satiated"		1430			educated guess
energy_from_fruits	energy gain from frugivory each timestep		73			educated guess
energy_from_foraging	energy gain from foraging each timestep		30			educated guess
energy_lost_traveling	energy loss from traveling each timestep		-10			educated guess
energy_lost_foraging	energy loss from foraging each timestep		-10			educated guess
energy_loss_resting	energy loss from resting each timestep		-6			educated guess
species_time	mean time spent feeding on an individual tree (feeding bout)		2			educated guess
duration	duration of resting behavior		4			educated guess
step_forget	Number of steps taken to reconsider revisiting a fruiting tree		87			educated guess
prop_trees_to reset_memory	Proportion of total trees that calls the *enhance_memory_list* procedure		2			educated guess

Parameter	Description	Guareí				Santa Maria		Suzano		Taquara	Source
month	Sampled month	Aug	Jul	Jun	May	Apr	Mar	Dec	Sep	Jan	empirical
timesteps	Amount of activity period (1 timestep = 5 min)	867	853	657	447	451	699	726	347	855	empirical
ndays	Number of observed/simulated days	8	8	6	4	4	6	6	3	6	empirical
mean_timesteps	Mean activity period duration	108	107	110	112	113	116	121	116	142	empirical
simulation time	Timestep when tamarins select a sleeping site and start travelling to it (10% of mean_timesteps)	97	96	99	101	102	104	109	104	128	educated guess
step_len_mean Foraging	Mean step length when the group is foraging	13.87	12.93	12.14	14.06	21.03	16.95	8.38	7.51	30.89	empirical
step_len_mean Travel	Mean step length when the group is traveling	25.30	25.20	25.44	23.43	35.97	32.37	17.49	17.94	39.31	empirical
max_random_angle 75q Foraging	Relative max angle deviation when the group is foraging	77.22	75.66	78.99	68.98	63.00	89.73	51.20	55.92	43.02	empirical
max_random_angle 75q Travel	Relative max angle deviation when the group is traveling	59.53	72.75	75.63	67.86	58.76	68.99	47.53	63.61	17.85	empirical
p_foraging_while traveling	Probability of foraging while traveling (estimated as p_foraging / p_foraging + p_travel)	0.70	0.54	0.47	0.36	0.61	0.59	0.21	0.31	0.21	empirical
GTT_mean	Mean gut transit time of seeds	19	13	18	17	16.6	16	21	26	16	empirical
n_trees_Frugivory	Number of fruiting trees that were consumed during the study period	77	86	43	28	43	61	46	27	58	empirical
n_trees_Sleeping site	Number of sleeping trees that were used during the study period	7	8	5	1	2	6	7	3	7	empirical
n_tamarins	Number of tamarins in the studied group	5	5	5	5	2	2	6	4	4	empirical

3.3.5 Implementation verification

The model was thoroughly tested for implementations in a step-by-step and multi run basis. As it is implemented in NetLogo, visual debugging was thoroughly done. The model also includes a “step” button, which prints different agent variables for each timestep, allowing stepwise debugging.

3.3.6 Model output verification

Model calibration was done using a genetic algorithm with a custom fitness function with the aim of gathering the most realistic parameter values for our simulations, the parameters that reproduce the multiple patterns observed empirically (e.g., DPL, home range size, etc.), reducing the uncertainty in the model structure and parameters, following the pattern-oriented modeling approach (Grimm et al. 2014). Variables were min-max normalized, and two weights were applied on its deviance to the observed patterns: 1) weight = 1 for more “important” patterns: number of visited trees, home range sizes (50 and 95% KDE), mean daily path length (DPL), movement rate (MR), path twisting (PT) and activity budget (proportion of frugivory, foraging, resting and traveling); and 2) weight = 0.5 for “less important” patterns: energy, DPL, MR and PT standard deviation. This calibration was done with the simdesign_GenAlg() function of the *nlrx* package, which uses the *genalg* package (WILLIGHAGEN; BALLINGS, 2022). We used an initial population of 100 chromosomes which ran up to 50 iterations, mutation chance of 0.1 and elitism = 2 (20% of the best fit chromosomes go to the next generation). As the optimized parameters vary widely from group to group, we did not use it to run further simulations. Instead, we used “*educated guess*” values (Table 2).

3.3.7 Model analysis

We ran sensitivity analysis with the R package *nlrx*. A first preliminary sensitivity analysis showed that the feeding bout parameterization did not consistently affect the energy and other parameters of tamarins in Guareí (**Text**

A2.2 in Anexos). Further, we used the Morris method (simdesign_morris() in *nlrx*) to estimate effects of parameters on the dispersal seed aggregation and tree visitation. Sensitivity analysis on the other patterns of interest is still under way (movement patterns: DPL, home range size, MR, PT; seed dispersal patterns: SDD). With this analysis, we could test if the parameterization of feeding bout duration was an important factor guiding model results. For each combination of parameters, we ran n = 10 replicates. This approach has the advantage of requiring much less computational power than a full factorial design and allows us to infer general effects and their consistency, while also allowing for identifying non-linear outputs.

3.3.8 Model output corroboration

We plan to use data from a fifth group, “Sede”, from the same locality as group Taquara, as a “*true validation*” case (Fig. 1). For a true validation, we will parameterize the model with Taquara’s movement parameters.

3.4 RESULTS

3.4.1 Calibration

The results of the genetic algorithm revealed low consistency in optimized parameters between areas (**Figure 2**).

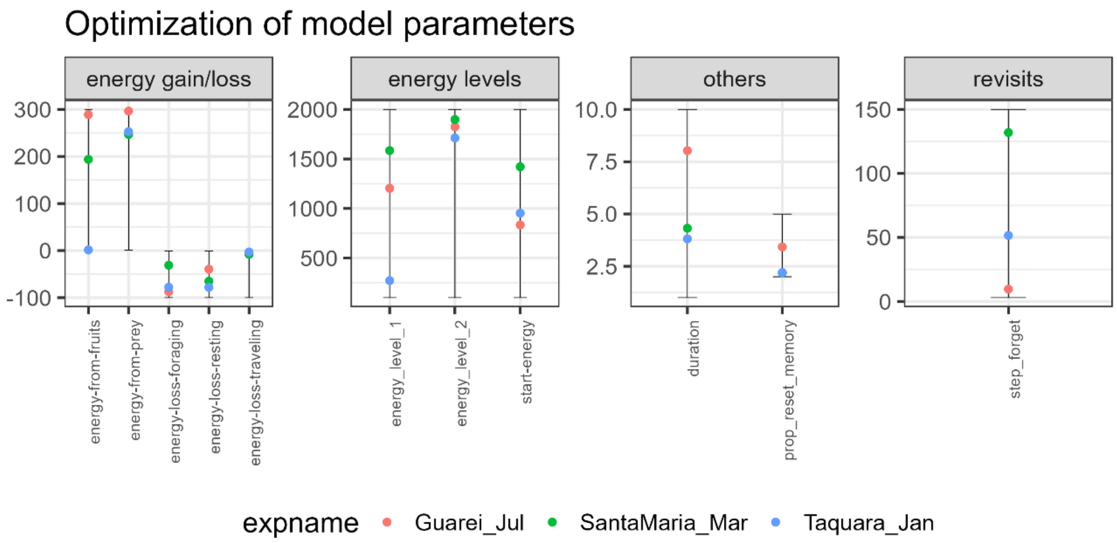

Figure 2 - Calibration of model parameters through genetic algorithm. For each category of parameters (gray labels), the error bars represent the range of parameters that were used to simulate multiple generations with distinct parameter combinations and the best parameter values (points) for each area which were selected through a genetic algorithm with a custom fitness function (detailed in *Methods*).

3.4.2 Sensitivity analysis

The Morris sensitivity analysis consistently revealed larger effects of parameters on seed aggregation and number of visited trees when feeding bout was parameterized **(Figure 3)**. This difference was more pronounced for the energy parameters (e.g., energy_from_fruits, energy_level_1), which are central in the model, suggesting that the feeding bout parameterization is an important factor in the model. However, no differences in the direction of effects (positive to negative and vice-versa) emerged when feeding bout was random (“off”). Furthermore, except for the energy-loss-traveling parameter when feeding bout was parameterized (“on”), all parameters showed high interaction between parameters and/or non-linear effects on the output as indicated by the sigma value.

3.4.3 Movement

Simulated home range (95% and 50%) sizes were very similar to the observed (**Figure 4a,b**), except for Taquara, which was 50% smaller. However, as the home range was similar or smaller to the observed, it was unexpected to find larger daily path lengths (DPL, **Fig. 4c**). This might have happened because tamarins in the model spent much more time traveling and less time spent consuming fruits (**Figure 5**). In turn the model failed to reproduce the patterns of movement rate and path twisting of the riparian forest (Suzano, although the MR was smaller than the other areas, consistent with the empirical cases), but consistently reproduced it for the other areas (**Fig. 6**).

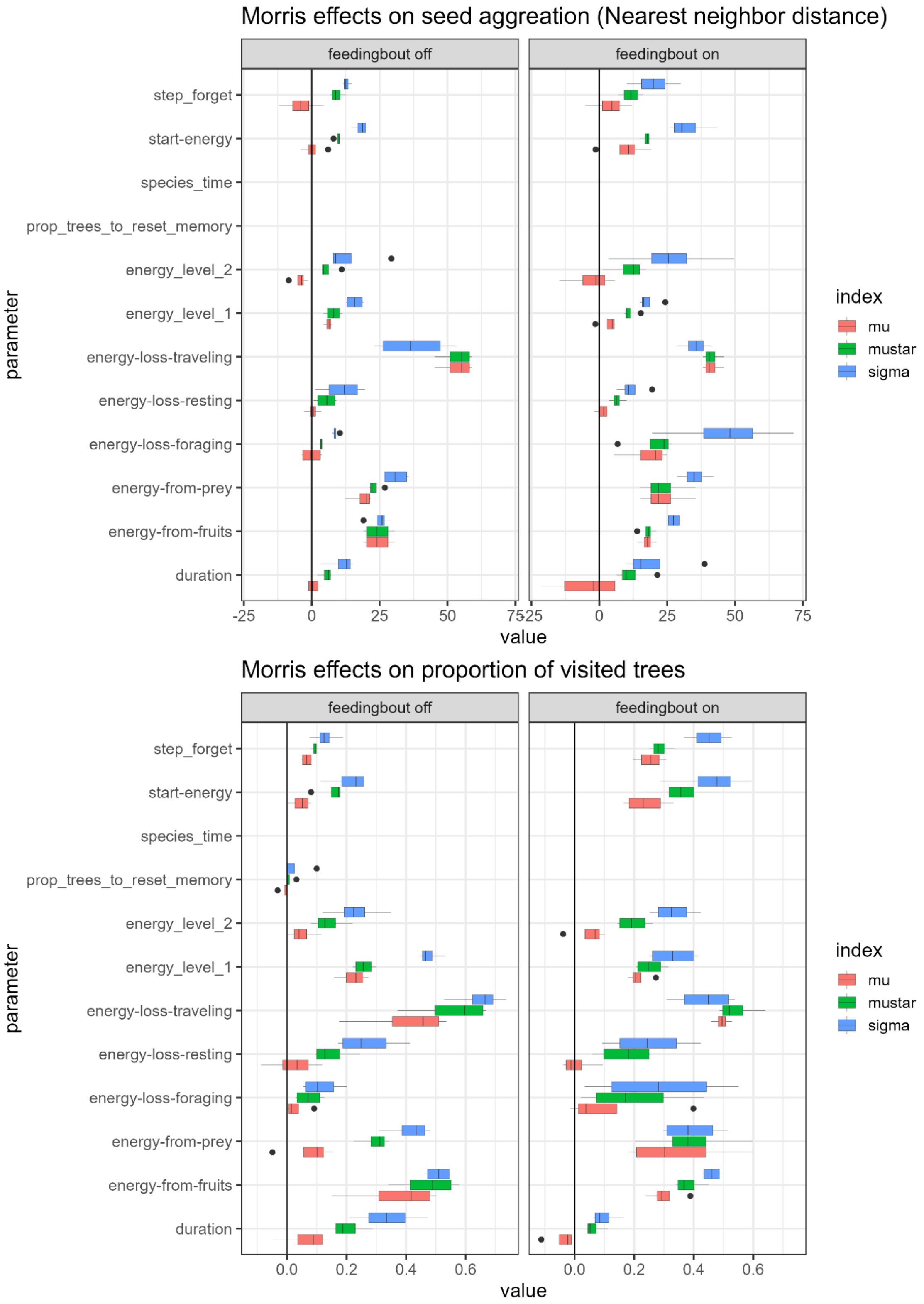

Figure 3 - Sensitivity analysis (Morris' method) showing the main parameters affecting the simulation output when feeding bout was parameterized ("on") or not ("off") in Guareí. A) number of visited trees; B) distance between dispersal events. μ (mu) indicates the direction of the effect, while μ* (mustar) is the absolute value of μ. High σ (sigma) indicates interaction between parameters and/or non-linear effects on the output. Boxplot quantiles not overlapping 0 suggest significant effects and black points represent outliers.

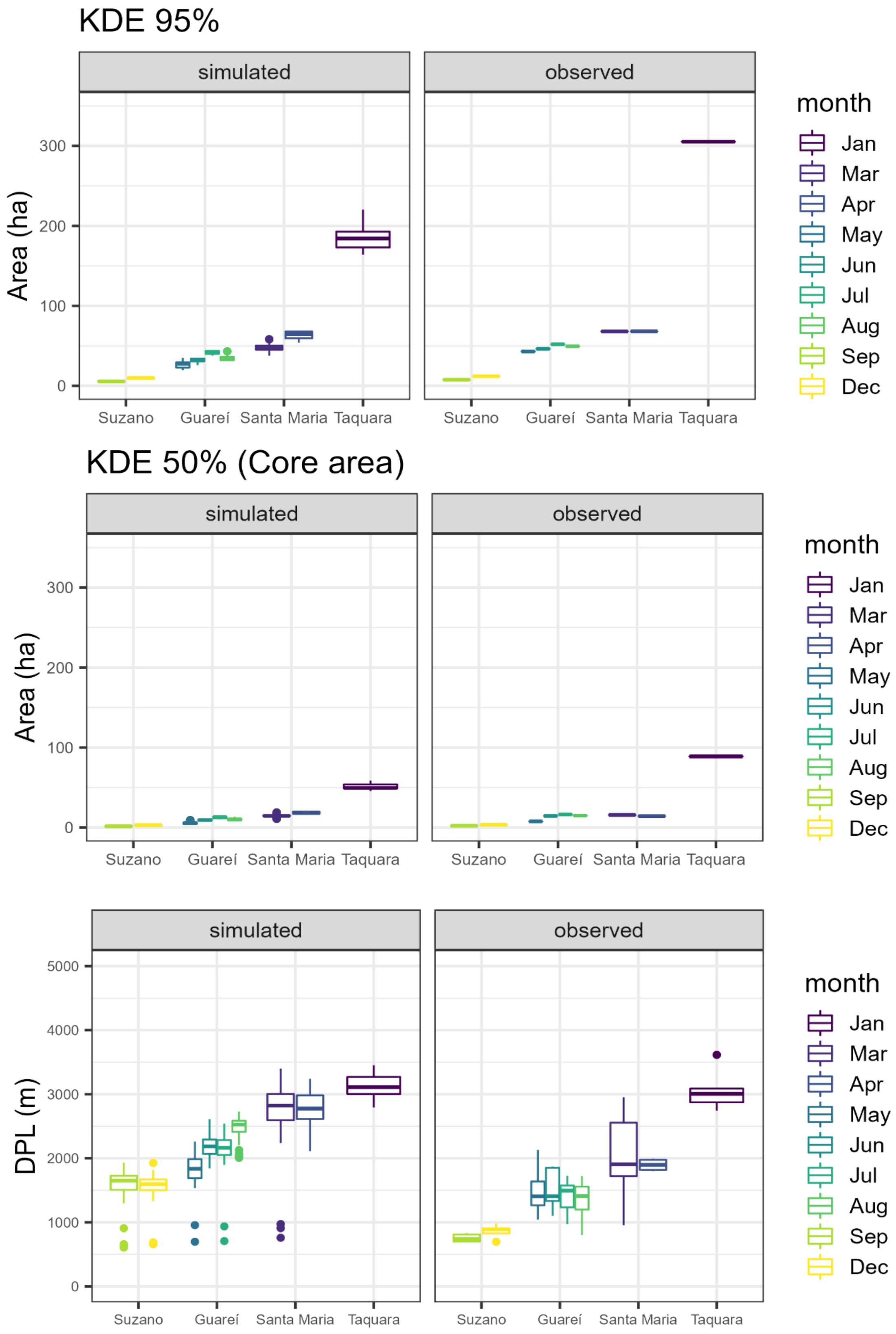

Figure 4 - Movement patterns of simulated and observed black lion tamarins. Each month represents 4 to 8 days of collected/simulated data. DPL = daily path length (in meters). Simulated (left) has ten replications (average of runs), observed values represent each day (average of days).

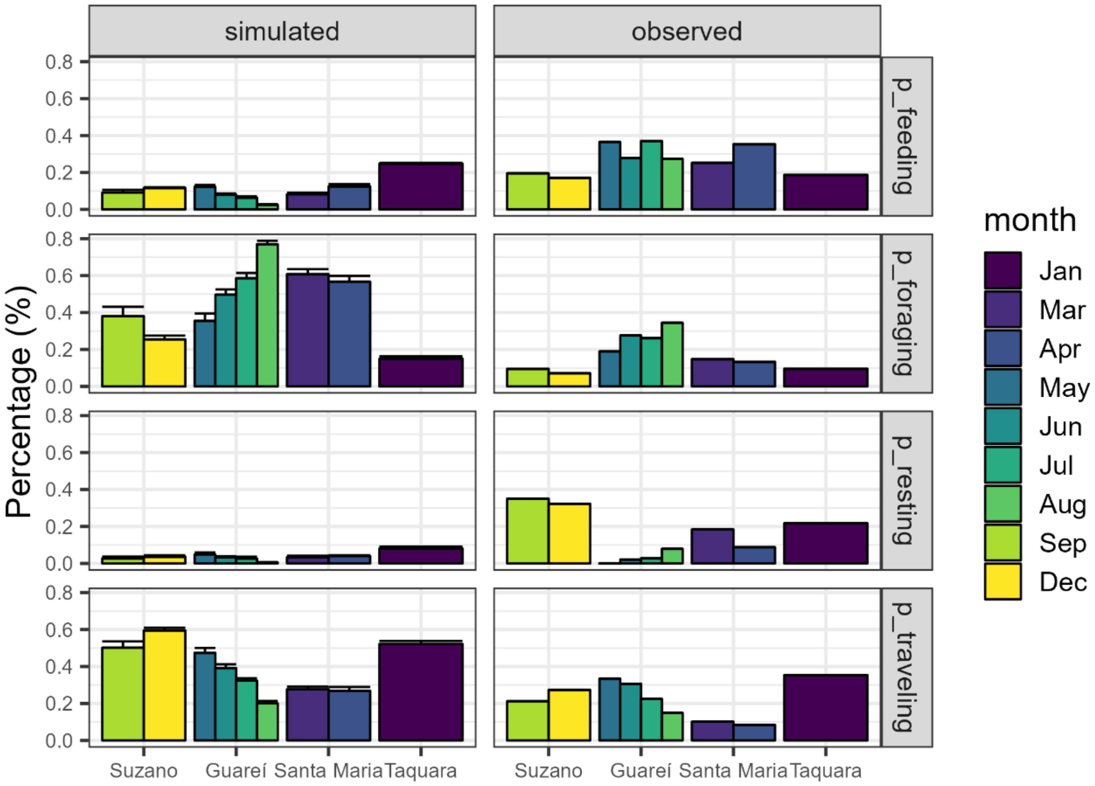

Figure 5 - Activity budget of simulated and observed black lion tamarins. Mean + sd values are displayed. Simulated (left) has ten replications (average of runs), observed values have no replication.

3.4.4 Seed dispersal

Seed dispersal distances were slightly overestimated (**Figure 7**), following similar trends with the exception of Santa Maria and Taquara, where simulations were under and overestimated, respectively. Example runs showing the seed shadow can be found in **Figure A2.1**. Defecation events were aggregated or randomly distributed and with values ranging from 0.5 to 1.2, while empirical values were consistently lower (more clumped) (**Figure 8**).

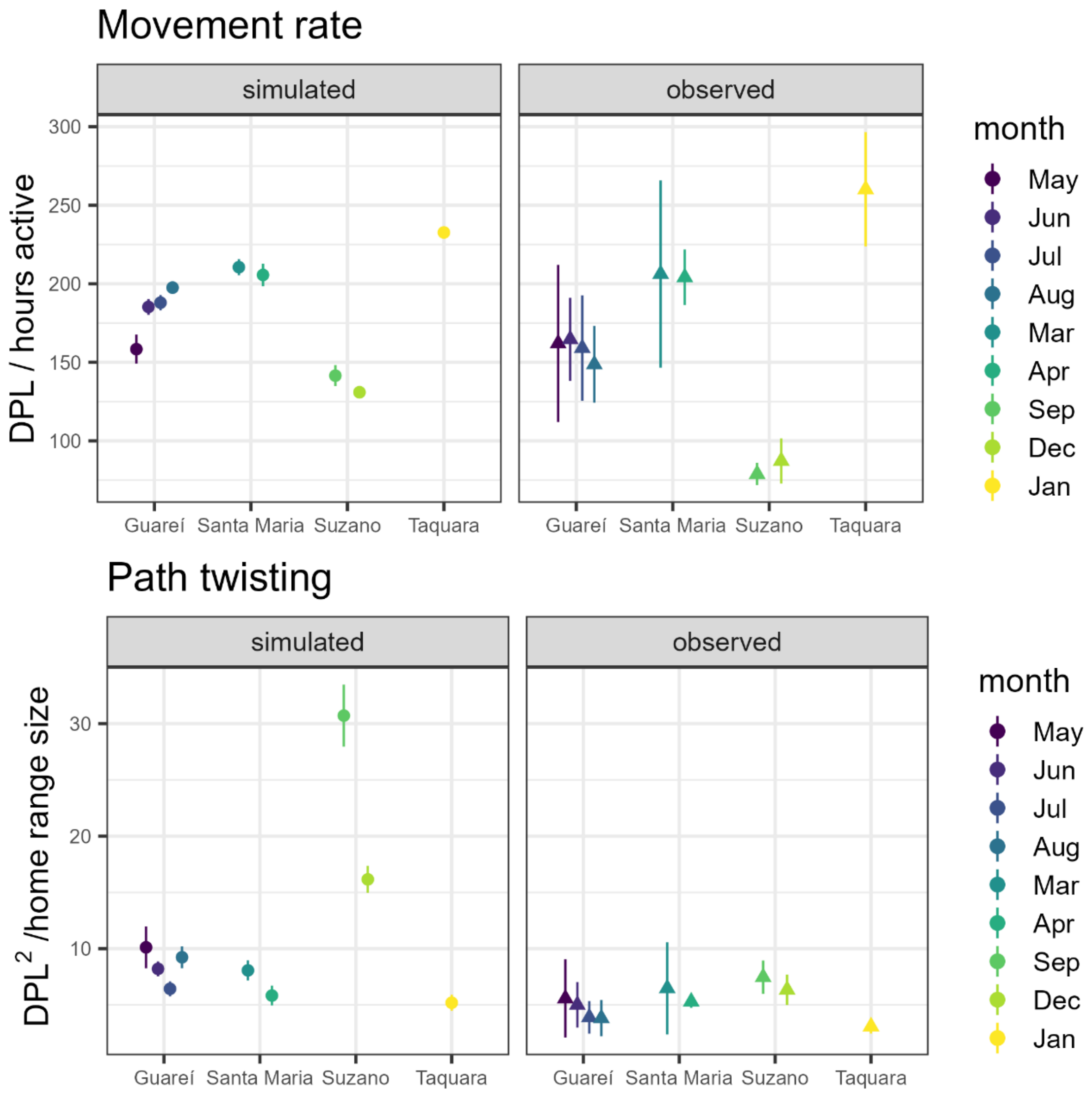

Figure 6 - Movement rate (MR) and Path twisting (PT) of simulated and observed tamarins. Simulated (left) has ten replications (average of runs), observed values represent each day (average of days).

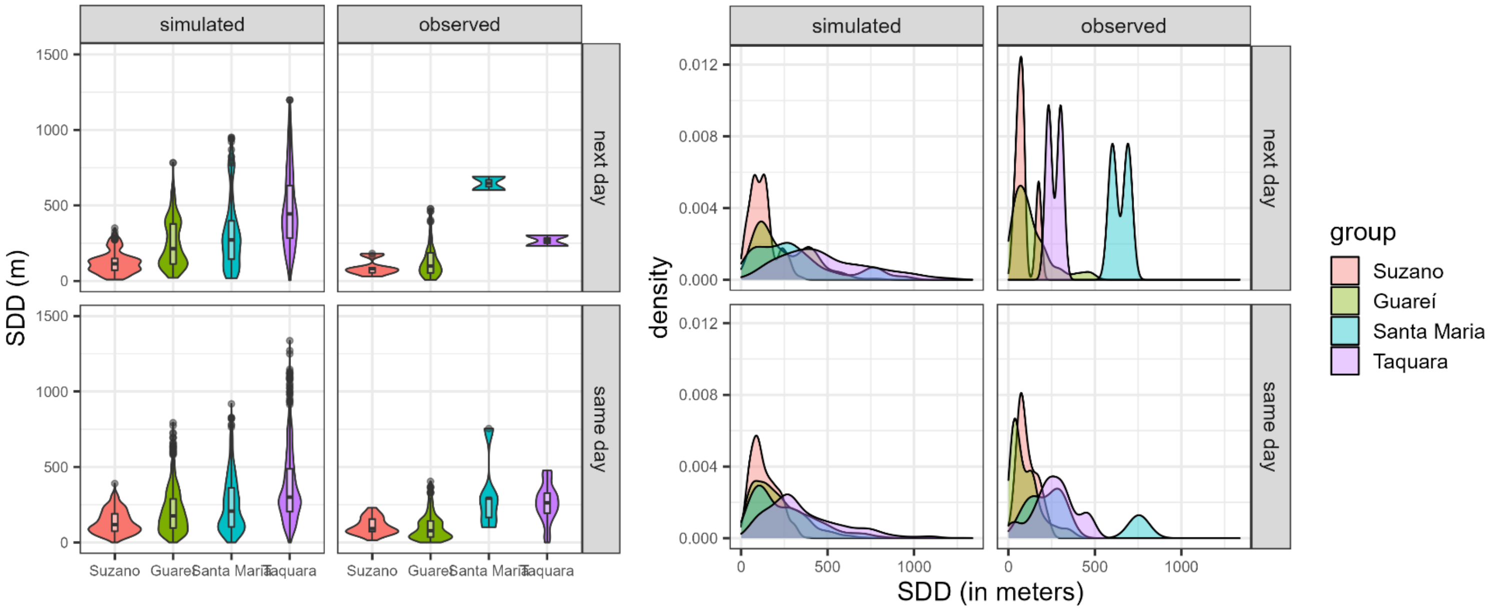

Figure 7. - Seed dispersal distance (SDD) of four black lion tamarin groups (empirical and simulated). A) Violin and boxplot showing the distribution of SDDs. B) Density plots of SDD per group (all available months). Same day and next day refer to seed dispersal events occurring on the same or in the next day following fruit consumption, respectively. Each group is represented by 1 to 4 months with 4-8 days each of collected/simulated data.

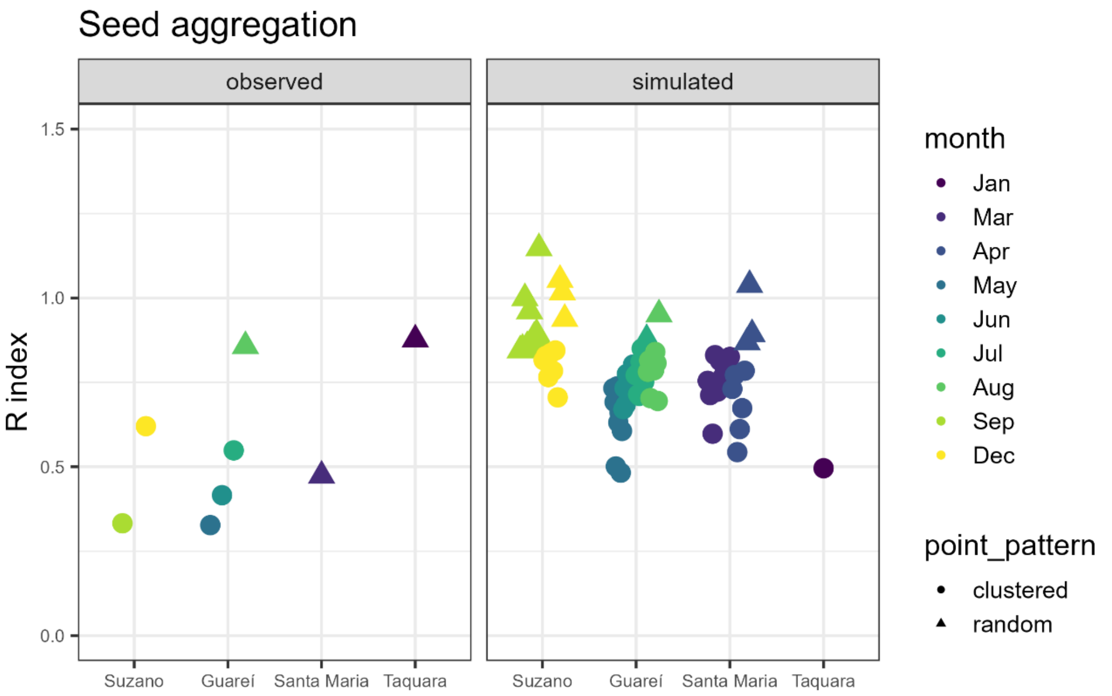

Figure 8 - Seed dispersal aggregation (measured from feces) of four black lion tamarin groups (empirical and simulated). Simulated (left) has ten replications (average of runs), observed values have no replication. We lack data for one time frame in Santa Maria (April).

3.5 DISCUSSION

The model was able to reproduce the observed patterns of seed dispersal of four groups of black lion tamarins inhabiting four distinct forest fragments in very fine scales of time (3 to 8 days) and space. The seed dispersal distance (SDD), although slightly overestimated, was quite consistent with the empirical (observed) data, apart from Taquara (continuous forest) and Santa Maria (medium forest) groups, for which the model predicted shorter and longer SDDs, respectively. Furthermore, the next day seed dispersal events did not match, once more, for Taquara and Santa Maria. The main cause of this might be linked to sampling limitations in our empirical dataset. These events were infrequent in our empirical dataset as these defecations are usually more difficult to find since they are produced very early in the morning when it is still quite dark in the forest**.** Thus, the empirical estimation of such dispersal events might have not been so accurate. Assigning which tree is the mother tree is not a trivial task and might require molecular methods (GELMI-CANDUSSO et al., 2019; HEYMANN et al., 2012). Indeed, many empirical defecation events are missed in the field or cannot be correctly assigned to a mother tree due to uncertainty about the potential candidates. Therefore, empirical data are usually not complete in terms of sampling coverage. In contrast, models allow to simulate every dispersal event, including those more difficult to identify in the field. Consequently, discrepancies observed in terms of SDD between empirical and simulated data can be due to incomplete empirical data collection or, as we will argue below, from the lack of representation of some processes related to ranging behavior and movement in the model.

Two drawbacks in reproducing the movement patterns were identified. The first is the possible effect of behavior (activity budget) on the resulting movement, especially the time spent traveling, which was longer than observed. Most likely, the main reason to this is because the activity budget in the model is simplified to four behaviors (assessed through group scans) (see example on Fig. 3 of Chapter 1), thus other behaviors such as *idle*, *social interactions* and *intergroup encounters* are dropped for simplification, thus leaving some timesteps (up to 20%) “free” for repeating the exclusive four implemented behaviors; Of course, a model with four behavior activities does not capture the whole complexity of such interesting species.

The considerably lower home range size for the group in the continuous forest was the second drawback. Raboy & Dietz (2004) assigned the search for fruiting trees and low number of available sleeping sites as factors driving movement of *Leontopithecus chrysomelas* (although the authors have not explicitly assessed it). Indeed, searching for fruiting trees seems to be enough for reproducing most movement patterns of tamarins in the model, but not of those in the continuous forest (Fig. 3). One possible explanation is the absence of monitoring territory borders as a behavioral activity in our model, which is likely to affect ranging movements recursion (BERGER-TAL; BAR-DAVID, 2015; WATTS; MITANI, 2001) and therefore, the monthly area used. Indeed, Peres (1989) suggests that the frequent use of borders by golden lion tamarins (with no distinction of habitat or territory borders) is a form of “interference and exploitative competition”. Qualitatively looking at simulated trajectories, it is easily seen that the tamarin routes circumventing the home range border do not emerge as frequently as in empirical data (*not shown*). Larger home ranges have been pointed out as a factor diminishing the frequency of territory defense in *L. Rosalia*, compared to groups with smaller home ranges (RABOY; DIETZ, 2004). Interestingly, tamarin intergroup encounters in the continuous forest are 1.5 less frequent than in a small fragment (Guareí), but their duration are three times longer (BURY, 2020). Despite a smaller probability of acquiring endoparasites (COSTA et al., 2022) and diminishing the chance of lethal intergroup encounters (CROUSE et al. 2022; which do not occur frequently in callitrichids: Heymann, (2022)), we are not sure about what leads lion tamarins to establish larger home ranges in continuous forests. A detailed study of the quality of resources and level of competition between groups should shed light on this question. Insofar during our implementations, we could not successfully include a behavioral activity that would lead the agent to monitor its territory border. Furthermore, we dropped the scent marking behavior, which showed little effect on ranging patterns in the previous version of the model (BIALOZYT et al., 2014) and because it seems more related to intragroup communication than territory defense (BURY 2020, HEYMANN 2022). Lastly, recent studies have contrasted the effect of resources and social factors in guiding group size and range dynamics of other primates, finding greater effect of social than ecological factors (ELLIS; DI FIORE, 2019). Whether social factors are as significant for determining tamarin range behavior and dynamics of tamarins as it is the resource distribution, it is still a matter of future exploration.

Notably, our model relies on resources, while the socioecological context (observed through intergroup encounters, home range overlap and dispersal) remains unaddressed. For example, a great review on home range overlap has found interesting relationships between home range size and animal density (PEARCE et al., 2013), which has been confirmed for multiple primate species (RAMSAY et al., 2023 and references therein). While future research should further investigate territoriality and intergroup dynamics of tamarins, grounding future model extensions, we argue that our model is a good candidate for predicting seed shadows of unknown tamarin populations, especially in small and medium sized (100 to 500 ha) forest fragments in fragmented landscapes, given the attention to its premises. The model reproduces well or partially most of our patterns of interest: the seed dispersal distance (SDD), home range size and daily path length (DPL), as well as other patterns that were not initially assessed (movement rate and path twisting), highlighting the multi pattern-oriented modeling approach (POM, Grimm et al. 2012) that guided the development of this model. Below, we discuss other caveats and possible future implementations.

3.5.1 Model limitations and further extensions

This model is still far from including all the possible processes that affect home range emergence and seed dispersal patterns. Potts & Börger (2022, fig. 3) formalize how spatio-temporal patterns can emerge from ABM modeling, comparing processes such as mutual avoidance, attraction to resources and central place attraction. Evidently, our model includes only attraction to resources. Implementing such processes and further comparing simulations with one of those factors dropped down can be quite rewarding in terms of understanding animal movement ecology. Anyhow, our model circumvents the lack of these processes in part by using the empirical home range and resources. Aiming at predicting movement and seed dispersal of unknown tamarin populations, one could do this by fitting a linear model of fragment size and animal abundance to predict home range sizes (analytic approach), although phenomenological.

Besides our focus on attraction to resources in our model, seed dispersal studies have shown that intraspecific variation in seed dispersal based on fruit abundance is common (SCHUPP et al., 2019; TONOS et al., 2021). Inter-individual variation of resource use patterns and consequently of seed dispersal might be as large as inter-specific variation (CANTOR et al., 2013; TSUJI et al., 2020; ZWOLAK, 2018), especially regarding tree visitation and fruit removal, and this effect on agent-based models decision making is acknowledged (DEANGELIS; DIAZ, 2019; MALISHEV; KRAMER-SCHADT, 2021). Thus, knowing which fruit species each tamarin group consumes, prefers, or even base its ranging behavior on, might enable us to better predict traveling and seed dispersal patterns when considering all trees in a fragment. For instance, our model does not rely on sampling all individual trees of the same tree species in the fragment. Instead, our model depends only on *observed* consumed tree individuals during a time frame. Other resources (fruiting trees of the same consumed species) are known to have been ignored while tamarins were traveling (i.e*.,* tamarins do not exploit all the available resources or fruiting patches in their way). Therefore, the step_revisit parameter might be a way of turning individual trees into “depleted” or “visited” patches, which can be further modeled by estimations of feeding bout, revisitation times and further fine-tuned by the estimated fruit and energy intake by agents, as done and discussed in other studies (BONNELL et al., 2013; BOYER et al., 2006; BOYER; WALSH, 2010; HOPKINS, 2016; JANSON; BYRNE, 2007).

Recent simulation studies have been using empirically estimated caloric values to determine behavior modes (BENTLAGE, 2022; MALISHEV; KRAMER-SCHADT, 2021). As more ecophysiological and nutritional studies are conducted on black-lion-tamarins (REZENDE et al., *in prep*; BUFALO et al., *in prep*), we will be able to parameterize the model with real caloric acquisition (estimated from energy intake and feeding bout duration). In this way, if our model structure is correct, not only travel patterns will emerge in a close match with empirical data, but also the feeding bout times. This distinction, together with a more comprehensive understanding of how fragmentation and habitat loss affect the vegetation structure and fruit availability might further increase the model prediction capacity, making it possible to test hypothesis about which factors governs tamarins (and other primates) ranging behavior, distinguishing between ecosociological factors (group size, territoriality, food preference) and ecological factors (food availability and distribution).

3.5.2 Seed dispersal

Seed aggregation and deposition sites

Seed dispersal is highly dependent on microsite deposition. Previous research has shown that side fidelity/adequacy can vary a lot from a disperser to another and within seasons (TOCHIGI et al., 2022). Here we show that seed dispersal by tamarins are mostly clumped, matching the observed patterns in nature. We are aware that the number of defecations collected in a study is prone to observer specificity and error. For instance, it is estimated that 1/7 of feces are seen during a field expedition in another callitrichid species (Heymann EW, *pers. comm.*). Despite this methodological problem in gathering fecal samples during empirical studies which hampers comparisons with simulated data as most point pattern analyses rely heavily on the number of observations (O'SULLIVAN; PERRY, 2013b; PETRERE, 1985), we highlight that the model is able to give a complete profile of seed dispersal events. As the probability of identifying one seed dispersal event diminishes the longer the seed takes to be defecated (because the criterion relies on the exclusive consumption of one feeding tree), this might be the reason why the SDD was slightly overestimated in the model. Furthermore, a complete profile of dispersal events can aid on the understanding of seed dispersal aggregation and the impact of Janzen-Connel processes in further plant development stages, especially if estimations on how many seeds are consumed and defecated are included in the model. However, more seed dispersal events are likely being generated in the model than in nature, because the defecation of seeds in the model depends uniquely on the parameterized gut transit time, while it might depend on other digesta passage times in the wild (FUZESSY et al., 2016).

Although seeds dispersed during travel behavior might result in higher dispersal success (RUSSO; AUGSPURGER, 2004), the high seed deposition of seeds in sleeping sites commonly seen in primate seed shadows (BRAVO, 2009; FUZESSY; SOBRAL; CULOT, 2021; GONZÁLEZ-ZAMORA et al., 2012, 2014) might not be always overcomed by Janzen-Connel effects, resulting in aggregated dispersal of seeds that survive and thus, in aggregated tree distributions (RUSSO; AUGSPURGER, 2004)). This might be one link between adult tree distributions and frugivore movement in the seed dispersal loop (BORAH; BECKMAN, 2021; CÔRTES; URIARTE, 2013; WANG; SMITH, 2002). The same might be valid for resting sites, which can contain higher density of seeds (MUÑOZ LAZO et al., 2011). However, we omitted resting locations from our model as our knowledge on tamarin resting sites availability and selection is limited. In this sense, the recent use of LiDAR to reveal forest structure effects on movement (e.g.*,* McLean et al. 2016) might ground the fine tuning of agent behavior decisions based on structural availability of resting sites, and therefore, of seed dispersal patterns.

3.5.3 Movement

Abiotic factors (temperature, slope)

Temperature might have a direct effect on primates’ velocity and home range size (CAMPOS et al., 2014; DI BITETTI, 2001). This factor is partially compensated by the step model parameterization, but not for daily fluctuations in temperature, which might alter the frequency of resting (but were partially compensated through the parameterization of the activity period and midday period). These daily fluctuations can be seen in the smaller variations of DPL and other movement metrics for the simulations in relation to the empirical data (Fig. 4 and 5). Furthermore, although our model does not include any type of resource selection, the utilization of mean velocities and maximum random angles was enough for reproducing most patterns of movement. Furthermore, as temperature might affect velocity and resting times, it will also affect seed deposition (MUÑOZ LAZO et al., 2011).

As slope emerges as frequent factors guiding movement behavior in other simulation studies (EVERAARS; SETTELE; DORMANN, 2018), we should further test how tamarins inhabiting forest fragments with peaks and slopes in their home range will affect the model prediction capability. However, as the slope will mainly affect velocity and route directionality, this effect should be implemented at the decision level of agents, which is not attainable with the present model, which uses constant velocity and straight-line movement to feeding resources.

Energy

The use of pure step models, disentangled from energy (internal state), are not always needed to predict seed dispersal (as shown by Bialozyt et al. 2014 and highlighted in the introduction of this chapter). Instead, these patterns (step length and turning angles) should emerge from the model (as it emerged in Ranc et al. 2022 model). Although a constant speed is enough to reproduce most tamarin patterns of our interest, multiple variables such as slope and temperature (discussed above), but also predator avoidance, intergroup encounters, and so on, would need a better understanding of the agent decision and how fast and directional they travel during each behavior to be implemented in the model and provide better estimates of long-term seed dispersal patterns.

As pointed by Malishev & Kramer-Schadt (2021), using simple algorithms as (correlated) random-walks neglect movement capacity and habitat-dependent strategies, energy use and predator avoidance, which in turn might be compensated by ABMs incorporating individual energetics (or **eABMs)**. Thus, using an energy submodel with a null movement model (such as in Ranc et al. 2022 and our model) might make the model more realistic, because it links physiological to movement processes. However, despite the high dependence on the energy levels, our model is still not parameterized with very detailed energy activity budgets (MALISHEV et al 2021), and our optimization resulted in inconsistent energy parameters. Both the use of accelerometers and metabolic rules might become a way of avoiding the highly variable *ad-hoc* estimates of energy intake and expenditure (MALISHEV et al. 2021). Our model assigns a unique value of energy per timestep, independent of fruit caloric content. Previous sensitivity analysis (**Text A2.2** in Anexos) suggested that feeding bout parameterization did not matter for Guareí, and that a general value (from 1 to 4 timesteps = ~ 5 to 20 min feeding on each tree, independent of species) did not make any significant change in model output. However, we did not test this thoroughly for all groups, and their frugivory patterns vary in terms of feeding bout and richness (**Figure A2.2**; BUFALO et al. 2022 *in prep*). Furthermore, according to optimal foraging theory, if animals spend more energy going to a resource, they might heavily deplete it and stay on it for longer times (Davis et al. 2022). Although we are certain that tamarins do not deplete much of the patches they visit, preliminary analysis have shown that they might take longer foraging times in patches that provide less energy per time unit, such as fruits with low pulp to seed mass ratio (KAISIN, 2022). Further studies comparing feeding bouts and fruit intake will shed light if this is important for predicting movement and seed dispersal patterns.

Cognition

Primates are provided with distinct cognitive and heuristics for traveling and finding resources (de Guinea et al., 2021). A consensus on which primates use different maps for navigation and to which extent does not exist. *Alouatta pigra* uses metric information (Euclidean maps), but shows "*high path recursion tendency, which limited their capacity to travel in straight lines and approach feeding trees from multiple directions*" (DE GUINEA et al., 2021b). In our model, we have implemented a Euclidean map-based navigation (i.e., agents know every tree location and travels to it in the closest path), but not route-based maps, as it might depend on unknown and complex landmarks in the landscape. Although not thoroughly tested, both our model and empirical data suggest tamarins approach resources from multiple directions, consistent with Euclidean maps at small-scale space (GARBER; PORTER, 2014). Furthermore, only the dynamics of going for the closest tree generated some recursion tendency (*qualitative* pattern), with tamarins tending to follow through similar paths in a route-like manner. This happened specially with resources near the edges of tamarin territories. Thus, we show that a simple rule (going for the closest tree) is enough to predict most tamarin movement and seed dispersal patterns. Further models such as those based on landmark navigation and on Jansen's Geometric Model (e.g., HOPKINS, 2016) should be considered in the future and thoroughly tested. For now, we can reasonably argue that Euclidean maps have been proven enough for *qualitatively* reproducing tamarin movement and ranging behavior.

We saw some incongruent paths in the model which likely emerged from the model simple decision rule: in some cases, the agent's energy levels dropped to below level 1 while traveling to a long-distance tree target, which make them change their target to the closest tree, thus making them turn around (up to 180° turning angles). This can be easily solved by implementing a sensing rule where agents know their distance to the target and decide to "stop by" another resource before proceeding to it. Furthermore, in very complex borders, our rules of movement showed one failure: agents got stuck in equidistant borders ("optimal" places) in some simulations in Suzano (the riparian forest). We tried our best to identify those runs and take them out from analysis. Implementations such as least-cost path (or an A* solver, FERNANDO SANCHO CAPARRINI, 2018) might easily solve this problem.

Feeding bouts, phenology cycles and synchrony

Making trees start and stop producing fruit (phenology cycle) is not occurring in the model, mainly because our time frames are < 9 days. For bigger temporal grains, phenology dynamics should be considered. For example, phenology synchrony is a factor affecting travel bouts in *Alouatta pigra* (DE GUINEA et al., 2021a; but see Jang et al. (2021) which shows that Javan gibbons (*Hylobates moloch*) do not select synchronous plant species). To our knowledge, no ABM has implemented such fine-grained variation in phenology (DURIEZ et al. 2009 *apud* DEANGELIS; DIAZ, 2019). How phenology cycles affect primate movement decisions as it interfaces temporal and spatial processes of frugivory at the same time are far from being understood (ARISTIZABAL et al., 2019; DE GUINEA et al., 2021a). We encourage further work on this subject. Further knowledge on how phenology synchrony and fruit availability guides fruit consumption (spatially) will make it possible to model all available resources in the home range of each group and how this guides frugivore behavior, fruit selection and resource defense.

3.6 CONCLUSIONS

The model reproduces quite well the observed SDD of four distinct groups of tamarins in distinct environments. This suggests that the model has predictive power. The exceptions were the activity budget, the home range size for continuous forest (underestimated) and path twisting for riparian forests (overestimated). The model also reproduces qualitative (path recursion) and other quantitative patterns (MR, PT) not initially assessed during the modeling cycle.

The model did not completely match some seed dispersal patterns, namely the seed aggregation. However, seed aggregation is very difficult to confirm in the field because researchers frequently do not see all defecation events. As the model does not depend on observer capabilities, nor on exclusive seed dispersal events, we hope future studies with genetic methods applied in the field will help confirm the model prediction capability (GELMI-CANDUSSO et al. 2019).

Despite huge sampling effort, understanding the drivers of movement behavior and seed dispersal of tamarins (and other vertebrates in general) is quite a significant challenge. Quoting Hess et al. (2020): “*A model is only as good as the input data that is used to parameterize and run a simulation*”. Here, we parameterized feeding behavior and movement of tamarins with empirical feeding bout durations and velocities, respectively. These parameters are pretty much *ad-hoc*, varying profoundly with the environmental context (MALISHEV; KRAMER-SCHADT, 2021). We encourage further modeling efforts to search for more mechanistic behavior rules which will avoid such multiple parameterizations that result in overly phenomenological models with low predictive power, namely those rules that are linked to the profound knowledge on tamarin natural history and its energetic relationships inside the frugivory loop.

3.7 ACKNOWLEDGEMENTS

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4. CHAPTER 3 - APPLYING THE SEED DISPERSAL MODEL TO DIFFERENT ENVIRONMENTAL CONTEXTS: A PRELIMINARY LOOK

4.1 INTRODUCTION

Efforts to link seed dispersal and frugivory has been astonishing in the last decades, ultimately enhancing our understanding of seed shadows and seed dispersal effectiveness (SDE) by vertebrates (CÔRTES; URIARTE, 2013; SCHUPP; JORDANO; GÓMEZ, 2010). As historically hypothesized, primates are important seed dispersers, representing core elements of dispersal in tropical forests (STEVENSON et al., 2015), composing up to 40% of frugivore biomass (CHAPMAN, 1995) and providing unreplaceable seed dispersal services (BUENO et al., 2013; CULOT et al., 2017). This service emerges mostly due to their movement patterns, with usually large daily distances and home ranges (CHAPMAN; RUSSO, 2007; FUZESSY; JANSON; SILVEIRA, 2017), high degree of frugivory and high richness of defecated intact seeds (BUFALO; GALETTI; CULOT, 2016; HAWES; PERES, 2014b), being one of the few taxa able to disperse large seeds by endozoochory (FUZESSY; JANSON; SILVEIRA, 2018). Therefore, that frugivorous primates play an important role in structuring plant communities is already well established (ANDRESEN; ARROYO-RODRÍGUEZ; RAMOS-ROBLES, 2018; CHAPMAN et al., 2013; GARDNER et al., 2019). However, most primate populations are declining mainly due to habitat loss (which might promote habitat fragmentation) and hunting, and it is still unknown how these anthropogenic activities affect primate functional roles (ANDRESEN; ARROYO-RODRÍGUEZ; RAMOS-ROBLES, 2018; ESTRADA et al., 2017).

Particularly to frugivorous Neotropical primates, this important functional role emerges mainly due to their high degree of frugivory (BUFALO et al., 2016; HAWES; PERES, 2014) and movement patterns (BORAH; BECKMAN, 2021; CHAPMAN; RUSSO, 2007; CÔRTES; URIARTE, 2013). Specifically, some Neotropical primates have long daily path length (DPL) with varying movement linearity (or path twisting, PT) and establish large home ranges, resulting in highly spread dispersal of seeds and therefore important dispersal services to the plant community (FUZESSY et al., 2017; FUZESSY et al., 2018). In this context, the factors determining ranging behavior in terms of DPL and shape are of overall importance in determining primate seed shadows.

Although fragment size, edge and vegetation have been demonstrated to affect primate behavior and their seed shadows, these effects are probably site-dependent (ARROYO-RODRÍGUEZ et al., 2013). At short time scales (ca. 3 decades after fragmentation), edge effects may be more important than area effects on vegetation structure (LAURANCE et al. 1998), which makes both fragment size and shape important variables to understand primate seed shadows. In a patch-scale perspective, variations of microclimate at forest edges (e.g.: increased temperature variance, increased wind throw) (LAURANCE; FERREIRA; LAURANCE, 1998; SAUNDERS; HOBBS; MARGULES, 1991) lead to possible changes in forest structure, fruit, and insect availability within varying distances from the edges, ultimately affecting primate feeding and movement behavior (ARROYO-RODRÍGUEZ; MANDUJANO, 2006; DUNN; CRISTÓBAL-AZKARATE; VEÁ, 2009). Compared to continuous forests, resource availability is usually lower in fragments. This is mainly attributed to fragment size, but also to fragment shape and isolation (ARROYO-RODRÍGUEZ; MANDUJANO, 2006). These small, fragmented patches, frequently lead to changes in primate movement patterns, resulting in shorter seed dispersal distances (SDD) and clumped seed dispersal, diminishing SDE (CHAVES; BICCA-MARQUES; CHAPMAN, 2018; GONZÁLEZ-ZAMORA et al., 2014; SERIO-SILVA; RICO-GRAY, 2002). For Neotropical primates, for instance, fragment size indirectly affects SDD by affecting home range size and daily path length (FUZESSY; JANSON; SILVEIRA, 2017). However, effects of fragment size, shape and resource distribution on primate seed shadows are still entangled and mostly unknown. Since all these above-mentioned factors interact in a traditional field study, it is almost impossible to isolate the effect of a specific patch or landscape attribute on primate movement pattern and its resulting seed shadow, hampering the clear understanding of the processes involved. Considering the high cost and effort to characterize and determine the factors driving primate seed dispersal spatial patterns, addressing this question may require a strong and comprehensive simulation approach. Therefore, modeling primate movement and seed defecation can help disentangling the effect of specific patch or landscape attribute on primate seed dispersal services.

Elucidating how the seed dispersal service is altered by habitat fragmentation is not an easy task; tracking the seeds to the source in different environmental contexts presents several methodological challenges (CÔRTES; URIARTE, 2013; NATHAN et al., 2012) and demands extensive field effort. However, the development of agent-based models (hereon “ABMs”) able to predict primate movement and their associated seed shadows opened new perspectives (BIALOZYT et al., 2014; CÔRTES; URIARTE, 2013). This tool can indeed, with a minimum of field effort, model the seed shadows resulting from pre-defined contexts and hence, help elucidating important questions related to theoretical and applied ecology.

Up to date, some ABM-based studies have directly shown the impact of environmental factors on movement behavior and seed dispersal. These studies have shown a strong effect of frugivore abundance (PEGMAN; PERRY; CLOUT, 2017) and spatial distribution of resources (FEDRIANI et al., 2018; PEGMAN; PERRY; CLOUT, 2017) on mean SDD, and explored potential outcomes on SDD and seed clumping in a landscape approach (NIELD et al., 2020). However, the effect of local environment characteristics, mainly driven by patch size and shape, has yet to be explored. The potential and power that ABMs allow to provide insights on the emergence of primate seed shadows is finally demonstrated with Bialozyt et al. (2014) work, which accurately predicted the seed shadows of two callitrichid species of one Amazonian plant species (BIALOZYT et al., 2014; GELMI-CANDUSSO et al., 2019). We adapted this model to the black lion tamarin (**Chapter 2**), which predicted well most movement and seed dispersal patterns of black lion tamarins in four distinct environmental contexts (small and medium sized forest fragments, continuous and riparian forests). Our model will run in a fine, small scale, irrespective of the landscape context, as some processes are most predicted by patch-scale variables (MAZEROLLE; VILLARD, 1999), including seed dispersal (SAN-JOSÉ et al., 2019).

By usually having large home ranges for its body size (REZENDE et al., 2021) which they frequently cross in a single day, black lion tamarins

(*Leontopithecus chrysopygus*, hereafter “tamarins”) are known to disperse viable seeds of more than 40 plant species at quite long distances (mean SDD of 150 to 280 m), especially of medium-sized seeds (ALCOLEA, 2016; DE ALMEIDA E SILVA, 2022; PASSOS, 1997). Given the different sizes and shapes of forest fragments that tamarins inhabit, we selected this species as a model to study seed dispersal in relation to these forest fragment attributes.

Here, we couple this previously developed model with a fragment and resource generator to answer the following questions: How can 1) fragment size, 2) fragment shape and 3) resource distributions affect tamarins’ movement and seed dispersal? Thus, we will ultimately link frugivory and animal movement to seed dispersal (CÔRTES; URIARTE, 2013; BORAH; BACKMAN, 2022), extending our understanding on primate seed dispersal (ANDRESEN; ARROYO-RODRÍGUEZ; RAMOSROBLES, 2018). We explore these questions with two *in silico* experiments (“*Scenario simulations*” described in the *Method* section) under the three corresponding hypotheses:

4.1.1 Hypothesis 1: Effect of fragment size

Home ranges are the spatial expression of the behaviors that animals perform to survive and reproduce (BURT, 1943 *apud* BÖRGER et al. 2008). A recent review on primate seed dispersal distances identified fragment size as indirectly affecting dispersal distance through effects on home range size and daily path (FUZESSY et al. 2017). As larger fragments are hypothesized to allow tamarin groups to have larger home ranges, probably due to unrestricted space, we first test this relationship with published and unpublished data. Based on a statistical model, we found that both forest fragment size and conspecific density are good predictors of home range size (see *Forest fragment and home range generation* topic in *Methods*). Therefore, we further simulate distinct fragment sizes for a given group of tamarins with the predicted home range size. In other words, we hypothesize that the variation on fragment sizes leading to distinct home range sizes will alter seed shadows. We expect larger seed shadows in larger fragments (Fig. 1a), namely longer SDD with lower degree of seed clumping, a presumed positive spatial pattern for avoiding density-related processes (COMITA et al., 2014).

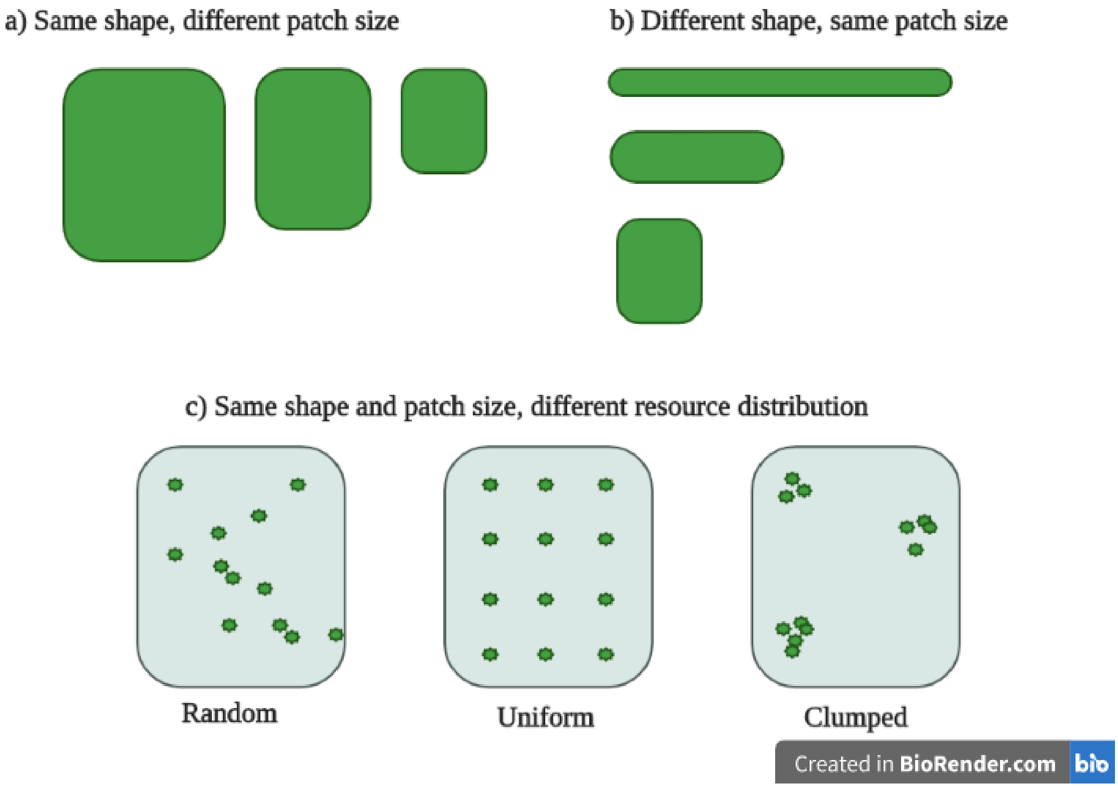


Figure 1 - Distinct environmental conditions where black lion tamarins (represented as agents) will be simulated based on hypothesis 1 (a), 2 (b) and 3 (c). Made in BioRender.com.

4.1.2 Hypothesis 2: Effect of fragment shape

Previous studies have linked edge effects with movement behavior and thus on seed dispersal, but this effect depends on the propensity of animals to respond to the edges (LEVEY et al., 2005; NIELD et al., 2020). Accordingly, primate responses to edges seem to be species specific (BOLT et al., 2020; BOYLE et al., 2009; LEHMAN; RAJAONSON; DAY, 2006; LENZ; JACK; SPIRONELLO, 2014). Tamarins persist in smaller and edgy fragments (e.g., riparian forests; (CULOT et al., 2015), where their home ranges are almost entirely constituted by edges. In Guareí (ca. 100 ha. Forest fragment), for example, they use the fragment edges intensively (Bufalo, F. unpublished). As riparian forests become thinner (e.g., 30 m from river to matrix), tamarin linear displacement (measured as mean step length) should be longer, thus altering seed shadows (Fig. 1b). As edge intensity increase and forest shapes get more complex (e.g., riparian forests), we expect a high intensity of use of the same areas, by means of frequent reuse of traveling paths, causing seeds to be dispersed in high density (i.e., a highly clumped pattern of seed deposition). Hence, the more complex the patch, the larger the mean SDD, but higher the seed clumping degree, with negative consequences on SDE.

4.1.3 Hypothesis 3: Effect of resource distribution

Spatial distribution of food resources (e.g., trees, lianas) and repeatedly used sites (such as resting and sleeping sites) are known to affect SDD, usually by reducing it as the degree of food resources clumping enhances (NIELD et al. 2020; PEGMAN et al. 2017). These patterns, although emerging from simulated generic frugivores, are similar for primates. For instance, *Alouatta palliata* mean SDD was found to be shorter when resources are clumped (SERIO-SILVA; RICO-GRAY, 2002), but this resource distribution was correlated with fragment size (smaller patches had clumped resources). Furthermore, resting and sleeping sites might receive more dispersal events, resulting in high seed density (RUSSO; AUGSPURGER, 2004; MUÑOZ LAZO et al. 2011), which presumably is negative due to Janzen-Connel effects (COMITA et al 2014). Therefore, we hypothesize that the distinct spatial distribution patterns of feeding trees (Fig. 1c) will influence the resulting simulated seed shadows. A general prediction is that tamarins' mean SDD will follow the same pattern found by Serio-Silva and Rico-Gray (2002), namely shorter SDD as the degree of clumping enhances. Thus, we predict that mean SDD will be longer when sleeping sites are dispersed within the home range (large nearest neighbor distance, NN) and the clumping degree of dispersed seeds (higher as the nearest neighbor distance between seeds decrease) to be higher if resources (feeding and sleeping trees) are clumped (PEGMAN et al. 2017).

As the relation between forest patch area and edge is negative (i.e., smaller patches tend to bear more edges and less core area, proportionally (SAUNDERS et al. 1991; FAHRIG 2003), we acknowledge that the above-mentioned hypotheses are non-exclusive and that area, edge and resource distributions may be collinear when considering movement and seed dispersal processes (**Figure 1**). Furthermore, as the tamarin population size (measure as density) is highly correlated with home range size (**Text A3** in Anexos), in order to test the effects of forest fragment attributes (large vs. small fragments, more edges vs. less edges, etc.), we will simulate scenarios where season and density are controlled.

4.2 METHODS

4.2.1 Model description

We used a previously validated model (cf. **Chapter 2**). The model works with the input of a forest fragment, the home range size for one group of tamarins (predicted based on the forest fragment size and tamarin density) and feeding and sleeping trees distributed within it (**Figure 2**). Fragment edges act as ‘constraints’ to animal movement (*sensu* Beyer et al. 2016), i.e., barriers that cannot be crossed nor circumnavigated and therefore impose absolute limits on distribution, as in other ABMs (Jones et al. 2017). Full description of the model can be found in the ODD protocol (**cf. Text A2** in Anexos; **Chapter 2**).

4.2.2 Forest fragment and home range generation

We developed a fragment generator for the purposes of simulating fragments with varying sizes and shapes. For the fragment size, we specify the number of cells of 10 x 10 m which corresponds to fragment sizes available throughout the tamarin distribution (50 to 1500 ha). For the shape, we use a field shape factor, which is an index representing how bigger a fragment is in one direction relative to its perpendicular direction (Figure 1).

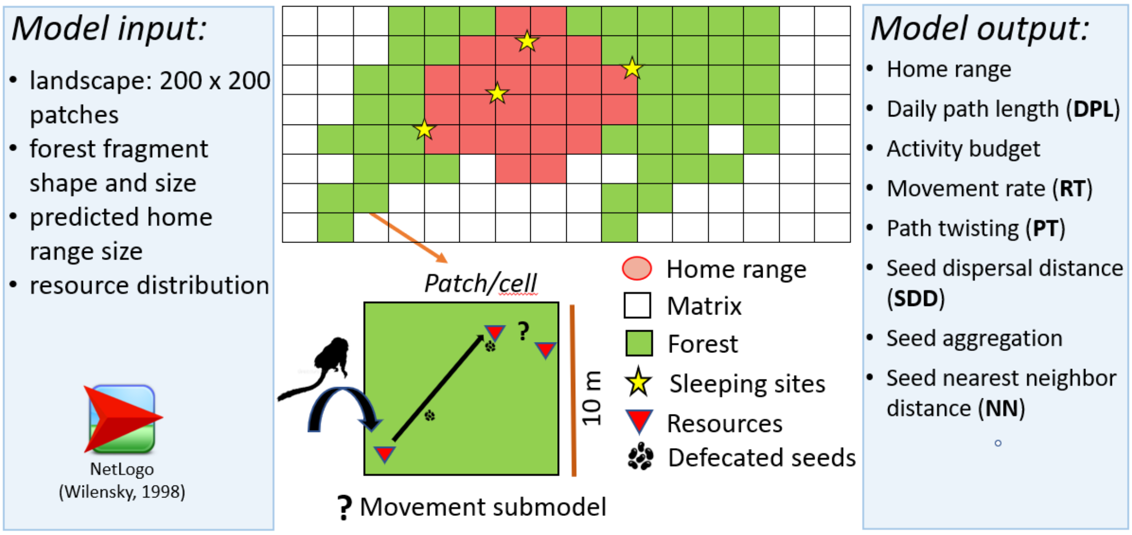


Figure 2 - Model overview showing the inputs and outputs (patterns) of interest. The model scheduling is described in detail in Chapter 2 (see ODD available in Text A2).

Previous studies have generated home ranges either by estimating energetic requirements and distributing it in a simulated landscape (ROHWÄDER; JELTSCH, 2022) or by using empirical home range sizes (LIU et al., 2013), or, still, a mix of both approaches (BUCHMANN et al., 2011). Preliminary analysis showed that home range and forest fragment sizes are correlated for tamarins. Here, we collected published and unpublished data on *Leontopithecus* spp. to understand the relationship of home range size and forest patch size while controlling for tamarin density (**Text A3** in Anexos)**.** We fitted a GLM with *lmer* package in R (BATES et al., 2015) with a Gaussian family distribution and log link. We log-transformed (log10) both the predictor forest size (in ha) and tamarin home range sizes (in ha). We used the predict() function in base R to predict home range sizes for a given forest fragment size and tamarin density.

For sure there is an interplay of resource availability with territoriality (BUCHMANN et al. 2011; PEARCE et al. 2013) and conspecific density, and these, in turn, with fragment size. But as far as we are aware, these distinctions are still not fully understood, and we only correct home range estimates for tamarin density in our model.

4.2.3 Resource generation

We used *second-order* Thomas process (O'SULLIVAN; PERRY, 2013a, p. 42) with varying degrees of clumpiness. For this, for a given numbers of points (feeding trees) of our interest, we used a fixed number of clusters ("originating" or "maternal" points), varying only sigma (sd-displacement), which represents the variation of distances from the cluster point, to generate feeding trees spatial patterns inside the home range borders. We used the generated feeding and sleeping trees locations as spatial windows (*owin*). We tested the resulting resource distributions for clumped, random or ordered patterns with Clark-Evans test (with clark.evans.test in *spatstat* package, BADDELEY; TURNER, 2005). Although the Clark-Evans test assumes homogeneous processes and we deliberately used a second-order homogeneous (Thomas) process, our aim was only to generate distinct patterns of resource distributions independently of the processes that generated it. We used significance (alpha ≤ 0.05) to classify resource distributions as clumped, random, or ordered. For sleeping trees, we randomly distributed *n* points inside the home range (*n* might vary from 1 to n days, i.e., when tamarins use only one sleeping site during the simulation period or one different sleeping site each day, respectively).

All forest fragments, home ranges and resource distributions are available as PNG files in the format of *export-world* function in NetLogo (**Supp. Mat. 2**).

4.2.4 Simulation scenarios

For each hypothesis, we varied the parameter of interest while keeping others constant. This resulted in two simulation scenarios, the first one (Experiment 1) related to the three ascribed hypotheses (**Table 1**) and a second one (Experiment 2) related to resource abundance.

Table 1 - Experiment design for each hypothesis with the range, number of replication and details of each varied parameter. Parameters in bold were varied to address each hypothesis of this study (see Introduction). Experiment 1 is related to hypotheses 1 and 2 (size and shape), and Experiment 2 to hypothesis 3 (resource distribution). Parameters in bold were varied to address each hypothesis of this study (see Introduction).

Experiment 1: effect of fragment size and shape				
Parameter	**range**	**values**	**replicates**	**n# sim**
fragment size	100, 150, 300, 500, 750, 1000 and 1500	7	5	35
fragment shape	according to field-shape-factor (1 to 3)	3	3	9
home range	predicted	1	5	5
density	0.035 and 0.14**	2	1	2
n-sleeping-trees	5	1	1	1
n-feeding-trees	50	1	1	1
clumpiness	R = {0.5 – 1.3}***	1	5	5
Total simulations				**2682*** **

Experiment 2: effect of resource availability				
Parameter	**range**	**values**	**replicates**	**n# sim**
fragment size	100, 500, 1500	3	1	3
fragment shape	according to field-shape-factor (1 to 3)	3	1	3
n-feeding-trees	10 – 100 (by 20)	5	3	15
resource clumpiness	R = {0.5 – 1.3}**	2	5	10
density	0.035 and 0.14*	2	1	2
home range	predicted	1	1	1
n-sleeping-trees	5	1	1	1
Total simulations				**1062*** **

* It corresponds to the density of tamarins in two areas: Fazenda Santa Maria and Guareí, located in the lower and upper Paranapanema river basin, respectively.
** considered clumped when R < 1 and p < 0.05, random when R approached 1 and p > 0.05.
*** Number of simulations may vary because the resource generation relies in a highly stochastic point-pattern process.
Values in bold are varied parameters, non-bold are constants.

4.2.5 Parameterization

As tamarin movement patterns differ extensively depending on the environmental context, likely upscaling with habitat availability and forest edges (**Chapter 1**), we use the set of parameters which correspond to the calibrated movement patterns and observed seed dispersal parameters of a specific month from group inhabiting a medium-sized forest fragment (515 ha) with low (0.035 ind./km²) tamarin density for every run ("Santa Maria" group in April month, **Table 2**). Moreover, we used calibrated parameters related with energy, memory and resting duration resulting from Chapter 2 (see genetic algorithm results cf. fig. 3). We did this because the calibrated parameters from a small forest patch (100 ha) and those of Santa Maria were relatively similar. As here we do not simulate riparian or continuous forest, we believe this is the best set of parameters scenarios involving isolated patches from 50 to 1500 ha. Furthermore, the movement patterns (step length and turning angles) of tamarins in the small and medium-sized forest were similar for most behaviors, thus justifying the use of the same parameters (cf. Chapter 1). Lastly, as the generated resources (fruiting trees) do not have any species identity, we specified the feeding bout times through the *species_time* parameter (the time spent, in timesteps, feeding in a specific individual tree) with the observed mean and standard deviation value sampled from a normal distribution (only positive values). For the gut transit time, the time it takes for a seed to be defecated after consumption, was assigned based on a Poisson distribution with mean = 16 timesteps.

Table 2 - Parameters used to run the simulations. Values correspond to the calibrated Santa Maria (April) of Chapter 2 (Figure 2).

Parameter	**Details**	**value**
Routine-related		
simulation-time	Timestep when tamarins select a sleeping site and start traveling to it	110
no_days	Number of simulated days	10
Energy-related		
start-energy	Initial level of energy at the start of each day	980
energy_level_1	Level of energy which below it the tamarin is considered “hungry”	1584
energy_level_2	Level of energy which above it the tamarin is considered “satiated”	1897
energy-from-fruits	energy gain from frugivory each timestep	192
energy-from-prey	energy gain from foraging each timestep	246
energy-loss-traveling	energy loss from traveling each timestep	-53
energy-loss-foraging	energy loss from foraging each timestep	-31
energy-loss-resting	energy loss from resting each timestep	-65
Seed dispersal-related		
gut_transit_time	mean gut transit time assigned for each seed in every frugivory event	16
Movement-related		
max_rel_ang_forage_75q	Relative max angle deviation when the group is foraging	74
max_rel_ang_travel_75q	Relative max angle deviation when the group is traveling	67
step_len_forage	Mean step length when the group is foraging	1.3
step_len_travel	Mean step length when the group is traveling	2.4
Behavior-related		
species_time	mean time spent feeding in na individual tree (feeding bout)	2.5
species_time_sd	standard deviation time spent feeding in na individual tree (feeding bout)	3
duration	duration of resting behavior	8

p_foraging_while_traveling	Probability of foraging while in traveling activity	0.61
Memory-related		
step_forget	Number of steps taken to reconsider revisiting a fruiting tree	265
prop_trees_to_reset_memory	Proportion of total trees that calls the *enhance_memory_list* procedure	2

4.2.6 Statistical analyses

We standardized all predictor variables with the scale() function in R. For the response variables, we square-root transformed those related to distance (SDD or NN distances) and log-transformed those related to area (home range and forest fragment size) when the Kolmogorov-Smirnov test was rejected (distributions tested: normal, Weibull, log-normal and Gamma, implemented in ks.test() function in R). When the KS test rejected all possible distribution families, we inspected density, cdfs, qqplots and ppplots with the *fitdistrplus* package (DELIGNETTE-MULLER; DUTANG, 2015), selecting the most appropriate transformation and family distribution. For each experiment, we used AICc as model selection criteria implemented in the MuMin package (BARTOŃ, 2022), selecting the model with the smallest AICc. We only used continuous variables with Spearman correlations $\rho < 0.75$ by using findCorrelation() function in *caret* package (KUHN, 2022).

For experiment 1, we fitted a GLM using a Gaussian error distribution with a log response (identity link) for both SDD and seed aggregation. We dropped the following variables from predictors: proportion of visited trees, number of visited trees, area used (KDE95 and KDE50), movement rate (MR) and standard deviation of path twisting (PT) (**Figure SM3-2**). For experiment 2, we fitted a GLM using a Gaussian error distribution with a log response (identity link) for both SDD and seed aggregation. We dropped the following variables from predictors: proportion of visited trees, number of visited trees, DPL, PT, KDE95 and standard deviation of DPL and PT (**Figure SM3-3**). We further simplified models with multilinear responses by dropping variables with high variance inflation (VIF) as diagnosed with the sjPlot package plot_model() function. Model validation plots are available in **Figures SM3-4 to SM3-7**.

4.3 PRELIMINARY RESULTS

4.3.1 Experiment 1

Neither fragment size (estimate = 0.004, p = 0.06) nor fragment shape affected SDD (**Figure 3**). Instead, mean seed dispersal distance (SDD) increased with daily path length (DPL) and decreased with path twisting (PT) (**Table 3**), being the best predictors of SDD. The same was valid for seed aggregation, which diminished with DPL and increased with PT, but in turn it was highly affected by the time spent feeding (p_feeding) and only slightly when fragments were narrow (field shape factor = 3). Furthermore, the clumping degree of feeding trees slightly increased seed aggregation (Table 3). In turn, clumping degree of sleeping trees did not influence SDD (contrary to expected), nor seed aggregation (Table 3).

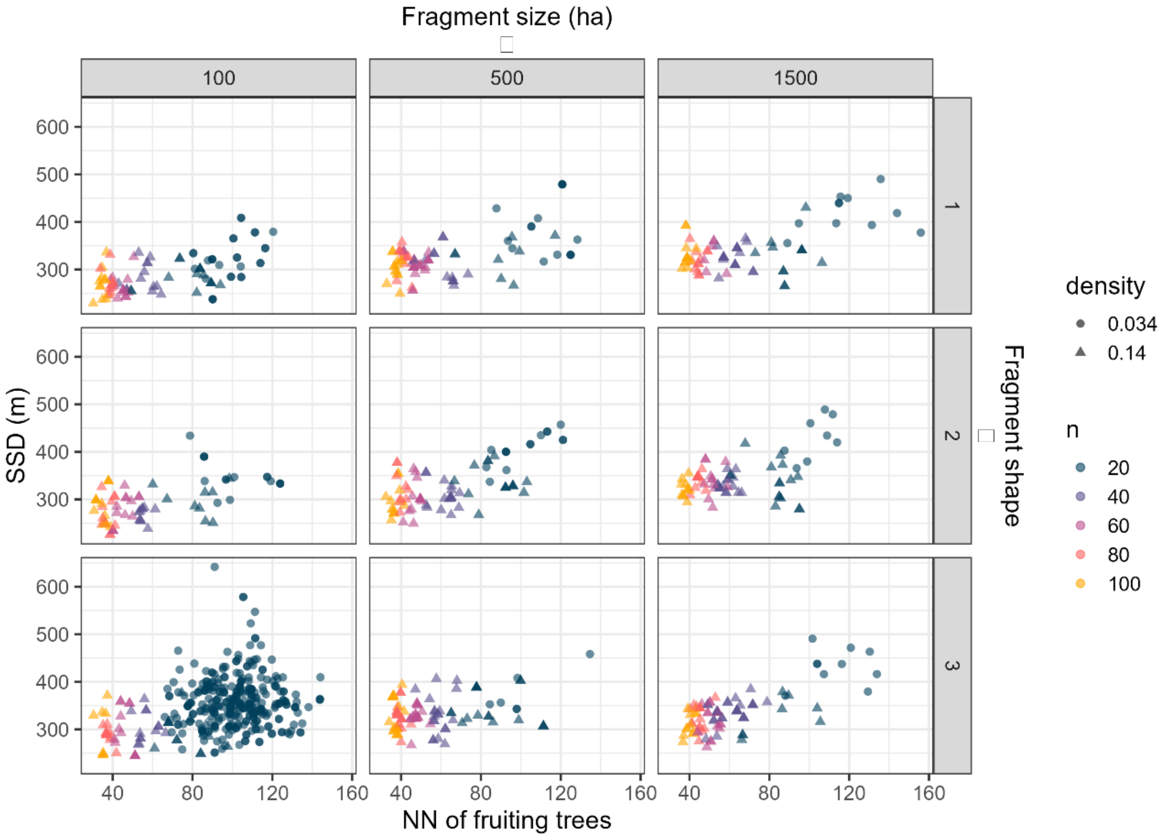


Figure 3 - Simulated seed dispersal distance (SDD) generated by one black lion tamarin group inhabiting forest fragments with varying size and shape. Density is the population density, which predicts home range size (see text).

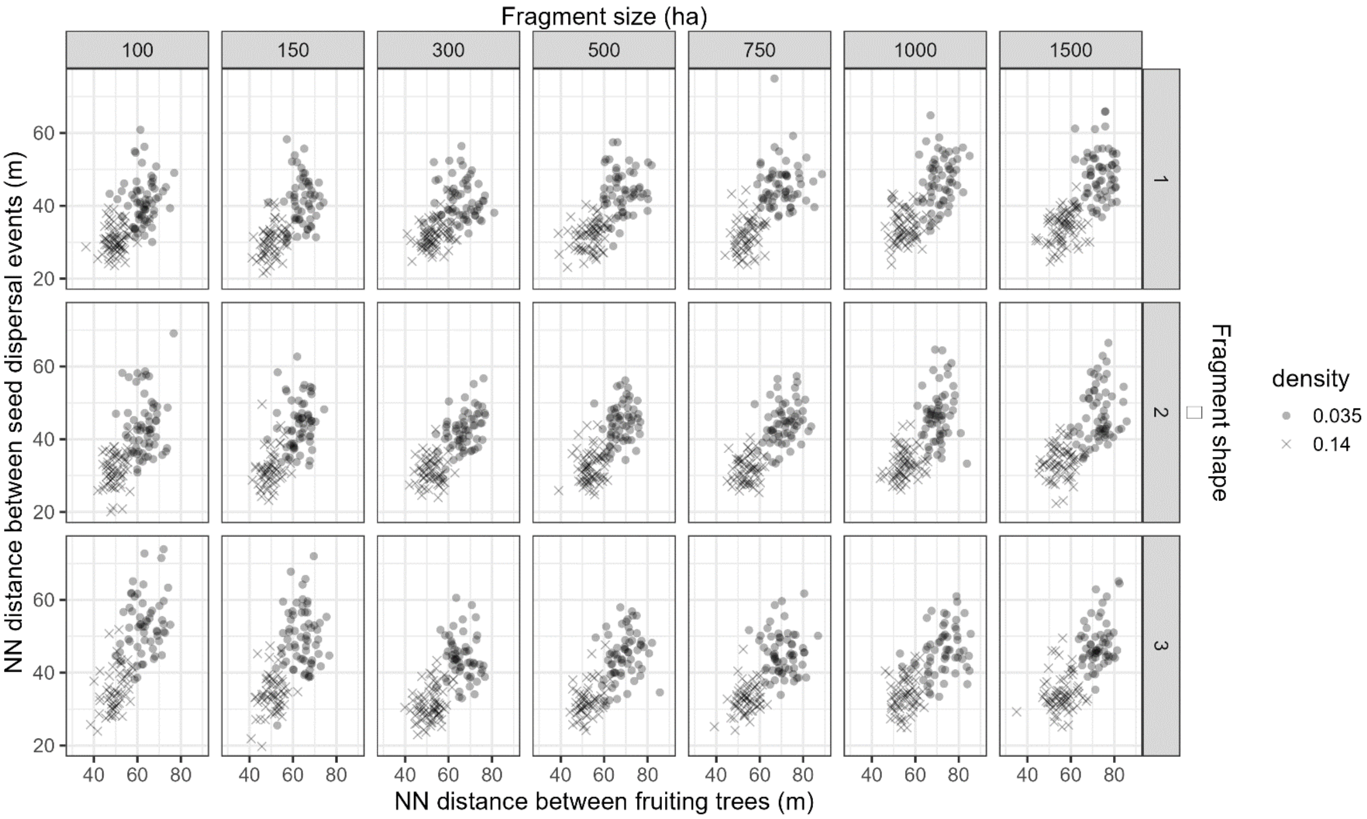


Figure 4 - Simulated seed aggregation of seed shadows generated by one black lion tamarin group inhabiting forest fragments with varying size and shape in relation to resource (feeding tree) aggregation. Density is the population density, which predicts home range size (see text). NN = nearest neighbor distance, a proxy of aggregation based on how close each tree is from its neighboring tree (in meters).

Table 3 - Predictors of seed dispersal distance (SDD) and seed dispersal aggregation (measured as NN distance) of seed shadows generated by black lion tamarins. KS test in bold indicates that the response variable does not follow the chosen distribution. Estimates values in bold denote important (>|0.1|) values. Non-significant parameters were dropped.

Experiment	Model	Response	KS test	Parameter(a)	Estimate	Std.Error	t.value	***p***
1	GLM (family: Gaussian, link: identity)	log(SDD)	D = 0.022216, p = 0.1456	Intercept	5.8342	0.0050	1167.7148	0.0000
				step	0.0144	0.0024	5.9445	0.0000
				DPL	**0.1472**	0.0050	29.1891	0.0000
				MR_sd	-0.0068	0.0022	-3.0400	0.0024
				PT	**-0.1086**	0.0051	-21.4702	0.0000
				n_unvisited_trees	0.0106	0.0024	4.3820	0.0000
				p_feeding	0.0128	0.0025	5.0524	0.0000
	GLM (family: Gaussian, link: identity)	log(NN_seeds)	D = 0.048342, **p = 8.202e-06**	Intercept	3.6540	0.0059	621.4420	0.0000
				density (0.14)	-0.0320	0.0099	-3.2450	0.0012
				field.shape.factor (3)	-0.0148	0.0052	-2.8356	0.0046
				NN_feeding_trees	0.0127	0.0038	3.3193	0.0009
				DPL	**0.1192**	0.0057	21.0814	0.0000
				PT	**-0.1039**	0.0060	-17.4389	0.0000
				n_unvisited_trees	0.0166	0.0029	5.8192	0.0000
				p_feeding	**-0.1130**	0.0071	-15.8431	0.0000
				p_foraging	-0.0189	0.0071	-2.6538	0.0080

Experiment	**Model**	**Response**	**KS test**	**Parameter(a)**	**Estimate**	**Std.Error**	**t.value**	***p***
2	GLM (family: Gaussian, link: identity)	log(SDD)	D = 0.038252, p = 0.09097	Intercept	5.6585	0.0137	413.6190	0.0000
				fragment_size (500)	**0.3251**	0.0162	20.0554	0.0000
				fragment_size (1500)	**0.3211**	0.0147	21.7726	0.0000
				n	-0.0576	0.0088	-6.5586	0.0000
				step	0.0302	0.0041	7.3641	0.0000
				energy_stored	-0.0090	0.0038	-2.3592	0.0185
				PT	**-0.1251**	0.0103	-12.1374	0.0000
				p_resting	-0.0399	0.0038	-10.4887	0.0000
				n_unvisited_trees	0.0333	0.0074	4.5065	0.0000
	GLM (family: Gaussian, link: identity)	log(NN_seeds)	D = 0.10579, **p = 1.088e-10**	Intercept	3.4745	0.0169	206.1880	0.0000
				fragment_size (500)	**0.3780**	0.0208	18.1917	0.0000
				fragment_size (1500)	**0.3707**	0.0192	19.2945	0.0000
				field.shape.factor (2)	-0.0219	0.0112	-1.9657	0.0496
				field.shape.factor (3)	-0.0382	0.0107	-3.5606	0.0004
				PT	**-0.1810**	0.0123	-14.7068	0.0000
				p_feeding	**-0.2026**	0.0077	-26.3100	0.0000
				p_resting	-0.0169	0.0049	-3.4381	0.0006

a. All parameters were Z-transformed, except factors (density and field shape in both experiments, and fragment size in experiment 2).

4.3.2 Experiment 2

When we varied the number of feeding trees, the SDD was longer with increasing fragment size and shorter with high PT, as predicted (Table 3). However, SDD did not vary in relation to clumping degree of fruiting trees (measured by the nearest neighbor distance, NN), contrary to expected, despite a positive trend (**Figure 5**, Table 3). Other factors such as the number of fruiting trees (and how many of them were visited) also affected SDD, but in much less extent than fragment size and PT (Table 3). Similar trends were observed for the seed aggregation, measured as the NN between defecated seeds. The major factors affecting seed aggregation was fragment size (positively) and PT (negatively), but also the proportion of time spent feeding, which increased aggregation. Despite a trend of diminishing seed aggregation with less aggregated resources (fruiting trees, **Figure 6**, but not sleeping trees, **Figure 7**), this was not significant.

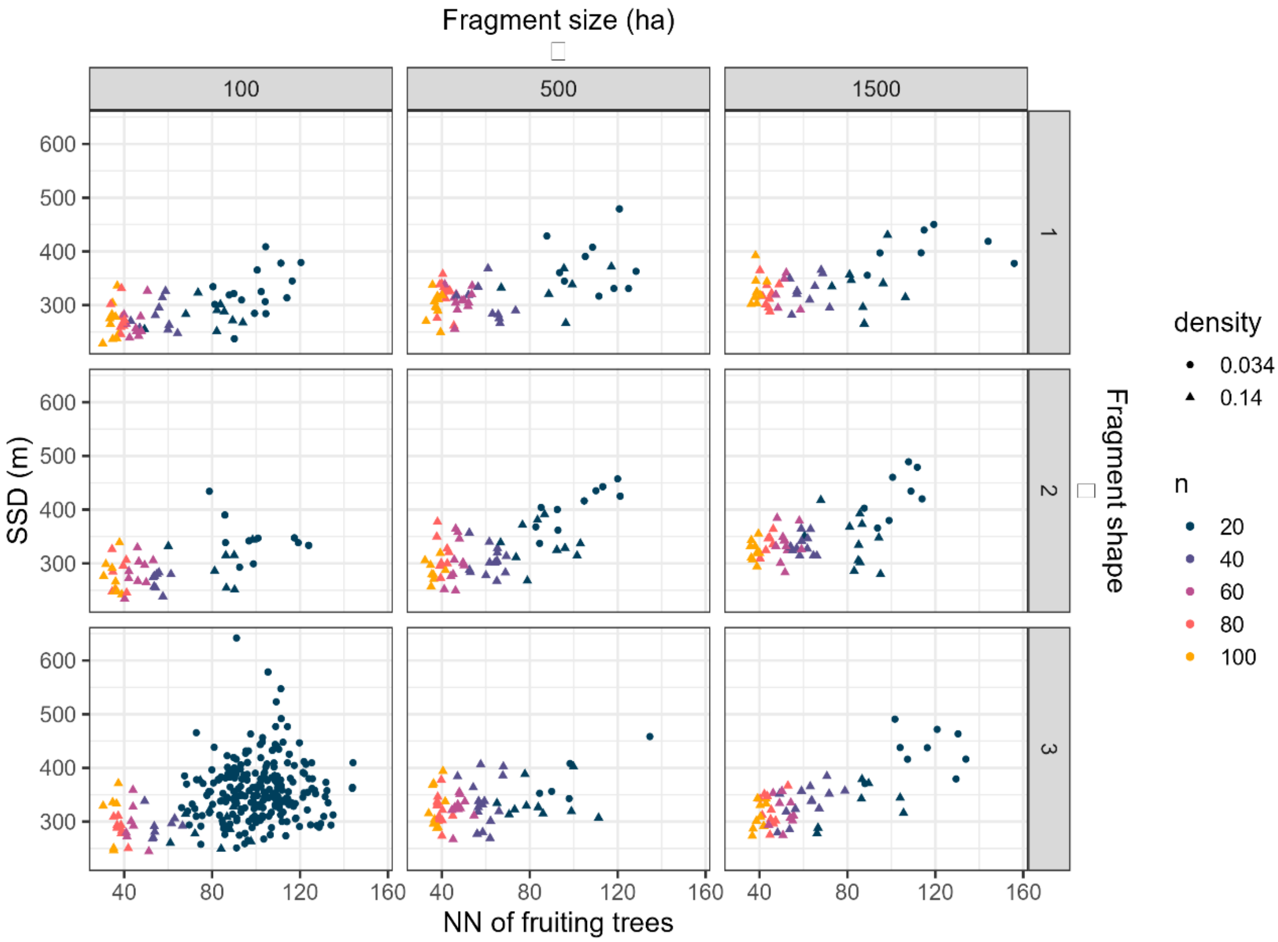


Figure 5 - Simulated seed dispersal distance (SDD) of one tamarin group inhabiting different environmental contexts with varying number of fruiting trees. Density is the tamarin density, which predicts home range size (see text), while “n” refers to the number of fruiting trees. NN = nearest neighbor distance, a proxy of aggregation based on how close each tree is from its neighbor tree, in meters.

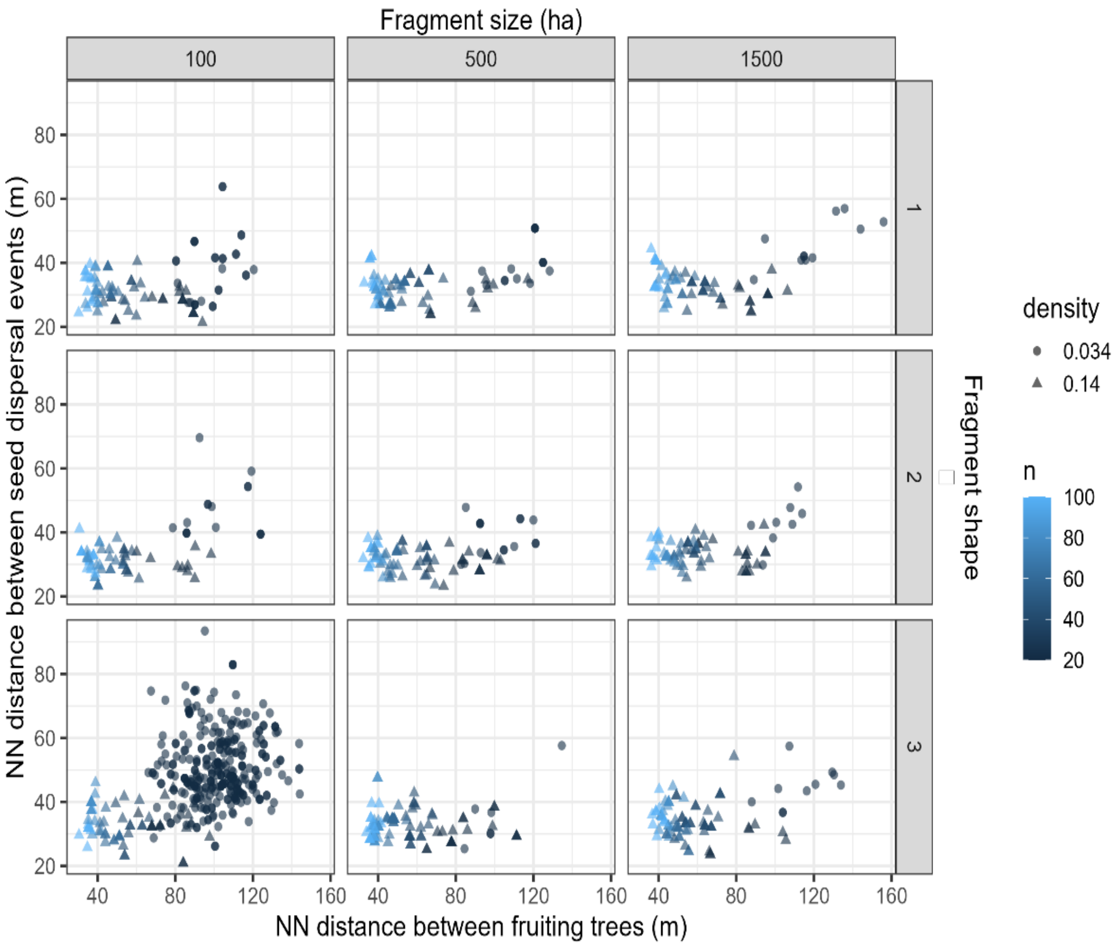


Figure 6 - Simulated seed aggregation, measured as the nearest neighbor (NN) distance, in meters, between seed dispersal events of one black lion tamarin group inhabiting different environmental contexts with varying aggregation of fruiting trees. Density is the tamarin population density, which predicts home range size (see text), while "n" refers to the number of fruiting trees.

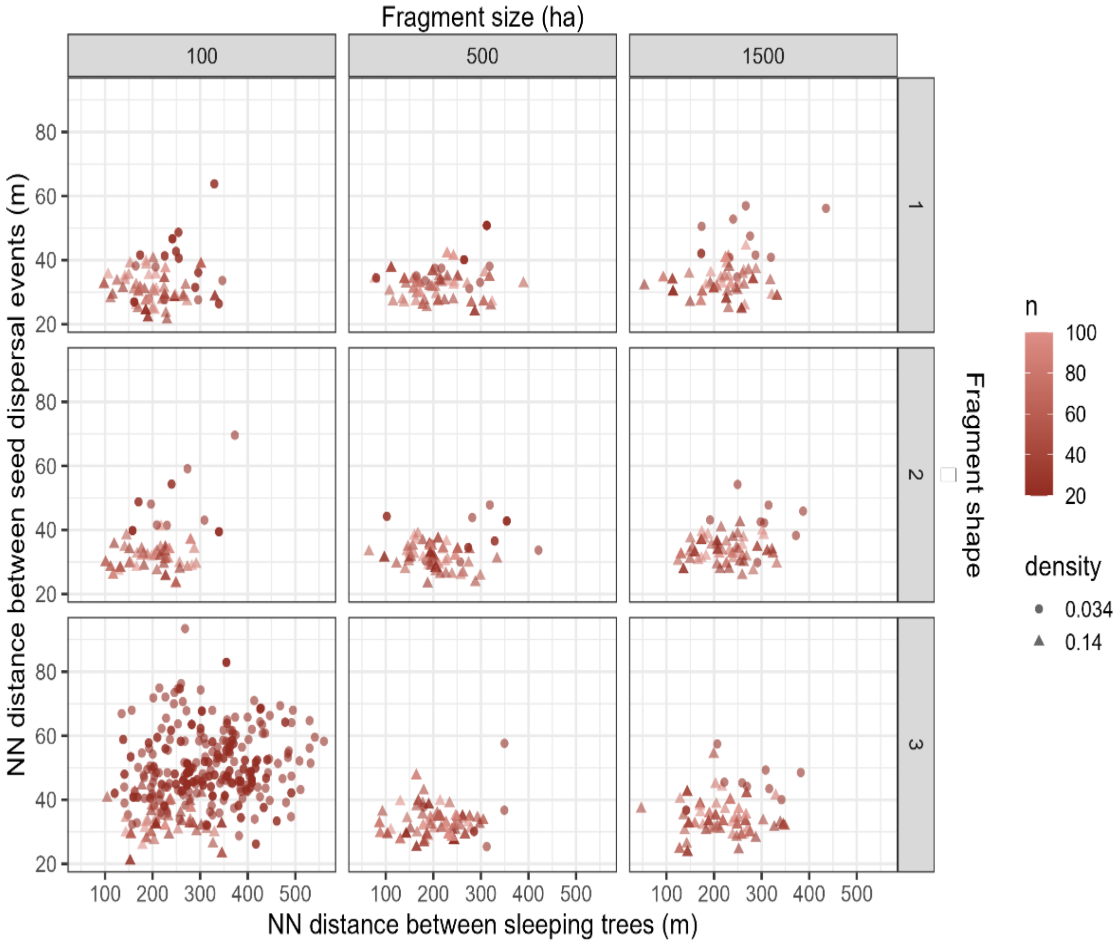


Figure 7 - Simulated seed aggregation, measured as the nearest neighbor (NN) distance, in meters, between seed dispersal events of one black lion tamarin group inhabiting different environmental contexts with varying aggregation of sleeping trees. Density is the tamarin population density, which predicts home range size (see text), while "n" refers to the number of sleeping trees.

4.4 PRELIMINARY DISCUSSION

The great effect of movement rate (MR) and path twisting (PT) on SDD (as inferred from the statistical models) was expected, given its high predictable power of SDD of Neotropical primates (FUZESSY et al. 2017). However, the much smaller contribution of fragment characteristics (such as size and shape) was not expected. This might happen because our simulations control for the scaling of movement patterns with increasing size and longer shape. Other factors, albeit secondary, also posed a significant influence on SDD, such as the population density of tamarins (which was used to generate home range sizes) and the number of visited trees, but much smaller effects were seen from the number and aggregation of fruiting trees, which are factors often claimed to have large effects on SDD in empirical studies (CHAVES; BICCA-MARQUES; CHAPMAN, 2018; DUNN; CRISTÓBAL-AZKARATE; VEÁ, 2009; GONZÁLEZ-ZAMORA et al., 2012; SERIO-SILVA; RICO-GRAY, 2002). These results show that SDD is indeed governed almost exclusively by movement patterns (NATHAN et al., 2012; SPIEGEL; NATHAN, 2007), namely by how much (DPL) and how tortuous (MR and/or PT) the animal travels.

On the contrary, the degree of seed aggregation was highly predicted by fragment size and time spent feeding, and then by movement patterns (DPL and PT). Although much smaller than expected, the increase of seed aggregation within more linear patches was confirmed. This reinforces the need of assessing not only seed dispersal distances, but also conspecific density of dispersed seeds in seed dispersal studies (MUÑOZ LAZO et al., 2011; RUSSO; PORTNOY; AUGSPURGER, 2006). These findings confirm other simulation studies that found a great effect of movement patterns and time spent feeding on seed dispersal distances and aggregation (JONES et al., 2017).

We are unaware of other studies spatially and explicitly testing the direct impact of resource (or patch) aggregation in primate movement patterns, although the hypothesis that this is an important factor is frequently stated (SERIO-SILVA; RICO-GRAY 2002; SPIEGEL; NATHAN, 2007; REYNA-HURTADO et al., 2018). Few exceptions apart, Ariztibal et al. (2019) tested the effect of resource aggregation on feeding selection by *Alouatta pigra*, but while aiming at understanding feeding patch (fruits or leaves) size. However, some studies have assessed the spatial distribution of defecated seeds, mainly building on the resulting patterns of sleeping site usage hypothesized by Champan & Russo (2006). For instance, Muñoz-Lazo et al. (2011) found higher seed density around sleeping and resting sites of Amazonian tamarins, and Gestich et al. (2019) found overall dispersed patterns of seeds dispersed by titi monkeys in the Atlantic Forest, with some sites close to the sleeping sites receiving more seeds. As for the sleeping site selection of golden lion tamarins (FRANKLIN et al. 2007) there might be other processes playing a role in the selection of trees by tamarins.

Apart from obvious geometric differences, previous studies have highlighted other discrepancies between isolated and riparian fragments. For example, riparian forests have been hypothesized to have either higher or lower resource availability than isolated forest fragments. Indeed, vegetation surveys throughout multiple tamarins' forest fragments showed that the riparian forests presented better habitat quality, based on vegetation structure and composition (as measured by Cibim 2022). While our team believes that riparian forests might contain more fruits for tamarins (KEUROGHLIAN; EATON, 2008; but see Pessoa et al., 2017 and Bolt et al., 2023) tamarins indeed have smaller home ranges and higher densities in riparian forests (CALDANO; MONTICELLI; GALETTI JR., 2016; MAMEDE-COSTA; GOBBI, 1998). This is in line with other simulation models, where home range size of herbivores is predicted to be smaller when resources are abundant (BUCHMANN et al., 2011).

Here we show that movement patterns (DPL, MR and PT) are much more important in predicting seed dispersal distances and aggregation than local fragment characteristics. In turn, we show that local fragment characteristics, especially size (and shape in a lesser extent), affect seed aggregation. This conclusion can be drawn because we used a simulation model with controlled factors (movement parameters, resource distributions and forest fragment shape and size), which give us a replication and predictive power that cannot be attained in empirical studies.

Callitrichids, different from the larger Atelids, disperse few seeds per dropping with high frequency, and are more likely to disperse seeds into secondary forests (BUFALO et al., 2016; CULOT et al. 2019; HEYMANN et al 2022). After controlling for the movement and the scaling of ranging (by using only calibrated values of one known group and predicted home range values, respectively), we suggest that tamarins' important role as seed dispersers in distinct forest fragments (the environmental contexts) is mainly driven by its emerging daily movement routine, rather than the forest fragment characteristics (shape and size). Thus, the events guiding their daily routine should be further investigated. Meanwhile, the resource distribution affected only slightly the seed aggregation, but not the SDD, as usually suggested in the literature. Future work should control for the movement scaling of tamarins, such as step length, turning angles and home range overlap between groups in given fragments in order to use the model in more predictive ways.

5. GENERAL DISCUSSION

Building from empirical data, here I identified a set of possible rules that might be or -much more importantly – might not be determining space use and seed dispersal by black lion tamarins (Chapter 1). Afterwards, I implemented these rules, other heuristics, and qualitative patterns to an agent-based model (ABM) able to predict most of movement and seed dispersal patterns of our interest (Chapter 2). Finally, I generated theoretical forest fragments to understand the effect of fragment size, shape, and resource distribution (Chapter 3), finding that mostly tamarin daily path length (DPL) and movement rate (MR) but not forest size or shape are the main predictors of SDD. The degree of resource aggregation, namely the distance between fruiting trees, emerged as much less influent on seed shadows than expected, affecting only the seed aggregation. Overall, we show that black lion tamarins vary in response to fragment size, shape, and resource distributions (the environmental context). In the following paragraphs, I make a general account on how this study has contributed to a general understanding of the seed dispersal processes, in particular the spatial result of it – the seed shadow. Given the difficulty to work with this elusive species, we expect this publication to stimulate well designed and framed ecological studies and we hope it represents a good contribution on primate ecology.

The recent conceptual review of movement ABMs of Potts & Börger (2022) contextualize these models in three generating processes: mutual avoidance, central place attraction and resource attraction. Notably, the model here developed only considers the last one, which is enough for predicting most patterns, albeit not on the continuous, more “pristine” forest. The further implementations of rules which represent these other two processes, namely rules related to the territorial behavior and territorial border patrolling of black lion tamarins, might reveal which of these three generating processes are indeed required. Overall, though, it seems that processes other than a simple heuristic of moving towards resources in a Euclidian world coupled with a homoeostasis/energy sub model is enough to reproduce complex patterns in nature, such as the movement and seed dispersal patterns of an arboreal frugivore.

Hereon, I frame the developed model into the phenomenological-mechanistic spectrum (GALLAGHER et al., 2021). The recent review of Morales & López (2022) puts in perspective the problem of implementing the mechanisms guiding movement and seed dispersal (previously discussed by Cousens et al., 2010). Our resultant model is phenomenological (and less mechanistic) in some extent because we “forced” the emergence of some patterns, for example the home range size (through the placement of known resources in predicted home ranges) and the mean travel velocity. As Matthias Spangenberg cited, it is similar to state that a lion moves with mean velocity of 0 m and turning angles of 360° and proceed to put a GPS collar into a lion trapped in a cage. This might sound too tough as I struggled to search for other mechanistic rules that could make the travel velocity to emerge. Although this statement bears some true, similarly to other (few) research that can see these small level patterns (step length and turning angles) emerge (RANC et al. 2020; VISSAT et al. 2023), at least I implemented a correlated random walk (by restricting the turning angle range) with a mean velocity, and I did not sample from an empirical distribution (the so-called step models), which might render pure stochastic variation that does not exist, and which the use of was criticized earlier (BIALOZYT et al. 2014).

More recently, though, Sengupta et al. (2018) have shown how the use of big data and new machine learning technologies could help us to find more essential, mechanistic rules that can be implemented in an ABM. This is further complemented by the recent launch of the *abmAnimalMovement* package in R (MARSHALL; DUTHIE, 2022) which will make access to these simulation models and “rule-hunting” and how to match the different fields and expertise of movement ecologists, modelers, GIS and GPS related technologies much easier. In accordance to reaching the so-called generality discussed in the introduction, Malishev et al. (2020) reviewed the ABM literature based on energy sub models, rendering further insights on fine-scale processes such as foraging, competition, risk perception and memory guided by bottom-up decisions related to energy intake and expenditure.

A main difference between the model here developed and other recent models should be stated, though. Different from other models, our tamarin model can be parameterized with data collected in small time windows (> 3 days), not depending on the more elaborated and less tangible (or hardly conceptualized) parameters such as the “tendency to Levy Walk” (GAVRILITCHENKO et al., 2022) or transition matrices (MARSHAL & DUTTIE, 2022), which are all – in some way – phenomenological (see Discussion in Vissat et al. 2023). Further, these models are frequently tested for only one group, environmental contexts, or regions, thus relying on parameters that are highly site-dependent (and therefore *ad-hoc*) and/or on knowing the emerging patterns beforehand (which goes against the philosophy of ABMs, which are built from ground up). In turn, our model builds up into the generality of movement and seed dispersal patterns. For instance, one could further understand the scaling of movement patterns (such as step lengths and turning angles) as I did in Chapter 3 in order to use the model in more predictable ways. With this understanding in hand, one could parameterize the model to predict seed dispersal patterns in all fragments that exist throughout the black lion tamarin geographic distribution. Lastly, with recent estimates of energy intake and energy expenditure, the last one passive of being acquired by biologging, it is likely that the models which represent unitary relationships and interactions, i.e., the ones building on elementary bottom-up interactions, are closer to represent the processes involved and thus, able to attain generality.

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.

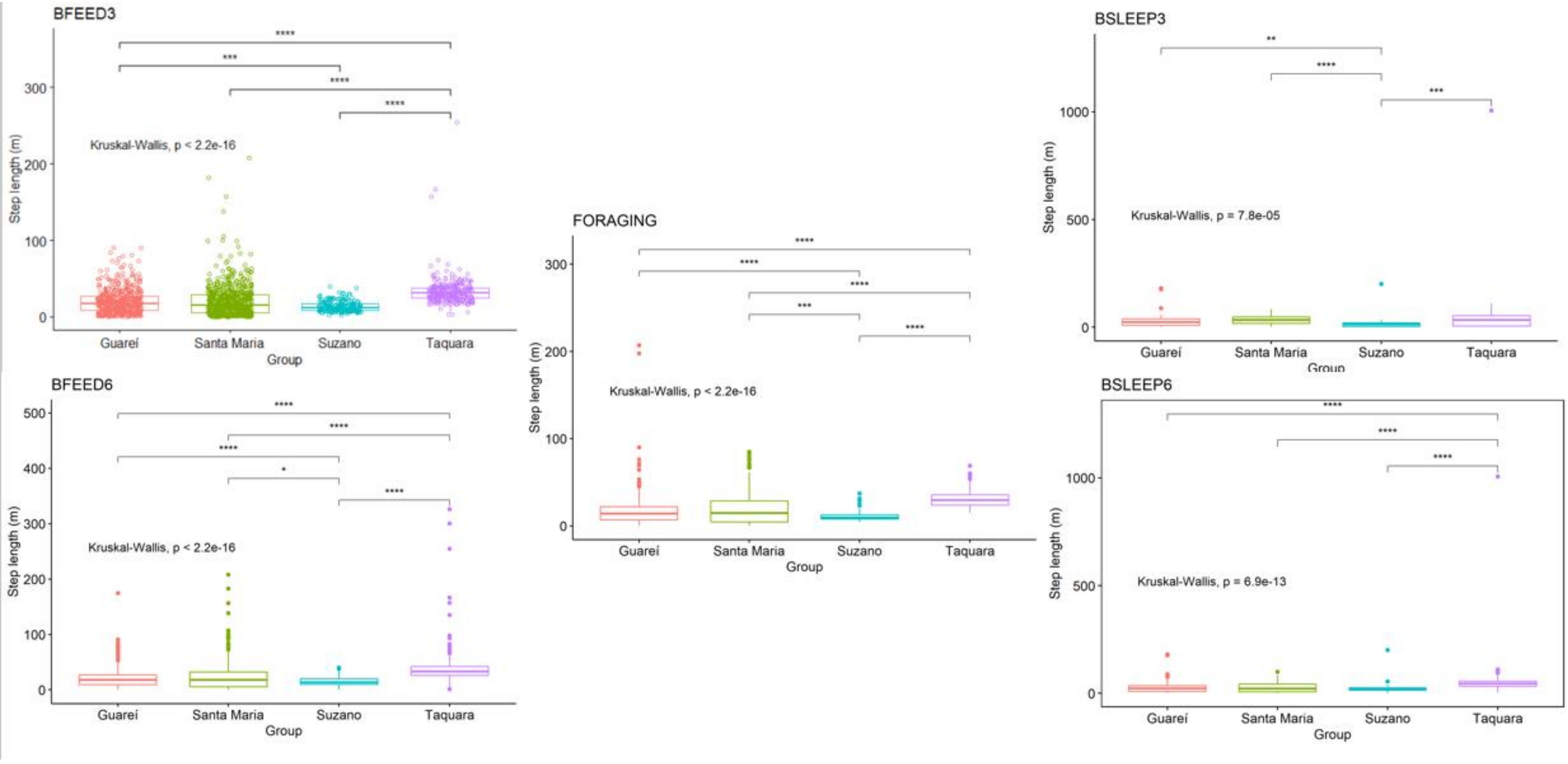
WILLIGHAGEN, E.; BALLINGS, M. **genalg: R Based Genetic Algorithm**. , 2022.

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

8. ANEXOS

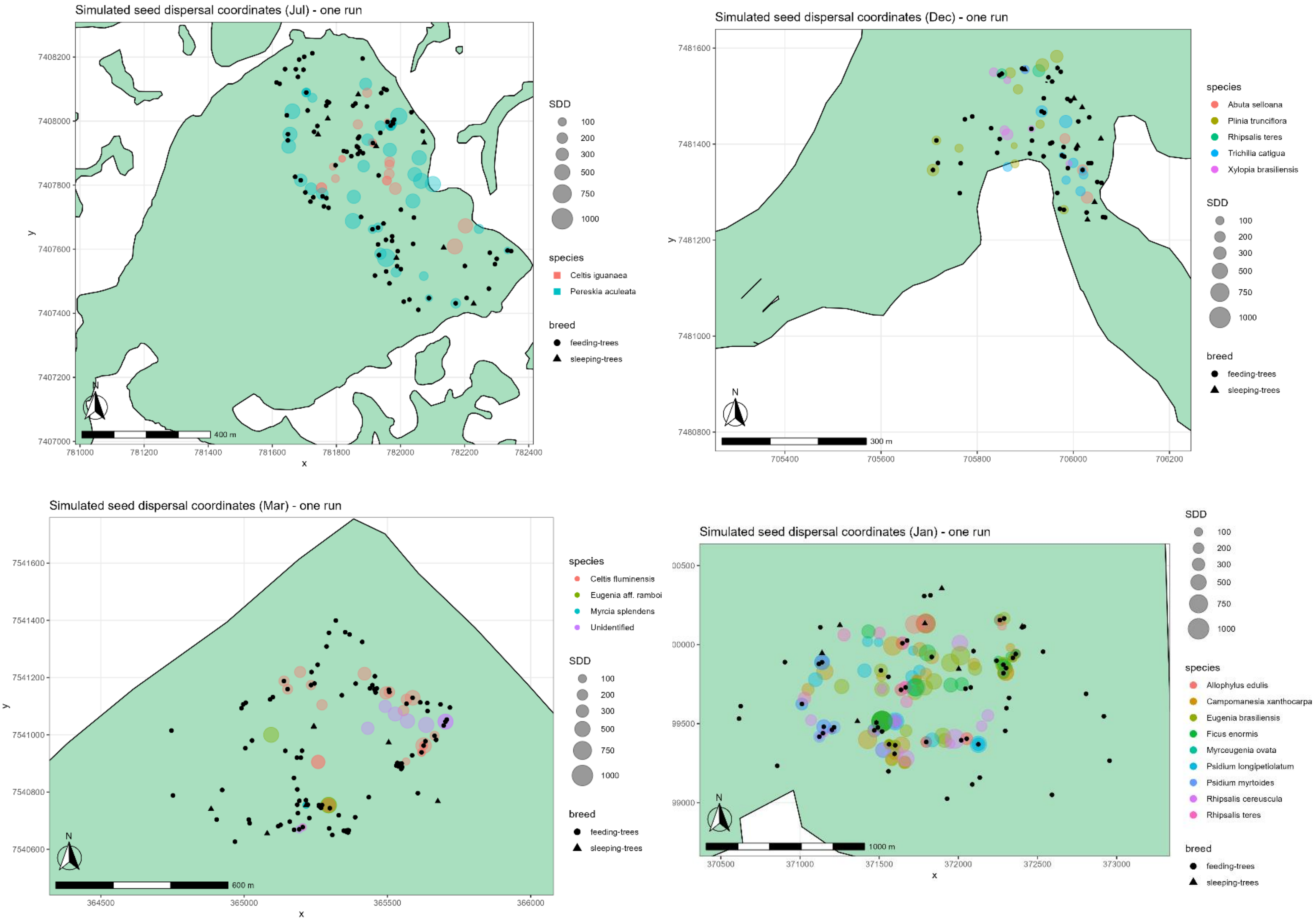
8.1 ANEXO 1

Figure A1 - Post-hoc tests of step lengths (velocity) of four groups of black lion tamarins inhabiting distinct forest fragments (environmental contexts). Asterisks denotes different levels of significance: *almost significant (0.05 ≤ p ≤ 0.1); ** significant (p ≤ 0.05); *** very significant (p ≤ 0.01); **** highly significant (p ≤ 0.001). Results of Kruskall-Wallis shown inset.



8.2 ANEXO 2

Figure A2.1 - Seed shadows of simulated black lion tamarins for a specific time period. See Table 2 for used parameters. Top left: small sized fragment; Bottom left: medium sized fragment; Top right: riparian forest; Bottom right: continuous forest.



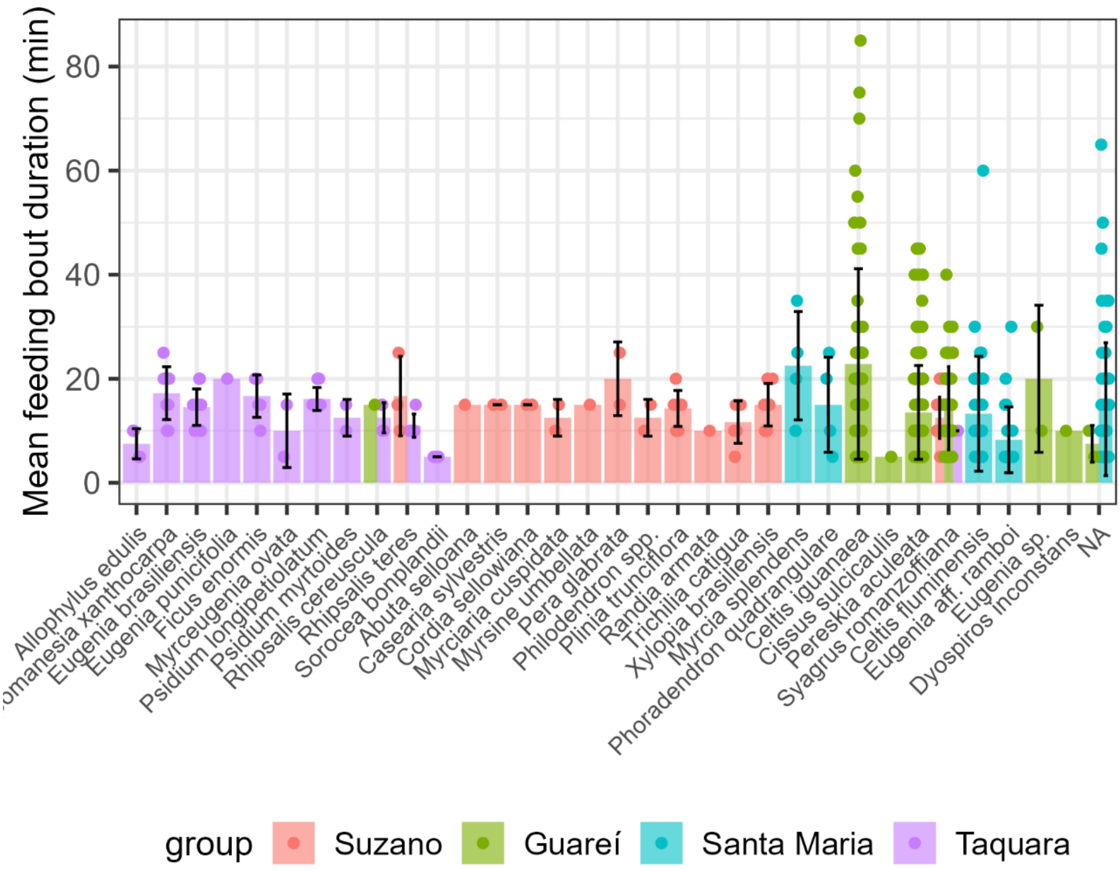


Figure A2 - Feeding bout parameterization for four simulated groups of black lion tamarins (riparian, small, medium, and continuous forest, respectively). Each timestep is equivalent to 5 minutes (the time interval between group behavior scans). These values were used for parameterization of feeding bouts. Error bar = sd.

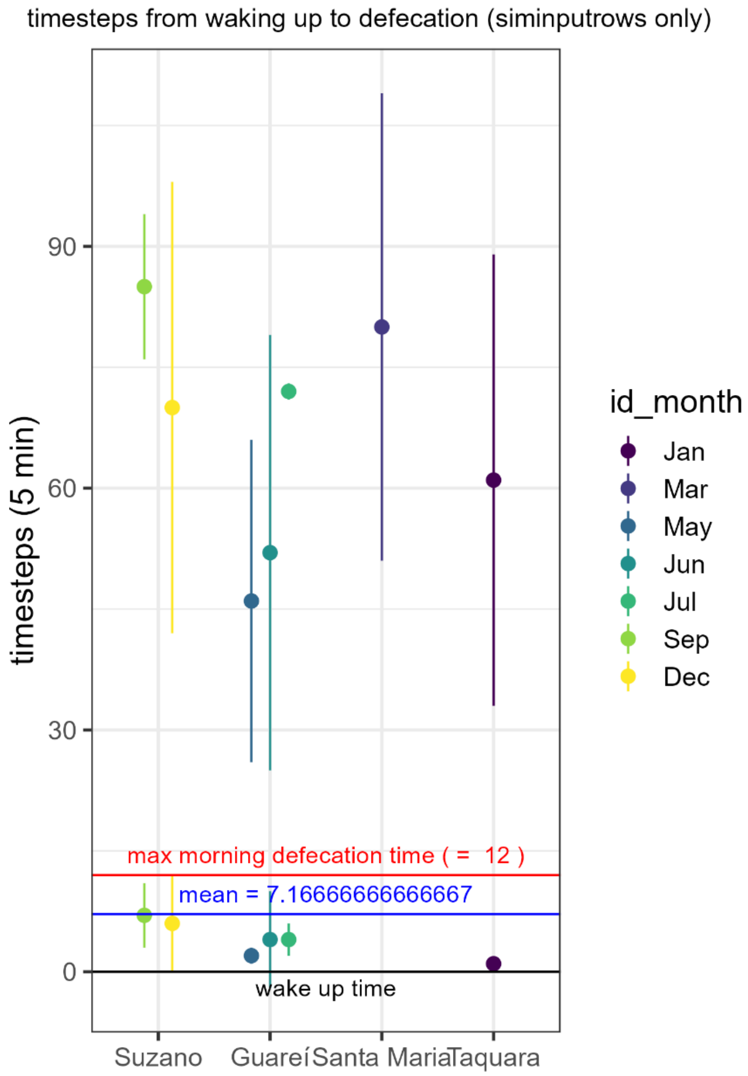


Figure A2.3 - Gut transit times parameterization of four simulated groups of black lion tamarins (riparian, small, medium, and continuous forest, respectively). Red, blue and black lines represent the max, mean and minimum values, respectively, for *next day* defecations (*morning-defecation* procedure).

Text A2.1. ODD Protocol

Our model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual and agent-based models (Grimm et al. 2006, 2010, 2014). Our model is implemented in NetLogo 6.2 (Wilensky 1999).

OVERVIEW

1. Purpose

The model was built with the aim of understanding behavioral and energetic responses guiding the ranging behavior and space use of black lion tamarins (*Leontopithecus chrysopygus*) and their effects on seed dispersal patterns in different fragmentation scenarios.

2. Entities, State Variables, and Scales

The model represents one tamarin group (as one super-agent), fruiting and sleeping trees (resources), seeds, and forest/non-forest patches (habitat). Only one individual is represented because tamarins are highly cohesive familiar groups. Patches are considered suitable or not according to the patch color state variable ("forest" or "matrix"). Patch size is 1 ha (Spatial grain) and does not vary between runs. Tamarin groups range through these patches while having the following state variables: *energy*, *behavior*, *action*, *travel-mode*, *tree-target*, *feeding-species-time* and *tree-memory-list*. Feeding and sleeping trees have state variable *tree-species*. Seeds have the state variables *seed-species* and *mother-tree*.

Patches together built into four different forest fragments ("environmental contexts") of varying sizes and shapes (spatial extent) used by four groups of real tamarins, and this forest is determined by loading a shapefile of the forest fragment. The matrix poses no unique effect for simplifying purposes. Tamarins do not leave the forest as they are highly forest dependent.

Each timestep represents 5 minutes to match empirical behavioral data collected on the tamarins in four distinct localities. Simulations run for a variable number of days (3-8, matching the empirical data collection time frame). Each day lasts 107 to 142 timesteps.

3. Process Overview and Scheduling

Agents start the day in a random sleeping tree. The movement generating process of the model is the homeostasis (Bialozyt et al. 2014). Thus, behaviors of the agents are decided based on its energy levels. Two levels are present, representing agent's internal state (Nathan et al. 2008): *energy_level_1* and *energy_level_2*, which corresponds roughly as "hungry" and "satiated" when agents have the *energy* below and above these levels, respectively.

Based on its energy level and time of the day (**Figure 1**) the agents will, at each timestep, either a) travel, b) consume fruits, c) forage for insects, d) rest or e) search for a sleeping tree. If tamarins travel or rest, they lose energy (*energy-loss-traveling* and *energy-loss-resting*). When tamarins feed or forage, they gain energy (*energy-from-fruits* and *energy-from-prey*). While traveling to known resources to feed and maintain homeostasis, tamarins defecate seeds of the consumed trees and lianas species based on empirical gut transit times.

During the course of one day (107 to 142 timesteps, corresponding to 8.91 and 11.83 hours, which are, respectively, the short and longest activity period registered in the field) and with low energy (energy < energy-level-1), the agent exhibits four main behaviors (red boxes in **Figure 1**). When hungry, it travels (a) to the closest feeding tree (short-distance *target-tree*) and consumes its fruits (b) when in proximity (representing the frugivory process) for a period in timesteps (defined by *feeding-species-time*). At each traveling step, tamarins have the possibility of foraging (c) while traveling defined by the slider *p_foraging_while_traveling* (empirically estimated by p_foraging/(p_foraging + p_traveling from empirical data), which roughly represents how much time was spent foraging mainly for insects.

When energy > energy-level-2, tamarins either rest (d) if it is midday (48 > timestep > 68) or travel (a) to a long-distance *target-tree*, also with the possibility of foraging (c). When daytime reaches the 90% of the estimated day duration (107 to 142 timesteps), tamarins select the closest sleeping tree and travel (a) to it for the number of necessary steps. At each movement step (travel or foraging), tamarins use constant speed (empirically estimated) and orient themselves to their *target-tree*. A random angle limited to the *max-random-angle* of each of these behaviors is drawn in order to generate stochasticity in movement.

At the end of each timestep, two sub models are executed: 1) the agents will defecate seeds according to *gut-transit-time* parameter (*defecation* procedure, see ***Seed dispersal*** **sub model**) and 2) they will take out the visited feeding tree from the subset of trees that they have visited (*memory-list*) and put it back in the list of potential feeding trees according to the *step_revisit* parameter (*forget-trees* procedure). Furthermore, a secondary function does the same for the trees in the vicinity (defined by the *visual* parameter, *forget-trees-in-radii* procedure, see ***Memory*** **sub model**). These procedures altogether represent resource monitoring and memory. A common characteristic of primates is to defecate in the mornings as soon as they leave the sleeping site. For these occasions, we implemented the *morning-defecation* procedure (see Seed dispersal sub model).

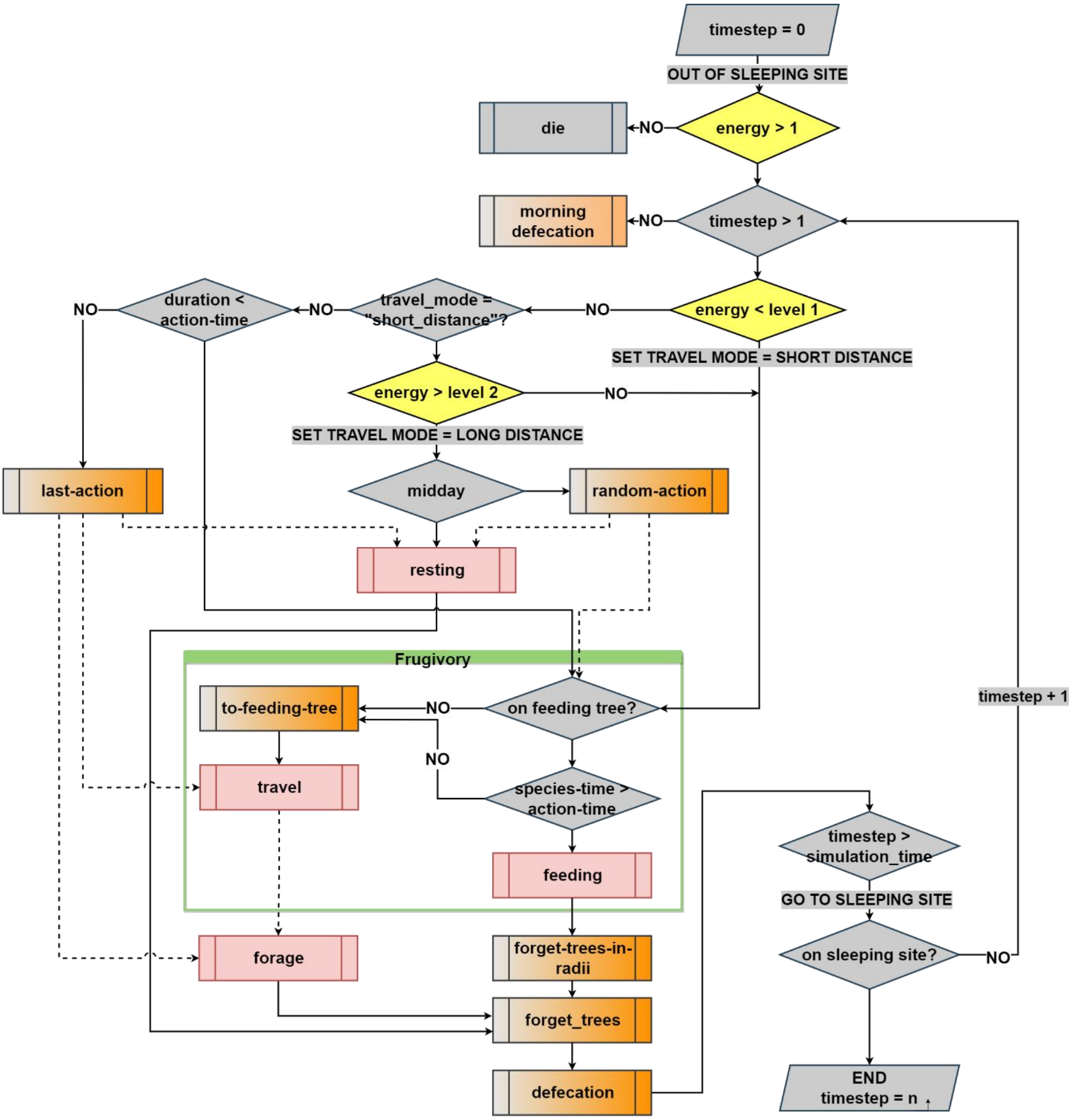


Figure 1 - Model overview and schedule. This flowchart represents the order in which the agents execute each procedure and behavior activity according to their homeostasis and day duration. Yellow diamonds represent the energy levels, red boxes represent the main behaviores exhibited by the agents, orange boxes represent procedures, and grey diamonds represent the model scheduling conditions. When arrows point downwards, it means that the condition was met ("YES"), while when it points sidewards, it means the condition was not met ("NO").

DESIGN CONCEPTS

1. Basic principles

The model was built with the aim of understanding the processes affecting seed dispersal patterns of black lion tamarins in different forest fragments. Constructed on a previous model on primate seed dispersal (Bialozyt et al. 2014), the present model implements new behavioral and resource-related movement. Some models in the literature have addressed similar questions (Pegman, Perry, and Clout 2017; Nield et al. 2020), but only on the landscape level or to very specific conditions or groups (Gazagne et al. 2022). Having a model for forest specialists with huge behavioral flexibility presents a new opportunity for understanding the processes linked to the patch level responses of frugivores. We built this model for first validating such variable emerging phenomena (seed dispersal) and its causal process: the movement.

2. Emergence

The truly emergent phenomenon in the model is the pattern of seed dispersal. The agent patterns of movement, ranging and foraging are highly variable in nature and emerge from multiple processes, which we are not completely aware of. Thus, we use empirical data to parameterize the agents' movement patterns.

We lack one process in our model that has been proving very important in defining home range size and ranging behavior (Bury et al. *in prep*.): territoriality. We circumvent the lack of this process by restricting the home range of the agents by making them able to move only to feeding and sleeping trees that were observed as being used. Thus, tamarins usually do not use the areas out of the Minimum Convex Polygon (MCP) of their resources.

One of the main variations on the model output is related to the agent response to the local resources (feeding trees) according to its energy. The implemented behavior rules, representing the hypothesis of movement drivers (not completely known), then generates the seed dispersal patterns.

3. Adaptation

Agents select the closest feeding-tree when energy < level 1 (short-distance target) and a random feeding tree when energy > level 2 (long-distance target). The target trees are selected from a memory-list (that modulates resource monitoring processes). Thus, no agent decision is involved, and agents do not rank alternatives, being the tree selection process derived from behavioral and energetic hypotheses.

4. Objectives

Agents' main objective is to keep homeostasis, and for this, they travel from feeding tree to feeding tree. They do this by getting "hungry" when energy < level 1. This energy measure does not represent real energy expenditure estimates and serves as a proxy to check which hypotheses of movement are unlikely through model implementation.

5. Learning

Learning is not implemented.

6. Prediction

Agents have no predictive capacities in this model, they only react to current state variables.

7. Sensing

Agents are assumed to know all the potential resources in their home range. They have complete awareness of their energy and select new target trees based on it. The only environmental variable they sense is if their patch-ahead is forest or matrix, thus avoiding the last.

8. Interaction

Agents interact directly with the feeding trees within their home range and within the forest fragment. No interaction with neighboring tamarin groups is implemented.

9. Stochasticity

Agents start in a random sleeping tree. During the routine loop (Figure 1), the *duration* parameter is used as a maximum number from where a random number is drawn, adding stochasticity to how long the agents spend repeating other behaviors than feeding and traveling (resting and foraging).

10. Collectives

The model includes no collectives. One agent represents one tamarin social group, which can vary from 2 to 8 individuals. As tamarins are familiar groups that travel in a highly cohesive manner, we model only one super-agent.

11. Observation

Observations are made on the agent level (which represents one social group). Four outputs are recorded *post-hoc* (after simulation finishes):

1) Home range: estimated by kernel methods (50 and 95%, representing core area and home range size) used during the data collection timeframe (from 3 to 8 days).
2) Daily Path Length (DPL): The sum of the realized step lengths for each simulation day. This value is based on the sum of realized step lengths, which is equal to the *travel_speed* (i.e., agents have constant speed) or, when tamarins are very close to targets, to smaller steps. All distances are calculated in patches and, afterwards, multiplied by *scale-size* (the spatial grain of 10 x 10 m).

3) Movement rate (MR) and Path Twisting (PT): these movement variables have been shown to be important predictors of SDD (Fuzessy et al. 2017). The MR is roughly equivalent to the distance traveled per hour, being usually correlated with DPL, but it is dependent on the amount of time spent traveling. The path twisting describes how long is the DPL in relation to the home range (or monthly area used), being thus a proxy of how sinuous the agent's daily routes are. These variables are estimated in the end of each run because it depends on the values of DPL for the simulated period.

4) Activity budget: the proportion of the four behaviors (travel, frugivory, foraging and resting). This variable is recorded as an agent list on each simulation day.

5) Seed dispersal distance and aggregation: These variables are calculated by taking each defecated seed and calculating its distance to the mother-tree and with a Clark-Evans test, respectively. The Clark-Evans test gives a value of R based on the nearest neighbor distance (NN) between point events, where R=1 suggests a random pattern, R < 1 suggests clumping/aggregation and R>1 suggests ordering/uniform pattern.

DETAILS

12. Initialization

Each of the three landscapes are settled based on a shapefile that draws the forest fragment where the tamarin groups live in São Paulo State, Brazil, and an ASCII (raster) file that defines the resolution and cell size. All 10 x 10 m patches (also called "cells") inside of this polygon are defined as "habitat", while the patches outside of it are defined as "matrix" and the patches falling on the fragment border are defined as "border". Resources (feeding and sleeping trees) are created based on a second shapefile of empirical tree coordinates (UTM) collected on each simulated time frame (each time frame is a 3-8 sequential days period in the same month). Then, the tamarin agent (n = 1) is randomly assigned to a sleeping tree before the simulation starts. The initialization is aimed at being generic to multiple field sites and tamarin groups. Only one type of agent is created during runs: the defecated seeds. This is described in the *Seed dispersal sub model.*

13. Input data

Two input files are used in the model: one .asc file defining the forest fragment boundaries and a .shp file defining tree point resources. Tree resources were assessed during multiple field expeditions from 2015 to 2019 (*unpublished data*), while BLTs were followed by foot. Furthermore, the agent movement sub model is parameterized with empirical velocities and turning angles (see Movement sub model). The time tamarins spend feeding in each tree species is also parameterized (see Seed dispersal sub model).

14. Sub models

Energy and movement sub model

The agents decide about which trees to move based on its own energy and distance to trees. They choose the closest feeding-tree while with energy < level 1 (“hungry”), and a random “long-distance” tree when energy > level 2 (“satiated”). At each timestep, they direct themselves to the target tree and travel to the short-distance targets up to the moment they reach it and feed on it, and they travel to the long-distance targets up to the timestep they reach it, or they energy gets below level 1, then they search for the closest feeding tree. While traveling, tamarins might forage (depending on the probability *p-foraging-while-traveling*). All steps are done with constant speed (step length) and with a maximum random angle uniform distribution soon after facing the tree target. If at the specified timestep they decided to “forage”, they randomly turn *turn_ang_75q_forage* and then walk the distance *step_length_forage*; If they are decided to “travel”, they randomly turn *turn_ang_75q_travel* and then they walk the distance *step_length_travel*.

When *simulation-time* reaches 90% of the *simulation-time*, they stop feeding and go to the closest sleeping tree for n timesteps (up to the moment then reach it).

In certain situations (especially in Suzano and Guareí), tamarins might face the problem of having matrix patches between themselves and the tree target. When this happens, another type of navigation enters in place, which is called by the procedure *avoid-matrix*. The agent looks at all patches around itself (in a radius of five patches) and selects the patch that is the closest to its target. Then, it moves *step_length_travel* to its direction up to the point that its path to its target does not contain any matrix patches.

Memory sub model

At the end of each timestep, the agent "memory" gets modulated in the following way:

1) The list of consumed trees (*tree-ate-list*) is paired with a second list (*tree-mem-list*) that counts the timesteps that have passed by since this specific tree was consumed. Each item of the *tree-mem-list* grows + 1 each timestep (with the auxiliary list *tree-add-list*), and when it reaches *step_revisit*, the feeding-tree is taken out of this list and added again to the *tree-potential-list*, the list of potential trees that can be targeted and consumed;

2) If the tamarins have fed on a specific tree, all the trees surrounding the consumed tree (defined by the *visual* parameter) are taken out from the *tree-potential-list*, thus being considered "visited" and further subjected to the same process as the consumed trees. This represents the cognitive process that this patch of resources was "visited" (but not necessarily depleted), making the agents search for other trees that are not necessarily the closest ones. The *visual* parameter is defined as the number of patches around the *target-tree*, thus giving and idea of radius (*forget-trees-in-radii* procedure);

3) If the *tree-pot-list* is smaller in size (because all trees are considered “visited” or “depleted” and are listed in the *tree-ate-list*) than (1 / *prop_trees_to_reset_memory*) of the total number of feeding trees, the *enhance_memory_list* function is called. This function takes (1 / *prop_trees_to_reset_memory*) – proportion of the initially consumed trees from the *tree-ate-list* and add them to the *tree-pot-list*, making these feeding trees “available” again. For example, if the total number of feeding trees is 30, this procedure will take place when the available number of trees (the length of tree_pot_list) reaches 14. This represents the process of avoiding revisiting recently consumed trees and is more important when the number of resources is small.

This type of memory might be described as *reference memory* instead of *working memory* (Van Moorter et al. 2009 *apud* Malishev et al. 2021) as we are not sure if the main factor driving BLT ranging patterns is energy acquisition or territory defense, or both. Thus, the aim of this submodel is to reference BLTs' home ranges. Furthermore, by taking out the roll of possible fruiting trees to visit (through *step_revisit*), we make BLTs' memory imprecise, which should be more realistic (Malishev et al. 2021) and we also simulate the process of patch depletion and high revisitation rates when resources are few (through the *enhance_memory_list* procedure).

Seed dispersal sub model

When the agents reach a target feeding-tree, they feed on it for timesteps = *species-time*, which represents the feeding bout tamarins spend in each tree species. The species-time is defined based on empirical data or in a random value of 1 to 6 if feeding bout parameterization is on or off, respectively). At each time-step, the agents consume 1 seed, which is added to the *seed-ate-list*. An auxiliar list keep track of the assigned *gut_transit_time* assigned to each seed by a Poisson distribution with mean μ estimated from empirical data.

At the end of each timestep, if timestep < 84 (representing 3 pm BRT) and if the *gut_transit_time* (the number of timesteps since fruit consumption up to seed defecation) is reached, agents will defecate *n_seeds_hatched*. If timestep ≥ 84, the seeds in the *seed-ate-list* are retained to the next day. When the next day starts, the agents defecate all seeds in the *seed-ate-list* in the previous day at timestep 1 or 2 (*morning-defecation*).

Text A2.2. Parameterization of the tamarin model with feeding bouts.

To test the effect of parameterizing the model with specific information of tamarin feeding bouts, we ran a sensitivity analysis for Guareí area (month of August) with the same parameter values bot only changed phenology “on” and “off”. The analysis showed that feeding bout parameterization does not seem to be important for explaining DPL or home range for Guareí (**Fig. A2.4**).

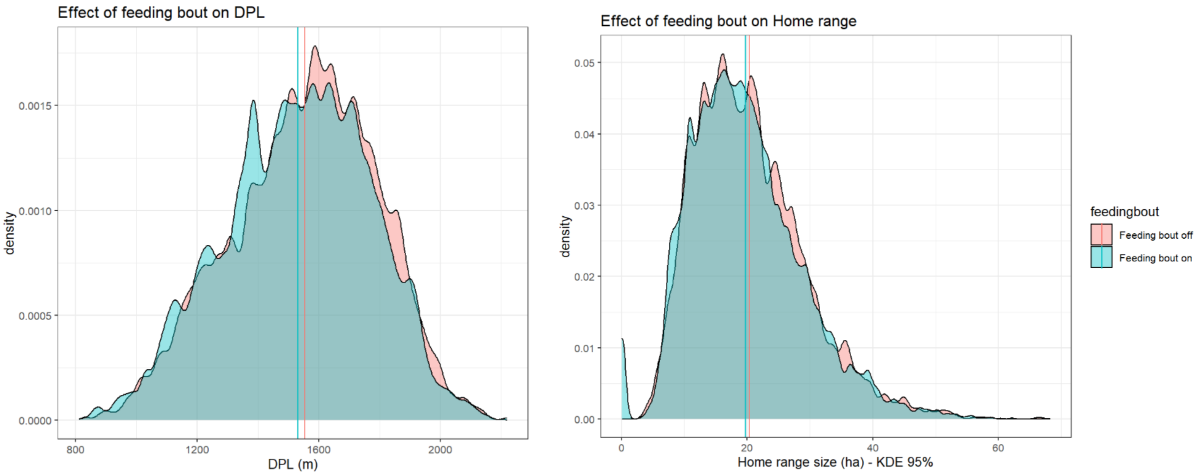
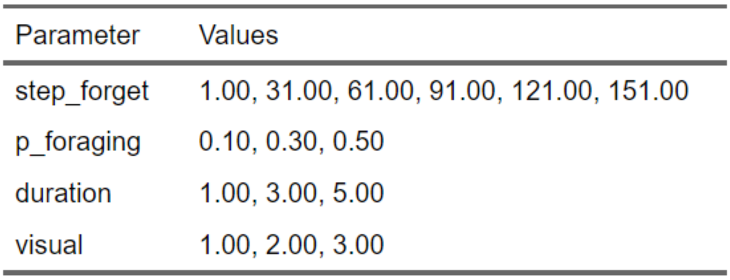


Figure A2.4 - Sensitivity analyses for testing the effect of feeding bout (time consuming each tree and liana species) parameterization for Guareí (August month).

Furthermore, we also varied four model parameters (**Table A2.1**) to estimate the effect of each parameter on the output movement emerging patterns (DPL and home range size). While runs with feeding bout on were more variable (wider quantile variation), it was not significantly different from the runs with feeding bout off (**Fig. A2.5**).

Table A2.1 - Parameters varied for sensitivity analysis. Runs were made only for Guareí (August month).



Parameter	Values
step_forget	1.00, 31.00, 61.00, 91.00, 121.00, 151.00
p_foraging	0.10, 0.30, 0.50
duration	1.00, 3.00, 5.00
visual	1.00, 2.00, 3.00

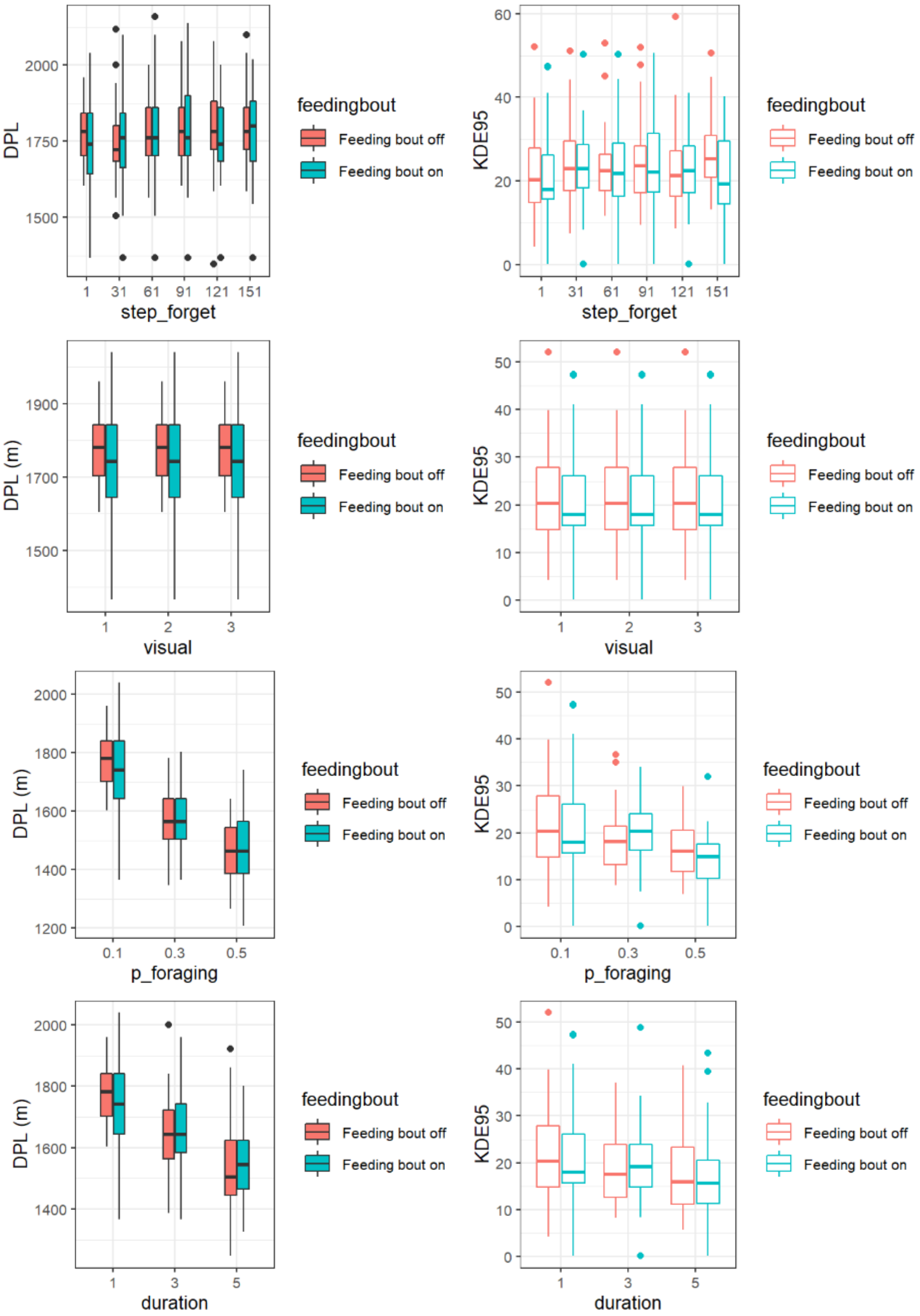


Figure A2.5 - Sensitivity analyses for testing the effect of feeding bout (time consuming each tree and liana species) parameterization on the emerging movement patterns (DPL and home range size).

8.3 ANEXO 3

Text A3. Analysis describing the relation between black lion tamarins' home range sizes, tamarin density and forest fragment size (habitat availability).

Smaller home ranges were linked to higher densities of *Leontopithecus* in previous studies (Nascimento et al 2011). Two patterns of home range usage have been suggested by Kierulff (2002) and discussed by Nascimento et al (2011): groups that use more intensively the core area and groups that use more intensively the borders, "patrolling" it. The latter has been more commonly seen in small fragments, while groups using the core more intensively have been seen in larger fragments with smaller population densities. Clearly there is a territoriality and encroachment role on home range size and use. Most of the data comes from what we call "continuous" areas, i.e., areas where the home range sizes are much smaller than the available forest, thus the response to fragmentation is more subtle. Here, we restrict our regression to ~3000 ha forest patches, which corresponds in max to the Caetetus Biological Reserve.

However, for our modeling purposes, we used a phenomenological approach to estimate the home range size based on patch size and density. We used published and unpublished data to develop a GLM which accounted for patch area and tamarin density. We fitted it with lme4 package in R (RMarkdown code available in "**Anexo3_code.pdf"**).

Although a highly phenomenological approach on modeling, this is the only possible way to predict home range sizes with available data and knowledge on *Leontopithecus* movement ecology. Other factors such as home range overlap (Pearce et al. 2013) should be considered in future studies.

Table A3.1 - Model selection.

	df	logLik	AICc	delta
glm4	5	1.2594418	10.63901	0.0000000
glm3	4	-0.4657329	10.93147	0.2924548
glm2	3	-2.1270116	11.39688	0.7578692
glm1	3	-2.2582055	11.65927	1.0202571

Table A3.2 - Best model (glm3).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.5726947	0.0758687	7.548493	0.0000002
patch_area_log	-0.0332960	0.0188532	-1.766067	0.0912599
density	0.6643348	0.3704420	1.793357	0.0866756

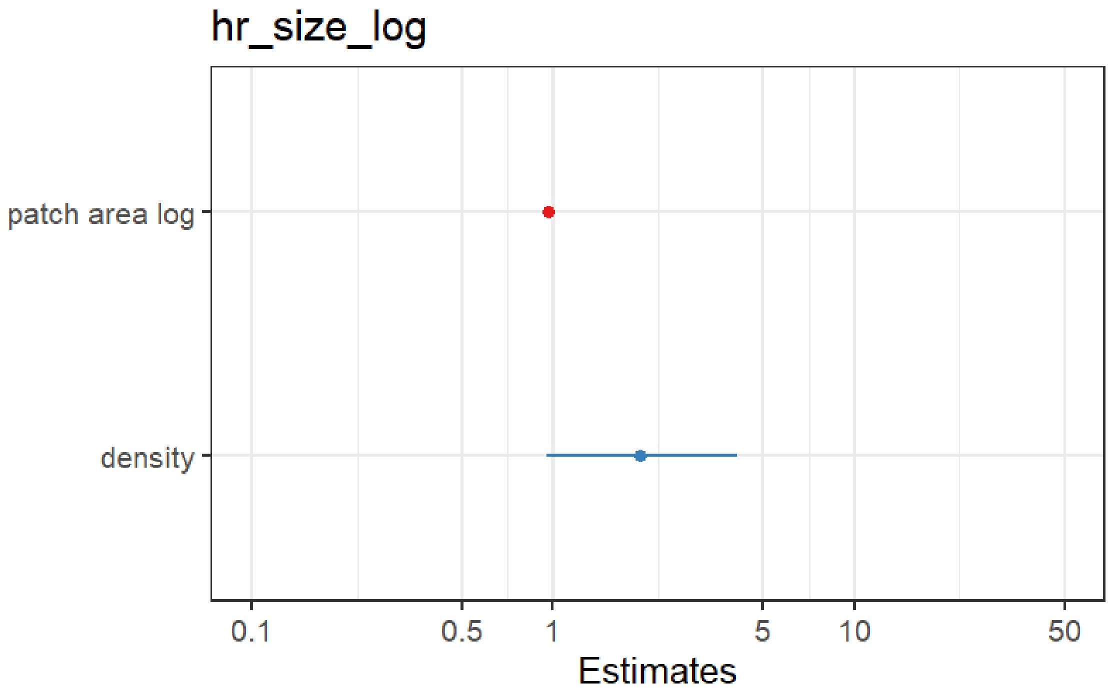


Fig A3.1. Model coefficients (glm3).

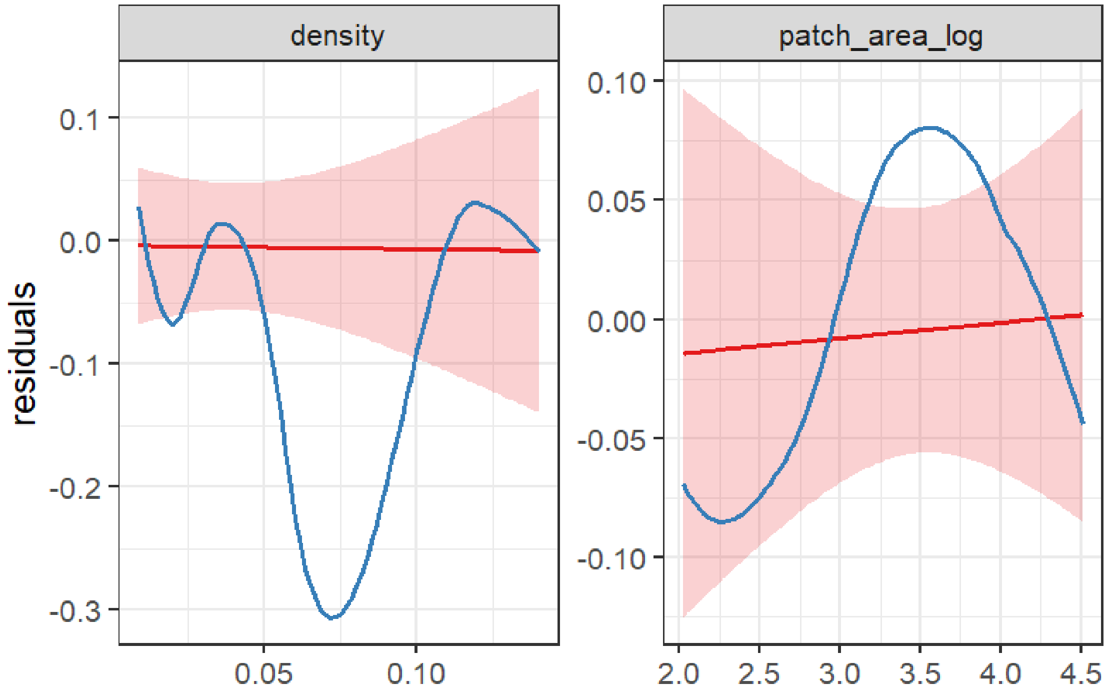


Fig A3.2. Model validation (glm3): residuals

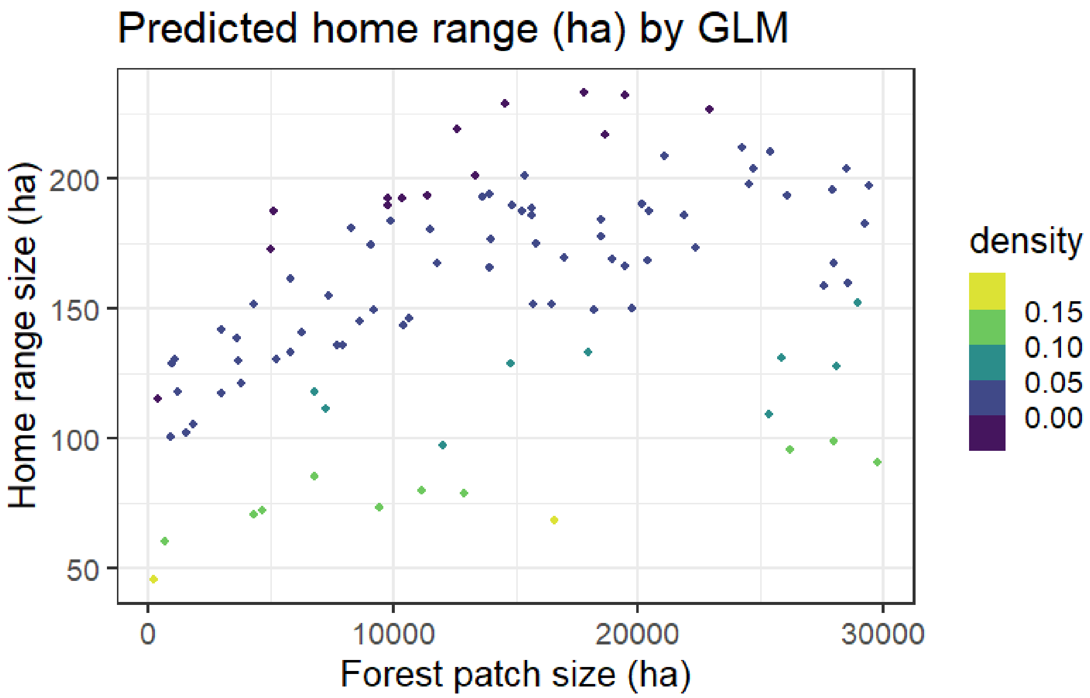


Fig A3.3. Model predictions from the best model (glm3) for *n* = 100 random fragment sizes and density values estimated with predict() function in R.

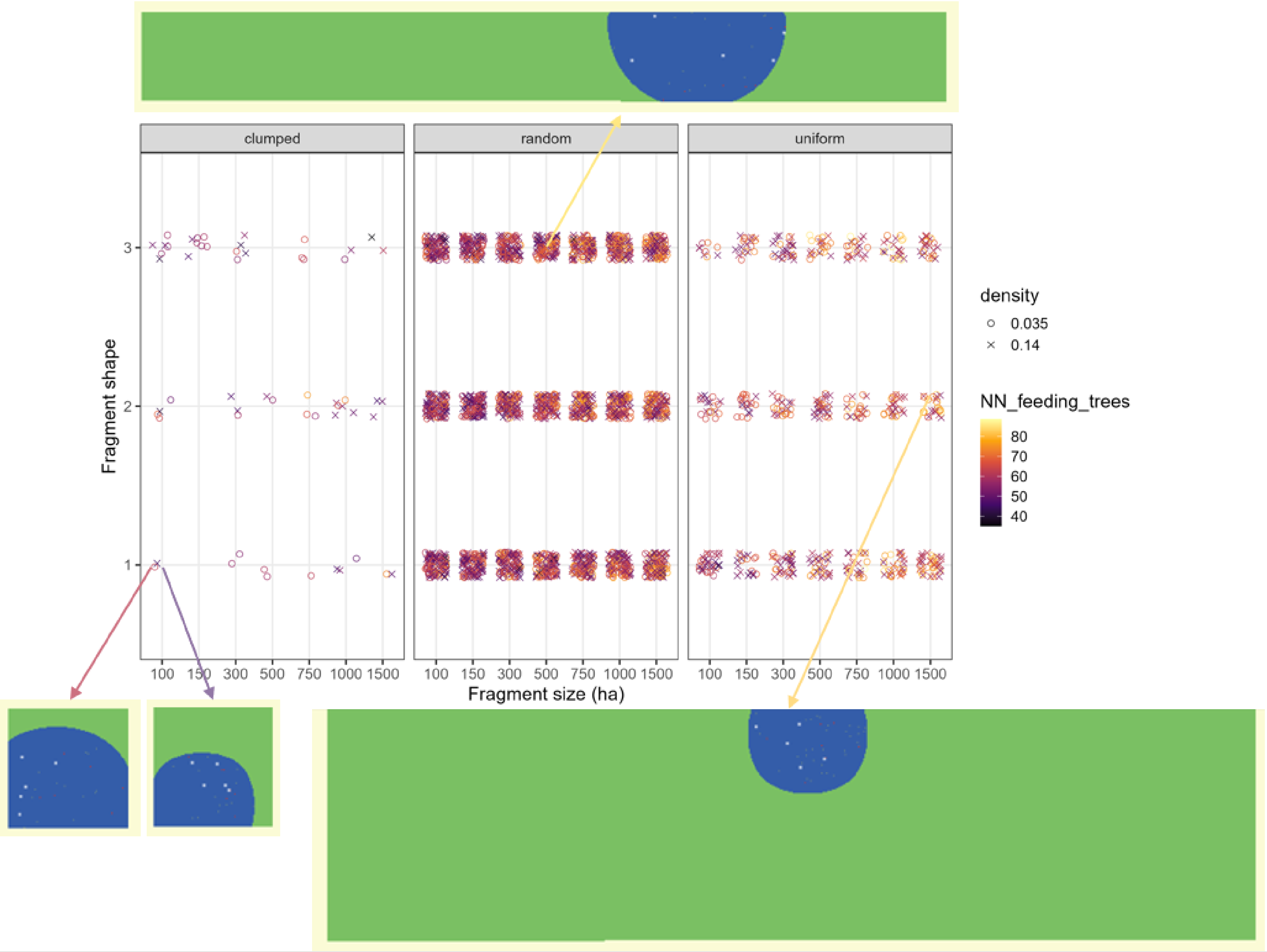


Figure SM3-1 - Example of generated forest fragments, home range sizes (jn blue) and resource distributions (red and yellow points, general pattern of feeding trees also denoted in the grey boxes). Insets are generated NetLogo worlds generated in PNG format with the *export-world* function.

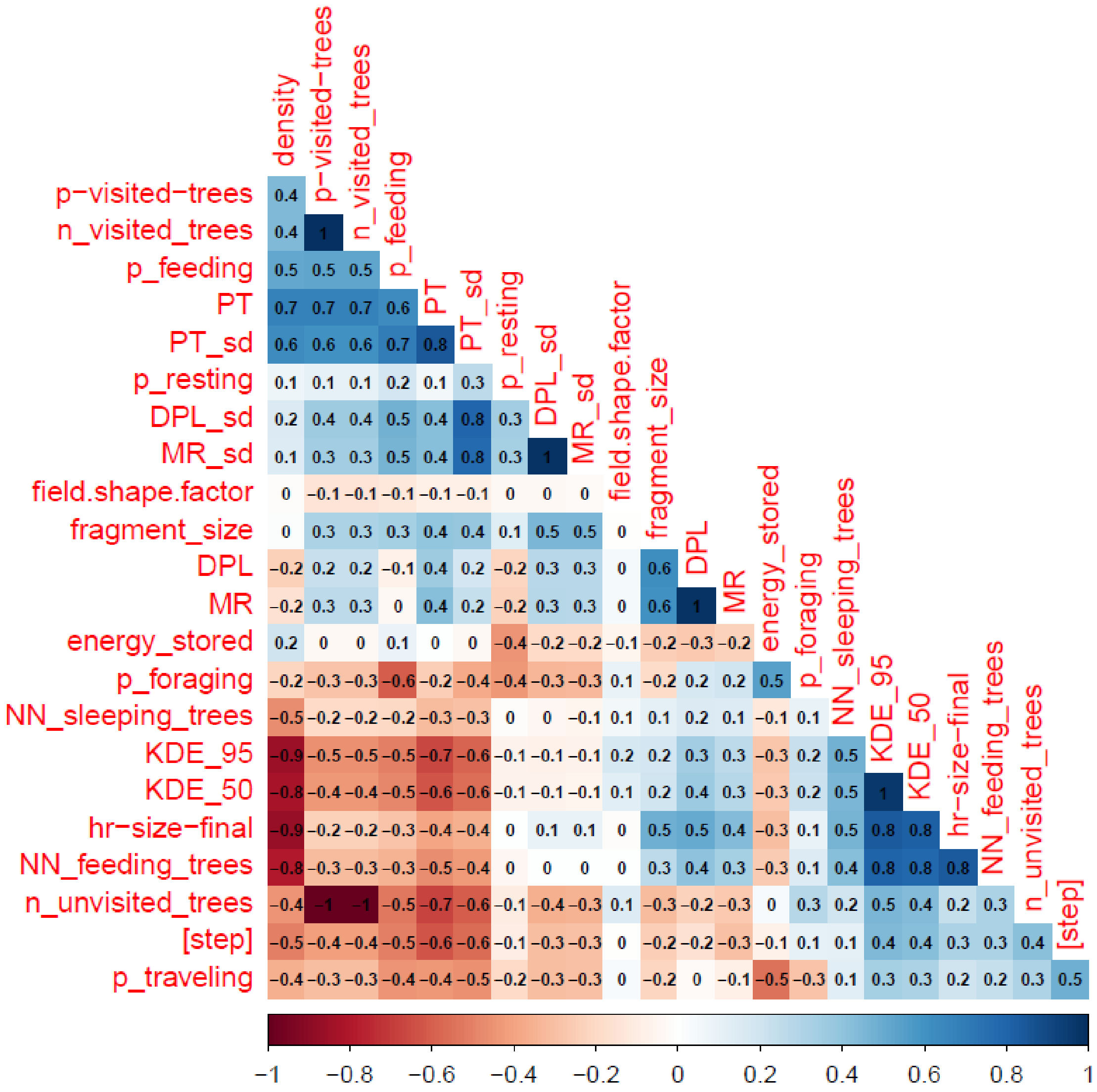


Figure SM3-2 - Correlation plot of predictors used in Experiment 1.

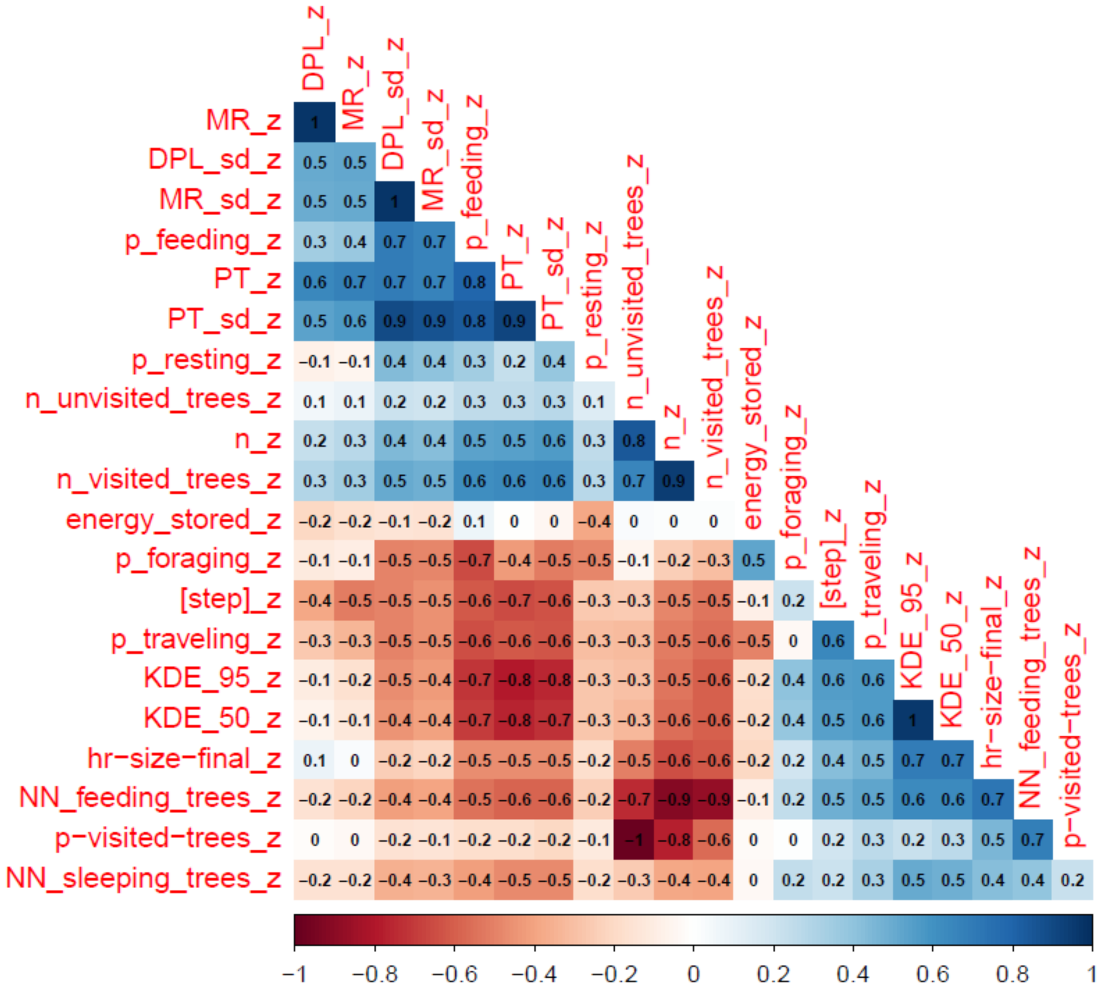


Figure SM3-3 - Correlation plot of predictors used in Experiment 2.

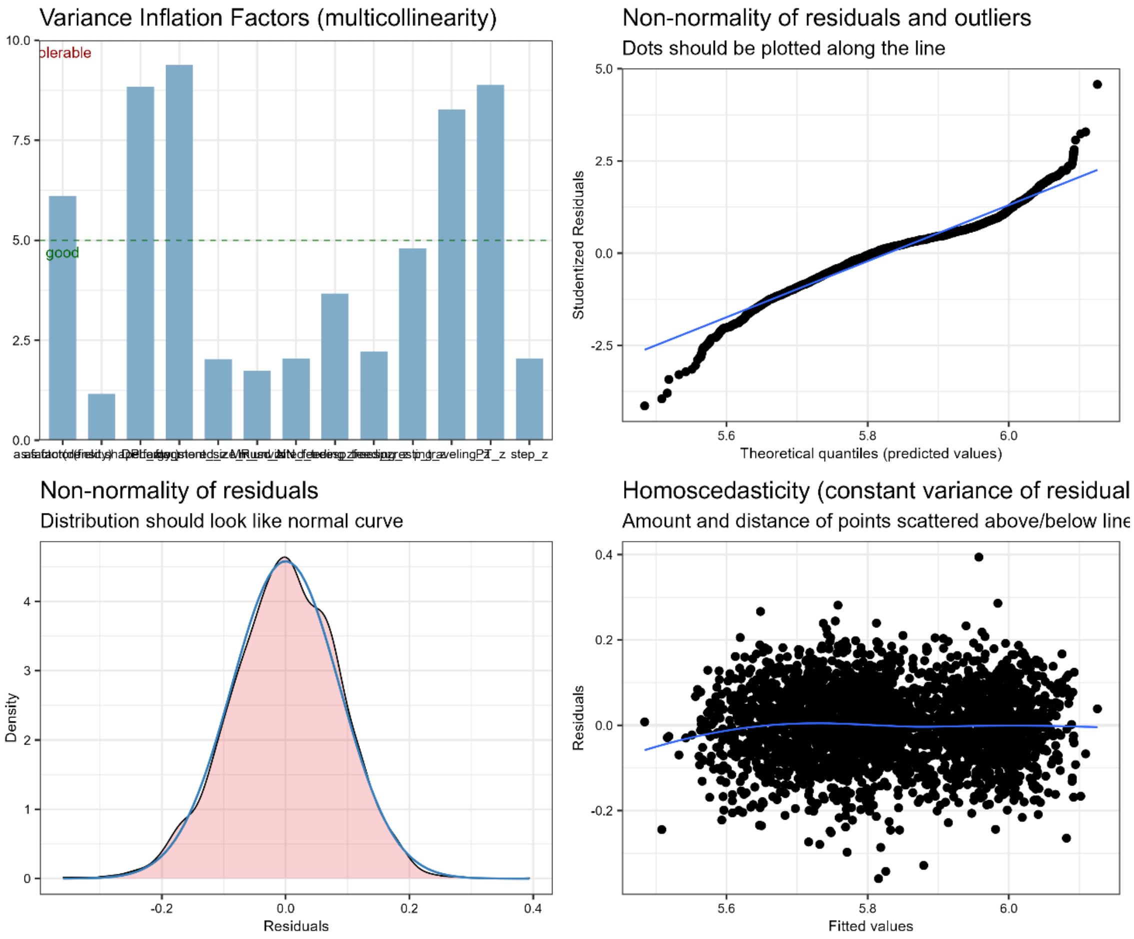


Figure SM3-4 - Model validation of the best model predicting seed dispersal distances (log-transformed) of Experiment 1.

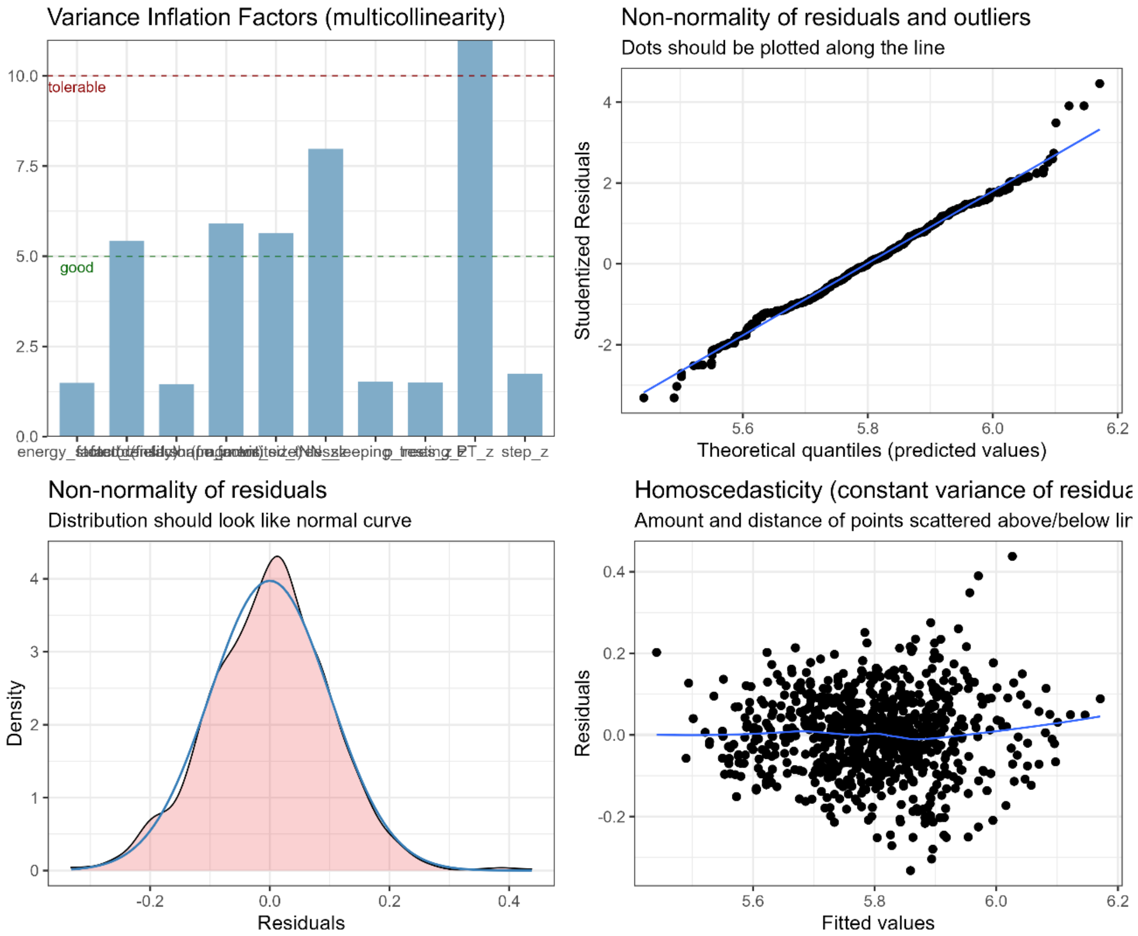


Figure SM3-5 - Model validation of the best model predicting seed dispersal aggregation (log-transformed) of Experiment 1.

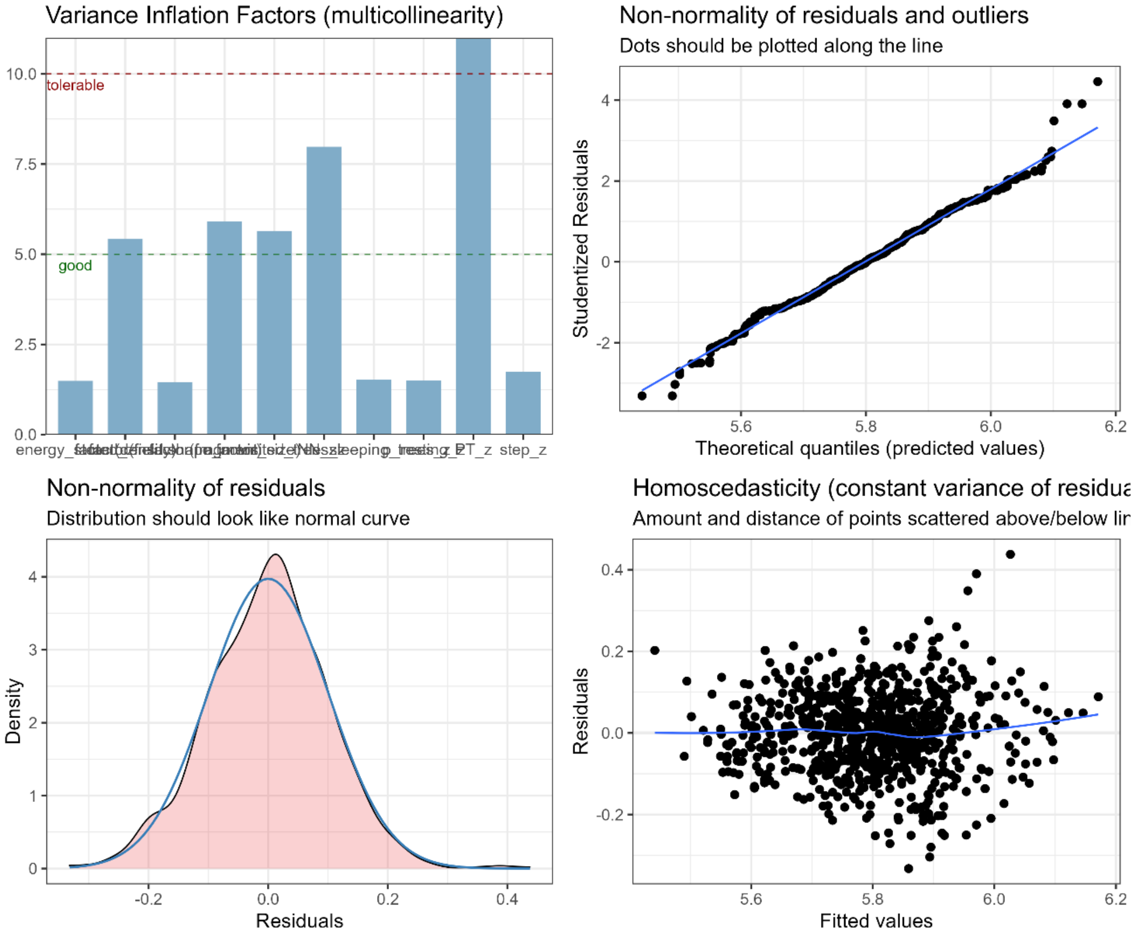


Figure SM3-6 - Model validation of the best model predicting seed dispersal distances (log-transformed) of Experiment 2.

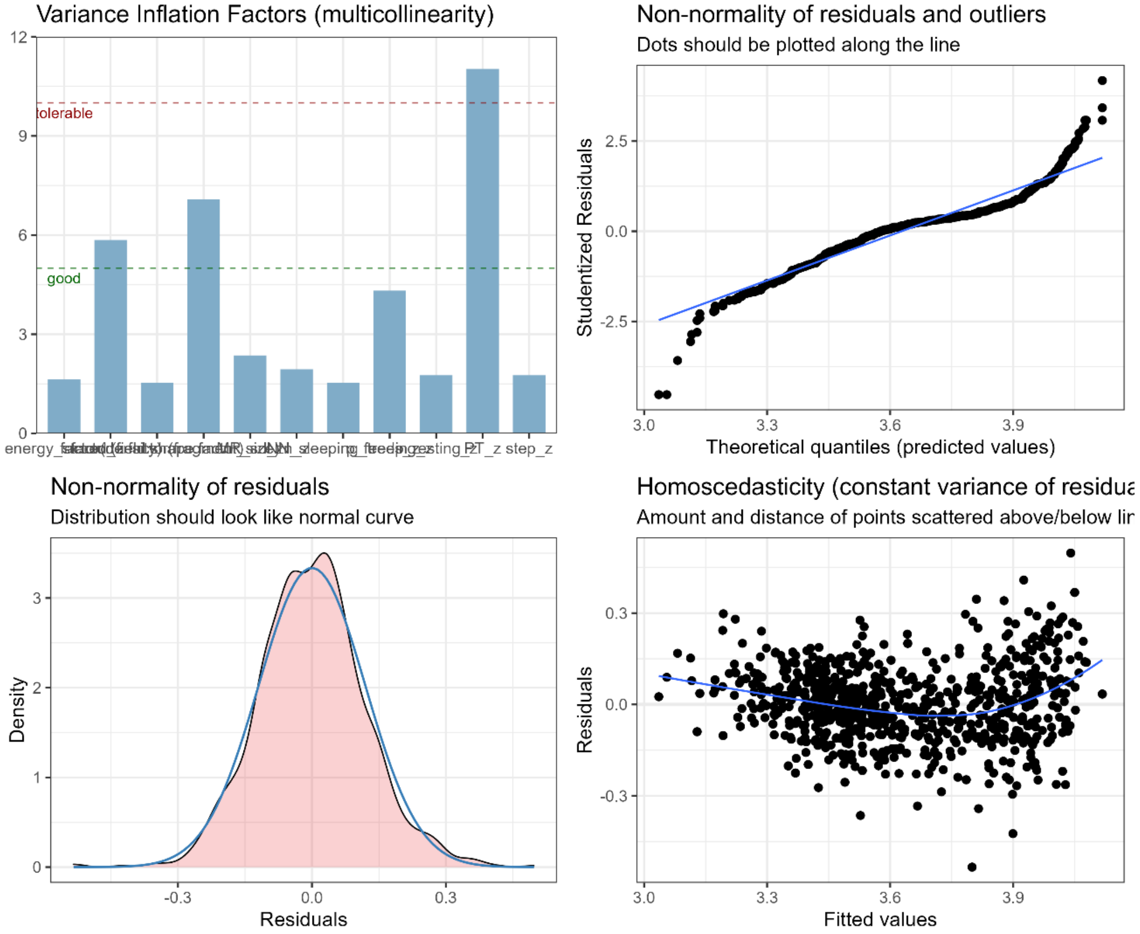


Figure SM3-7 - Model validation of the best model predicting seed dispersal aggregation (log-transformed) of Experiment 2.