

Predicting frugivore generated seed rain in different environmental contexts: a modelling approach applied to a forest specialist

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ABSTRACT

Frugivorous primates play a key role in the regeneration of tropical forests, ecosystems that have been heavily deforested and altered, by dispersing viable seeds via endozoochory. Due to their highly contingent and site-specific behavioural and ranging responses to habitat change, simulation models can help to better understand the consequences of different environmental contexts on their seed dispersal services.

Here, we extended a previously developed agent-based model (ABM), to reproduce, *in silico*, the spatially explicit seed dispersal pattern (seed rain) of an endangered Neotropical primate, the black lion tamarin (*Leontopithecus chrysopygus*). The model focused on behavioural modes, thus integrating responses to resources (fruiting trees) with motion capacity and internal energy state. We validated the model with data from four lion tamarin groups inhabiting forest fragments of different sizes: one small (100 ha), one medium-sized (515 ha), one continuous (33800 ha) and one riparian forest.

In all four forest types, our model produced realistic movement patterns as well as seed dispersal patterns generated by these lion tamarin groups, suggesting it captured most of the processes resulting in the seed rain. We compared the simulated patterns with observed patterns by comparing the used area (hectares), daily path length, activity budget, movement rate, path twisting and the defendability index (all related to movement). Simulated used areas only matched with empirical observations after the implementation of resource monitoring behaviour at the territory border. This underlines the need of specific behavioural rules based on the pattern-based modelling approach to successfully generate the observed patterns. The model slightly overestimated the seed dispersal distance (SDD) and the pattern of seed deposition was less aggregated than observed empirically, but still congruent with sampling limitations.

The model can run on a small set of parameters that can be estimated within a few days of data collection (feeding and sleeping tree coordinates and group behaviour sampling), thus having the potential to predict the seed rain from multiple groups of lion tamarins. Finally, we discussed potential improvements and encouraged replication of such modelling efforts to other forest dependent species, enabling a spatially explicit evaluation of the processes guiding the seed rain by forest specialists in different environmental contexts.

Abbreviations: ABM, Agent-based (or Individual-based) Modelling; DI, Defendability Index; DPL, Daily Path Length; GTT, Gut Transit Time; KDE, Kernel Density Estimator (either 95 % or 50 %); MI, M Index of defendability; MR, Movement Rate; POM, Pattern Oriented Modelling; PT, Path Twisting; SDD, Seed dispersal distance.

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1. Introduction

The spatial patterns of seed dispersal involve steps that are inherently dependent on the movement of dispersers (Borah and Beckman, 2022; C  rtes and Uriarte, 2013; Morales and Mor  n L  pez, 2022). While the seed shadow refers to the spatially explicit result of seed dispersal of an individual plant, the sum of seed shadows results in what is called the seed rain (Jordano, 2007). The seed rain generated by endozoochory by a single frugivore is a function of the frugivore's interaction with the environment (such as plant spatial distributions) and its inherent traits, such as handling behaviour, sociality, body size and ranging patterns. (Chapman and Russo, 2007). However, such ranging patterns are known to be affected by habitat loss, fragmentation and other anthropogenic impacts, as well as resource distributions, in hardly predictable manners (Borah and Beckman, 2022; Chaves et al., 2015; Chaves et al., 2018; C  rtes and Uriarte, 2013; Gould et al., 2020; Tucker et al., 2021). In this context, modelling emerges as a promising tool to understand how variation in primate movement patterns affects their seed dispersal services by endozoochory.

Fragmentation and habitat loss drastically impair 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-Rodr  guez and Mandujano, 2006; Serio-Silva and Rico-Gray, 2002) or even changing forest community dynamics as a whole (e.g., Chaves et al., 2018; Gonz  lez-Zamora et al., 2014, 2012). These changes mainly result in shorter seed dispersal distances (SDD) and clumped seed deposition, potentially leading to lower seed dispersal effectiveness (Schupp et al., 2010; but see Chapman and Russo, 2007). This lower effectiveness is mostly due to the diminishing probability of seed and seedling survival by distance-dependent processes such as pathogen attacks and granivores (Janzen-Connell hypothesis: Comita et al., 2014, but see Beckman et al., 2012). Indeed, fragment size has been shown to indirectly affect Neotropical primate ranging behaviours by diminishing daily displacements and home range size, thus resulting in shorter SDD (Fuzessy et al., 2017).

Progress in understanding animal-mediated seed shadows has been recently supported by an increasing number of simulation and modelling studies. In an early study providing empirical evidence linking edge effects with simulated movement behaviour in birds and, consequently, seed dispersal, Levey et al. (2005) suggested that this effect is influenced by the propensity of animals to respond to habitat edges. Similarly, a simulation study by Uriarte et al. (2011) found that, although movement and foraging behaviour changed according to matrix/habitat type (primary vs. secondary forest) and edges, 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 an approach at the forest fragment level, as some processes are driven by fragment-scale variables (Mazerolle and Villard, 1999), including fruit production, granivory and seed dispersal (Brudvig et al., 2015; Faria et al., 2023; San-Jos   et al., 2019).

Primate movements are governed primarily by their diet, but also by seasonality, according to food availability and distribution. For instance, their primary food resource may be more evenly (e.g., leaves) or patchily distributed (e.g., fruits, flowers, seeds, etc.), driving primarily folivorous primates to show Brownian-like movements (or random searches), while primarily frugivorous ones tend to show non-Brownian or L  vy-walk movement patterns (Reyna-Hurtado et al., 2018). However, primate trajectories within their home ranges are not adequately modelled by random movements. Instead, they move according to intrinsic (e.g., physiology) and extrinsic (environmental) factors (e.g., intergroup competition, predation pressure). The interactions among such factors determine how frugivores forage and consequently disperse seeds over space and time (C  rtes and Uriarte, 2013; Cousens et al., 2010; Morales et al., 2013). Furthermore, intra and interspecific responses of primates to fragmentation, habitat loss and anthropogenic disturbance are not consistent (Almeida-Rocha et al., 2017; Carretero-Pinz  n et al., 2016;

Gould et al., 2020; Kaisin et al., 2021; McLennan et al., 2017). For instance, as fragment size diminishes, more circularity in movement (resulting from high revisitation to fruiting trees), more time feeding and a decrease in home range size, amongst other effects, were found (Boyle et al., 2009; Gal  n-Acedo et al., 2023; Carretero-Pinz  n et al., 2016). Thus, developing a model of movement and seed dispersal that works in different forest fragments becomes a non-trivial task.

While a handful of models have been developed to estimate primate generated seed rain, each one with advantages and disadvantages (Chapman and 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). Previous models of primate movement and seed dispersal depend strictly on data of a single group and draws steps (lengths and angles) randomly (e.g., Raghunathan et al., 2020; Gazagne et al., 2020). Thus, they lack interfacing with the processes behind the movement decision and, therefore, they lack predictive power for other groups. 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 and Grimm, 2012; Russo et al., 2006). It is thus important that, while modelling the seed rain, models 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 or individuals of the same species in different environmental contexts). Individual or agent-based models (ABMs) can handle such context-dependent particularities. ABMs are models that simulate agents as unique and autonomous entities that interact with their peers and their environment locally, thereby allowing our understanding of collective effects of agents on the modeled system and vice-versa (Railsback and Grimm, 2012). Hence, the general advantage of ABMs is to rely on bottom-up approaches. For instance, one can model behavioural responses and the agent's internal decision or "rules" (i.e., the motion capacity of animals *sensu* Nathan et al. 2008), which are more likely to remain constant than their response to outer, variable environmental parameters. This leads to a better understanding of the underlying processes generating the aggregate patterns (such as movement, DeAngelis and Diaz, 2019; Malishev and Kramer-Schadt, 2021). Indeed, this approach has been proven to be beneficial for reproducing seed shadows and seed rain of different plant species *in silico* (Bialozyt et al., 2014; Gazagne et al., 2020; Gelmi-Candusso et al., 2019; Nield, et al., 2020; Pegman et al., 2017).

Here, we extend a previously developed ABM (Bialozyt et al., 2014) to diminish this site-dependency in two ways: by modelling movement decisions of more than a single group and by drawing steps according to each specific behaviour (thus avoiding the use of pure random steps), which we show is more robust to simulate the seed rain. We reproduce, *in silico*, the seed rain of four groups of an endangered primate, the black lion tamarin (*Leontopithecus chrysopygus*, hereon "lion tamarin"). Lion tamarins are small, arboreal, frugivorous-insectivorous, and territorial primates that inhabit the highly fragmented Atlantic Forest of the State of S  o Paulo, in southeast Brazil (Rezende et al., 2020). This Neotropical primate shows flexibility in terms of habitat use since they can be found in continuous forests to small fragments and riparian forests (Culot et al., 2015; Garbino et al., 2016). Previous analyses have shown that their movement patterns vary widely in terms of ranging (i.e., daily path length, home range size, step lengths and turning angles) and foraging patterns (i.e., revisitation to known fruiting trees, duration of feeding bouts), among others. For instance, one group inhabiting a continuous forest travelled three times faster and had home ranges ten times larger than groups inhabiting riparian forests (Zanette, 2023). By having larger than expected home ranges in relation to their body size (Ferrari, 1993; Gal  n-Acedo et al., 2023), which they can cross in a single day (Bury, 2022), lion tamarins are known to disperse viable seeds of more than 40 plant species at mean distances of 150 to 280 m, especially medium-sized seeds (de Almeida e Silva, 2022).

We explore if the same movement rules are sufficient for predicting seed dispersal patterns of four lion tamarin groups inhabiting distinct forests with varying characteristics (i.e., size, shape, and resource distribution). We are particularly interested in answering if we can predict lion tamarin's generated seed rain in distinct forest fragments, as it is important to develop a model with enough power to predict its seed rain in forest fragments we still lack data on. First, we explore how energetic and movement rules (i.e., energy levels, feeding bout duration, etc.) affect the emerging patterns of tamarin movement and seed dispersal such as daily path length (DPL), area used (in hectares), activity budget, and seed rain (SDD and seed aggregation). We do this by means of a sensitivity analysis. Secondly, we explore an optimization algorithm (genetic analysis) to estimate unknown parameter values, especially the ones related to energy gains and losses. Finally, we explore how accurately the model predicts lion tamarin movement and seed dispersal patterns by comparing observed and simulated patterns (validation). With few exceptions, we find a good predictability of movement and seed dispersal while discussing the model generality in face of the ecological processes at hand.

2. Methods

2.1. Study species and sites

The black lion tamarin mostly occurs in seasonal Atlantic forests of the State of São Paulo (also known as semideciduous forest; [Valladares-Pádua and Cullen Jr, 1994](#)). Tamarins inhabit very distinct environmental contexts throughout their highly anthropized geographical

range, such as riparian forests, small non-protected forest fragments, and continuous forests in protected areas. Most of them are found in the Paranapanema river basin, dominated by semideciduous forest, which has a warm and humid season (summer) and cold and dry season (winter) ([Veloso et al., 1991](#)).

Between 2015 and 2019, over varying periods of time, four tamarin groups were studied in four distinct areas ([Fig. 1](#)). The groups varied in terms of size and composition ([Table 1](#)). Data from each group was collected by different researchers. Firstly, the riparian forest group lived in an area owned by the Suzano forestry company, inhabiting a different environmental context than the other groups of this study. This group ranged mostly through the Rio Claro farm (ca. 4000 ha in size), of which 1799 ha are native Atlantic Forest distributed in one private protected area (RPPN Olavo Egydio Setúbal) and the rest of it in small fragments between *Eucalyptus* spp. silviculture and riparian forests. This group's home range was, in almost its entirety, composed of linear riparian forest and was estimated as one of the smallest for the species (22.5 ha KDE95 %, de Almeida e Silva, *pers. communication*). The small forest fragment (Guareí) is a privately owned forest of 100-ha surrounded by cattle ranches and sugarcane farms and *Eucalyptus* spp. silviculture. Three groups of tamarins were known to occur in it (ca. 0.15 individuals/hectare, Bufalo F. *pers. comm.*), with the studied group having approximately 40 to 50 hectares of home range. Here we use data from one group which occupied the northeastern and eastern part of the fragment (40.3 ha, [Bufalo et al., 2024](#)). The medium-sized forest fragment (San Maria) is a 515-ha forest surrounded by sugarcane plantation and a road. Lion tamarin population size was recently estimated to be around 18 individuals (0.035 ind./ha, [Forero-Sánchez et al., 2024](#)). The

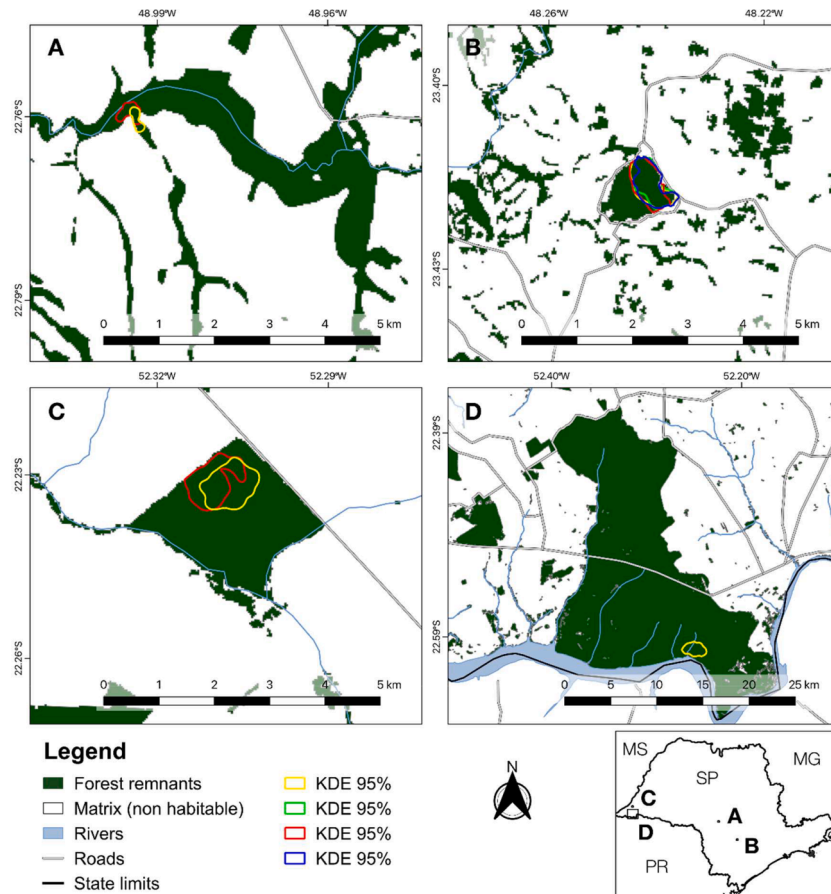


Fig. 1. Study sites and estimated area used by four lion tamarin groups throughout the species distribution. A) Riparian forest group in the Fazenda Rio Claro. B) Small-sized fragment group in a 100 ha privately owned farm (Guareí). C) Medium-sized fragment group in a 515-ha forest (San Maria). D) Continuous forest group in the Morro do Diabo State Park (MDSP, Taquara group). Outset: São Paulo State, Brazil. Each isopleth (colors) refers to the area used in a specific month (see [Table 1](#)). Notice the different scale in A. KDE: Kernel density estimator.

Table 1

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

Group	Fragment size (ha)	month/ year	Group size	Composition
Suzano	Riparian forest (Undefined)	Sep/ 2018	4	two adult males two adult females
		Dec/ 2018	6	two adult males two adult females
Guareí	Small-sized (105)	May/ 2019	5	two adult males
		Jun/ 2019		three adult females
		Jul/2019		
		Aug/ 2019		
San Maria	Medium-sized fragment (515)	Mar/ 2015	2	one adult male
		Apr/ 2015		one adult female
Taquara (MDSP)	Continuous forest (33,845)	Jan/2018	4	one adult male three adult females

studied group had an estimated home range of 85.7 ha (KDE 95 %, [Messaoudi, 2015](#)). Conversely, the Taquara group inhabited the Morro do Diabo State Park (MDSP), a large-sized (which we consider “continuous”) protected forest with low lion tamarin density (0.035 ind./ha, ind/ha) and a lot of environmental variability ([Paranhos, 2006](#)). This group had an estimated 316 ha year-round home range (KDE 95 %, de Almeida e Silva, *pers. communication*).

2.2. Model design

The main assumptions of the model is that lion tamarins structure their routine according to their level of energy (homeostasis) and that they can directly approach known feeding trees. Below, we briefly summarize the first three topics (“1. Purpose and Patterns”, “2. Entities, State Variables, and Scales” and “3. Process Overview and Scheduling”) of the ODD format (Overview, Design concepts and Details, [Grimm et al., 2020](#)) and further describe the *evaluation* process ([Augusiak et al., 2014](#)). A complete and detailed description of the model following the ODD format is available in **Appendix A**. The model is spatially explicit and agent-based and it is implemented in NetLogo 6.3.0 ([Wilensky, 1999](#)). All simulations were run through the *nlrX* package ([Salecker et al., 2019](#)). We used the SimpleR and GIS extension for NetLogo ([Baker, 2023](#); [Russell and Edelson, 2012](#)). All analyses were done in R 4.3.1 (R Core Team, 2023) and all codes are available in a github repository: <https://github.com/edimizac/predicting-seed-rain>.

2.3. Overview, design concepts and details (ODD)

The model was built with the *purpose* of understanding behavioural and energetic responses guiding the ranging behaviour and space use of lion tamarins and their effects on seed dispersal patterns (seed rain) in different forest fragments (“environmental contexts”). We built this model to predict lion tamarin’s seed dispersal (the emergent phenomena) and its causal process, their movement, answering the following *question*: can we predict the seed rain generated by lion tamarins in distinct environmental contexts based on the same movement rules?

Movement *patterns* were estimated through the *amt* package ([Signer et al., 2019](#); [Signer and Fieberg, 2021](#)). We estimated the area used by the group (in hectares) as our estimates were done in a 3- to 8-day time window, with the 95 % and 50 % Kernel density estimator (KDE95 and KDE50, respectively), and therefore do not represent the home range

concept ([Börger et al., 2008](#); [Jacobson et al., 2023](#); [Potts and Börger, 2022](#)). We also refer to the KDE50 as ‘core area used’. From the daily trajectories, we derived daily path lengths (DPL, in meters), movement rate (MR = DPL/activity time in hours) and path twisting (PT = DPL²/KDE95 in square meters). MR and PT have been shown to be important predictors of SDD ([Fuzessy et al. 2017](#)). We also calculated the Defendability Index ($DI = DPL / (4 KDE95 / \pi)^{0.5}$; [Lowen and Dunbar, 1994](#); [Mitani and Rodman, 1979](#)) as it captures the extent to which animals are able to cross their home range in a day ([Bury, 2022](#)). We also explored the M index ($MI = N(s * DPL / d^2)$, ([Lowen and Dunbar, 1994](#)), where *s* is the detection distance and *d* is the diameter of the circle equivalent to the used area), which, contrary to the DI, corrects for the territory boundary, an important factor considering the fragmented landscape where lion tamarins inhabit. For such, we used a detection distance of 90 m as the distance of detection and response to long calls as reported in [Ruiz-Miranda et al. \(2019\)](#) for golden lion tamarins (*L. rosalia*).

We assessed two seed dispersal *patterns*: 1) SDD were estimated by the linear distance of the defecation point to the mother tree/liana and 2) Seed dispersal aggregation, estimated by the R index from the Clark-Evans test in R (clark.evans function in spatstat package, [Baddeley and Turner, 2005](#)). This index is based on the nearest neighbor distance between point events (unique defecation points).

The model *initializes* with three *entities*: patches (cells), trees and lion tamarins. Only one individual is represented because lion tamarins are highly cohesive familiar groups, thus they are modelled as one agent. Each of the agents bear multiple *state variables* (listed on **Table A1**). Patches are 10 × 10 m (spatial resolution *scale*) and together compose a landscape with a forest fragment (habitat) and matrix (non-habitat) covering the expected home range and some additional surrounding area (**Fig. 1**). The trees are then positioned inside the forest according to their empirical location. The fourth entity is created when lion tamarins move around and defecate seeds from the visited fruiting trees.

Each timestep represents 5 min, which is the temporal *scale* of the empirical data collection. The model runs for *n_{days}*, matching the *temporal extent* of empirical data collection for the number of days collected in each time window (roughly three to eight sequential days in a single month). The length of each day is defined by the *simulation time* parameter, which represents the mean empirical activity period of lion tamarins for each time window (**Table 3**).

The most important *processes* of the model, which is repeated every time step, are the selection of known fruiting trees and the monitoring of these trees at the territory border of the simulated lion tamarins. These parameters were chosen with the aim to maintain the lion tamarins’ homeostasis by reaching a balance between energy expenditure and intake. At the end of the day, lion tamarins retreat to a sleeping tree. Based on estimated gut transit times, lion tamarins disperse seeds throughout their home range as they move, creating a seed rain.

The most important *design concept* of the model is the *interaction* between lion tamarins and their resources because, together with their energy levels, they represent the main process guiding ranging patterns. As a result of these inferred movement drivers, the seed rain *emerges*. While previous models have addressed similar questions ([Nield et al., 2020](#); [Pegman et al., 2017](#)), they examined these patterns at the landscape level or focused on specific conditions for a single group ([Gazagne et al., 2020](#); [Hopkins, 2016](#)).

The model has six *sub models*. The first – and most important - is the *movement sub model*. The most frequent driver of route directionality in the studied groups, assessed through a change point test, was feeding tree locations, representing 22.2–67.1 % of the change points ([Bufalo et al., 2024](#)). In the model, lion tamarins have two modes of moving: one when energy is low (triggered when energy is below level 1), representing a “hungry” state when they travel to the closest feeding tree; and a second one when lion tamarins are satiated (above level 2), when they travel randomly to any known feeding tree in the home range border (defined by *p_{defended trees}*) in the forest (**Fig. A1**). Both moving modes

are parameterized with empirical velocities (meters moved in one timestep, Table 3). 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 that draws random step lengths and turning angles for each step, thus lacking the ‘why to move’ component (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 lion tamarins will spend on each tree (“feeding bout on”). If feeding bout is “off”, the same time constraint (a random integer between one and *species_time_val*) is used. After approaching and feeding on a fruiting tree, lion tamarins will stop feeding on it when the empirical feeding bout is reached. On each timestep feeding on fruiting trees, the lion tamarins receive an amount of energy, which is constant. This rationale is a workaround the scarce information available on nutritional content of fruits native from the Atlantic Forest. However, we understand that this solution might incur in incorrect estimates of energy intake and other errors and should be treated with caution (Chivers, 1998; Zinner, 1999; Rothman et al., 2012). Empirical feeding bouts are available in Fig. B5. Although exudate consumption is important for callitrichids and might represent considerable energy intake when resources are scarce (Lambert and Rothman, 2015), we disregard it from the model as it was negligible for the time periods we modelled (0–2.07 % of behaviour observations). Lastly, we dropped the scent marking behaviour, which showed negligible 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, 2022; Heymann, 2022).

The second sub model is the *energy sub model*, which handles the *stored energy* of lion tamarins. In a very simple way, as the lion tamarin behaviour depends on the energy levels and not all energy that they consume is immediately available (it will eventually be stored as glycogen or fat), every time lion tamarins peak in energy (after consuming fruits), a procedure called *store energy* is triggered, storing the surplus energy they have above *energy_level_1*. This energy will be used (by the *get_stored_energy* procedure) when lion tamarins have less than 70 % of their *energy_level_1* available. This process represents catalysis. Conditions for this sub model are checked every timestep.

The *avoid matrix sub model* is called when the straight-line path between lion tamarins and their targets are intertwined by a non-habitat patch (“matrix”). When this happens, the movement of lion tamarins is guided by the *in-cone* procedure in NetLogo, which results in a set of forest patches. The patch which has the smallest distance to lion tamarins’ target will be chosen as their temporary target, thus avoiding the matrix.

The *sleeping sub model* starts when simulation-time reaches 95 % of the *simulation_time*. At this point, lion tamarins will stop feeding and go to the closest sleeping tree for *n* timesteps (up to the moment then reach it). Their speed is doubled, reflecting what happens in nature (Zanette, 2023).

The *memory sub model* regulates the available tree targets that a given lion tamarin group can choose from. This choice is important because it will ultimately determine which trees were recently visited and aid on their resource monitoring. Otherwise, agents would stick to the same tree and keep feeding on it. Although conceptually simple, this sub model involves at least three lists (Appendix A).

The emerging pattern of seed dispersal happens not only through movement, but also through a *seed dispersal sub model*. In short, each timestep the lion tamarins feed on a fruiting tree, one seed is consumed, and each seed receives a gut transit time value. Since the seed species characteristics may vary, leading to distinct gut transit times, this value is based on a Poisson distribution with mean empirical values for each seed species. It also determines if they are going to be defecated on the same or in the next day based on the time of the day. Multiple seeds might get defecated at the same time. Empirical gut transit times for each lion tamarin group is available in Table 3.

2.4. Model evaluation

2.4.1. Data evaluation

We used empirical movement and seed dispersal data of four groups of lion tamarins for model parameterization (Table 3). Empirical data was restricted to those months with at least three full consecutive and complete days of data collection by following lion tamarins by foot (sleeping site to sleeping site, *n* days) with a handheld GPS. Their positions and behaviour were recorded at 5 min intervals over a varied time (Table 1). Behavioural data were recorded through instantaneous scan sampling based on a standardized set of activities (resting, locomotion, feeding (on fruits), foraging, socializing, and other). When the group was in a stationary phase (e.g. resting, feeding in the same feeding tree) for several behavioural scans, we unified all consecutive GPS positions with a distance inferior to the estimated GPS error (8–12 m) because these spurious steps can lead into extreme relative turning angles (Hurford, 2009). Based on the activity period of lion tamarins, we derived simulation times, which varied between 8.91 to 11.83 h, representing the shortest and longest activity period registered in the field, respectively. The final dataset included 3 to 8 full days (from sleeping tree to sleeping tree) for each lion tamarin group and month combination.

From the GPS data, we derived multiple parameters (Table 2): mean step length and maximum random angle values for the specific behaviours of traveling and foraging (i.e., searching for fruits and mostly for invertebrates). To parameterize the movement model, we used the observed mean step length and 75th quantile of turning angles as the maximum angle turned during these behaviours (Table 3; see Hopkins, 2016 for a similar approach). Simulations were run for each specific group and month.

Seed dispersal events were monitored in the field through direct observation. Each seed dispersal event consisted of the observation of the consumption of fruits from a specific fruit tree, which was identified to species level and marked in the field, until the consequent defecation of its seeds later in the same day or in the next morning after leaving the sleeping site. We collected the feces from all observed events of defecation for identification and quantification of the seeds. When the lion

Table 2

Model input parameters (for all groups of black lion tamarins and month combinations). All values except *p_timesteps_to_rest* (which is empirically estimated) are educated guesses.

Parameter	Description	Value
<i>energy_level_1</i>	level of energy at the start of each day. Below it, the lion tamarin is considered “hungry”	900
<i>energy_level_2</i>	level of energy above which the lion tamarin is considered “satiated”	1150
<i>energy_stored</i>	Energy available in case of energy shortage buffering the lion tamarin against short-term energy expenditure	1000
<i>energy_from_fruits</i>	energy gain from frugivory at each timestep	73
<i>energy_from_foraging</i>	energy gain from foraging at each timestep	30
<i>energy_lost_traveling</i>	energy loss from traveling at each patch (10 m)	–15
<i>energy_lost_foraging</i>	energy loss from foraging at each timestep	–10
<i>energy_lost_resting</i>	energy loss from resting at each timestep	–5
<i>species_time</i>	mean time spent feeding on an individual tree (only when feeding bout is “off”)	2
<i>p_timesteps_to_rest</i>	proportion of total <i>simulation_time</i> at the start and end of the day (defined by midday) when the lion tamarin is not allowed to rest	0.15
<i>p_disputed_trees</i>	proportion value defining the number of trees at the border of the fruiting tree distribution which are going to be potentially visited when the lion tamarin is considered “satiated” (resource monitoring)	0.25
<i>step_forget</i>	number of steps taken to reconsider revisiting a fruiting tree	87
<i>div_to_reset_memory</i>	Denominator which results in the proportion of total trees left ($1 / \text{div_trees_to_reset_memory}$), to visit that calls the <i>enhance_memory_list</i> procedure	3

Table 3

Model input parameters for specific groups and months. All values were estimated based on empirical data.

Parameter	Description	Riparian		Small				Medium		Continuous
<i>month</i>	Sampled month	Sep	Dec	May	Jun	Jul	Aug	Mar	Apr	Jan
<i>timesteps</i>	Amount of activity period (1 timestep = 5 min)	347	726	447	657	853	867	699	451	855
<i>n_days</i>	Number of observed/simulated days	3	6	4	6	8	8	6	4	6
<i>simulation_time</i>	Mean activity period duration	116	121	112	110	107	108	116	113	142
<i>duration</i>	Maximum number of sequential steps spent resting	14	20	5	5	5	16	21	11	16
<i>step_len_mean_Foraging</i>	Mean step length (in meters) when the group is foraging	7.51	8.38	14.06	12.14	12.93	13.87	16.95	21.03	30.89
<i>step_len_mean_Travel</i>	Mean step length (in meters) when the group is traveling	17.94	17.49	23.43	25.44	25.20	25.30	32.37	35.97	39.31
<i>max_angle_75q_Foraging</i>	Relative max angle deviation (in degrees) when the group is foraging. Values are drawn randomly.	55.92	51.20	68.98	78.99	75.66	77.22	89.73	63.00	43.02
<i>max_angle_75q_Travel</i>	Relative max angle deviation (in degrees) when the group is traveling. Values are drawn randomly.	63.61	47.53	67.86	75.63	72.75	59.53	68.99	58.76	17.85
<i>p_foraging_while_traveling</i>	Probability of foraging while traveling (estimated as $p_{foraging} / (p_{foraging} + p_{travel})$)	0.31	0.21	0.36	0.47	0.54	0.70	0.59	0.61	0.21
<i>GTT_mean</i>	Mean gut transit time of seeds	26	21	17	18	13	19	16	16.6	16
<i>n_trees_Frugivory</i>	Number of fruiting trees that were consumed during the study period	27	46	28	43	86	77	61	43	58
<i>n_trees_Sleeping site</i>	Number of sleeping trees that were used during the study period	3	7	1	5	8	7	6	2	7

tamarins consumed fruits from another individual of the same tree or liana species prior to defecation, these dispersal events were discarded (Heymann et al., 2012). We derived mean gut transit times for each seed species by calculating the time lapse between observed feeding events and when the seeds were found in the lion tamarins' feces. These values were used to parameterize model runs (Table 3; see Appendix A for details). For estimating seed dispersal aggregation, we considered each defecation event with seeds as a point.

Finally, we also included the empirical trees in the model. The number of sleeping trees (either tree hollows or liana crowns in the canopy) varied from 1 to 7 and of fruiting trees varied from 27 to 86 according to the site and time window (month).

2.4.2. Conceptual model evaluation

Throughout model development, we evaluated two main processes related to the movement patterns: 1) the effect of feeding bout duration parameterization and 2) the effect of selecting random trees or trees on the border (hereon “border monitoring”, a proxy for territoriality). The feeding bout duration may vary depending on plant species, and as we did not have any energy estimates, we explored the results of the model with a sensitivity analysis comparing parameterized (feeding bout “on”) (see values in Fig. B3) and non-parameterized feeding bout (feeding bout “off”, Table 2). Border monitoring was implemented in the final model because the model with random targets failed to accurately reproduce the home range size, especially in the more pristine forest (see comparable results presented in Appendix C). This might be called a ‘robustness analysis’ (Grimm and Berger, 2016).

2.4.3. 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. Daily travel paths were compared visually either in NetLogo or in R (e.g., Fig. B2).

2.4.4. Model output verification

Throughout model development, we used *face validation* for model output corroboration (Augusiak et al., 2014). In other words, we visually compared mean, median and variation of output variables (i.e., used area and core area used, DPL, activity budget and SDD) to determine if they corresponded to the empirically observed values. If this was not the case, we refined the model and went through the modelling cycle once again. During model development, other patterns emerged as candidates for validation, following the pattern-oriented modelling (Grimm et al., 2014). These variables were: movement rate (MR), path twisting (PT)

and seed dispersal aggregation, as well as the Defendability Index (DI) and M Index (MI).

Three emergent patterns can be verified on the NetLogo interface: DPL, Activity Budget and SDD. All other patterns required the *Simple R* extension to be estimated. The output was captured through the *nrx* package in R.

Model calibration was done using a genetic algorithm using a custom fitness function with the aim of gathering the most probable parameter values for our simulations – i.e., the parameters that reproduce the multiple patterns observed empirically (e.g., DPL, area used, etc.) – following the pattern-oriented modelling approach (POM, Grimm et al., 2014; Gallagher et al., 2021). The parameter range is available in Table C1. This calibration was done with the *simdesign_GenAlg()* function of the *nrx* package, which uses the *genalg* package (Willighagen and Ballings, 2022). We used an initial population of 121 chromosomes (square of parameter number, 11^2) which ran up to 100 iterations, mutation chance of 0.1 and elitism = 2 (20 % of the best fit chromosomes go to the next generation). Variables were min–max normalized from 0 to 1, and we estimate the fitness of each chromosome as the sum of the inverse of the difference to the observed patterns ($|simulated - observed|$), following the below equation.

$$fitness = \left(\frac{1}{KDE_{95}} + \frac{1}{KDE_{50}} + \frac{1}{DPL} + \frac{1}{MR} + \frac{1}{PT} + \frac{1}{p_{fru}} + \frac{1}{p_{for}} + \frac{1}{p_{res}} + \frac{1}{p_{trav}} \right) \quad (1)$$

Eq. (1) was applied to “important” patterns: area used (50 and 95 % kernel density area; KDE_{95} and KDE_{50} , respectively), mean daily path length (DPL), movement rate (MR), path twisting (PT) and activity budget (proportion of frugivory, foraging, resting and traveling; p_{fru} , p_{for} , p_{res} and p_{trav} , respectively). Spatial models usually require recalibration and are computationally expensive (Kang et al., 2022). We acknowledge that both between-site and seasonal variations (e.g., Kaisin et al., 2023) might affect the comparability of these results. Thus, we ran the calibration for all group-month combinations. As the results of calibration varied inconsistently (Appendix C), we proceeded with the model analysis using the educated guess parameter set (presented in Tables 2 and 3).

2.4.5. Model analysis

We ran a global sensitivity analysis with the Morris method (Morris, 1991) implemented in the R package *nrx* through the *simdesign_morris()* function to estimate effects of movement and energy related parameters on model outputs (dispersal patterns: SDD and seed aggregation; movement patterns: DPL, area used, MR, PT and number of visited trees). 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 (Campolongo et al., 2007). With this analysis, we also tested if the parameterization of feeding bout duration (i.e., how long lion tamarins feed on each tree species) was an important factor guiding model results (C  rtes and Uriarte, 2013) by comparing runs with this parameterization "on" and "off". For each area-month combination, we ran eight values (sampling density) of each parameter with 20 random seeds with five replicates, resulting in 1300 and 1400 runs for each

timeframe ("on" and "off", respectively). We counted the number of runs that were not viable (lion tamarins died) and discarded those runs from the Morris effect estimation. For the first-order effects, μ indicates the direction of the effect (negative or positive), while μ^* is the absolute value of μ , indicating important (high μ^*) and unimportant (low μ^*) parameters in the model. High sigma (σ) indicates interaction between parameters and/or non-linear effects on the output. Reference lines for interpreting proportional first-order effects (slope = 1 or -1) and monotonic, non-monotonic and non-linear relations (slope = 0.1,

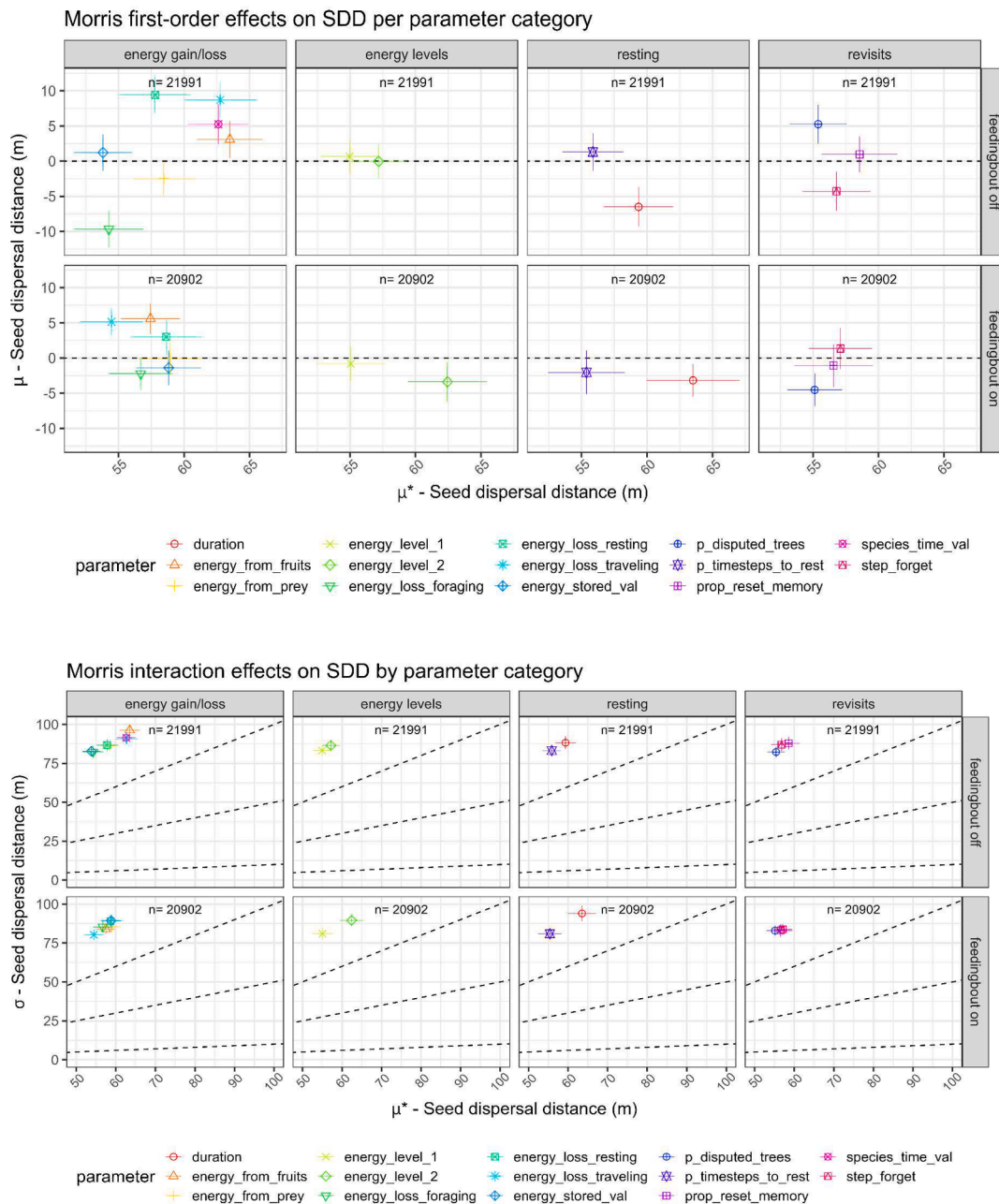


Fig. 2. Sensitivity analysis (Morris' elementary effects) showing the average ($\pm$ sd) effect of parameters on the average seed dispersal distances (SDD) when feeding bout was parameterized ("on") or not ("off") on all group-month combinations (four black lion tamarin groups inhabiting four distinct forests sampled in nine different months). **Upper plot (first-order effects):** μ indicates the direction of the effect (negative or positive), while μ^* is the absolute value of μ , indicating important (high μ^*) and unimportant (low μ^*) parameters in the model. Reference dashed line shows average effect = 0 (the parameter generates both positive and negative effects on SDD). **Lower plot (interaction effects):** High sigma (σ) indicates interaction between parameters and/or non-linear effects on the output. Reference lines show linear (slope = 0.1), monotonic (slope = 0.5) and non-monotonic (slope = 1.0) interaction effects. Average values represent nine different mean values of 20 independent runs (random seeds) for each group-month combination. Morris effects by group-month combination on seed aggregation and on other output variables (DPL, MR, UD, etc.) are available in **Appendix B Text**. Inset numbers show total number of model runs for each parameterization (feeding bout "on" and "off"). Numbers differ because different parameter sets result in different survivability of the agents.

0.5 and 1.0, respectively) were plotted to visually identify the less important parameters (Hess et al., 2020; Menberg et al., 2016).

2.4.6. Model output corroboration

The model has not been validated with fully independent (i.e., not considered during model development) data. Instead, we looked at and extracted parameters from the empirical data which we used to validate the model.

3. Results

3.1. Calibration and sensitivity analysis

The results of the genetic algorithm revealed low consistency in optimized parameters between areas (Fig. C1). The continuous forest had the lowest fitness values. For instance, the energy acquired for each timestep consuming prey was unexpectedly minimized in some fragments and months. However, it has maximized the proportion of defended trees (fruiting trees at the border of their used area) in most fragments, which makes sense since lion tamarins frequently present routes circumventing their home range borders. Similarly, the calibration suggested that runs with low energy from fruit and high energy spent resting in the riparian forest was the best fit. This is in accordance with the observed decrease of activity of some primates in small fragments, although consistency in this effect is weak (Carretero-Pinzón et al., 2016). Given this low consistency in optimized parameters between areas, we continued our model validation and analyses with the set of educated guess parameters (Tables 2 and 3).

The sensitivity analysis (Fig. 2) revealed that feeding bout parameterization (“on”) made the resting time *duration* and the *energy_level_2* more influential (larger μ^*) on the SDD, usually diminishing it (negative μ). The same was shown for energy acquired from fruits (*energy_from_fruits*) and energy spent resting (*energy_loss_resting*), which usually enhance SDD (positive μ). The *species_time* (which restricts the amount of time spent in each tree, used only when feeding bout is “off”), had large average effects on SDD, likely as a result of lion tamarins spending more time moving between fruiting trees as the parameter value decreased. No unique parameter was identified as important (Appendix B Text 1). Instead, important parameters changed for each area and month combination (not shown). As our focus was validation, we followed our analyses with the feeding bout parameterized with empirical data (“on”). Moreover, all parameters presented non-linear and interaction effects (high σ , Fig. 2, Appendix B Text 1), even when group-month combinations were analysed separately (not shown). All results presented are respective to viable runs, i.e., runs where lion tamarins’ energy did not reach 0. This might have led to less than 20 replicates in some cases (Figs. 3–6).

3.2. Movement

Most simulated movement patterns were very similar to those observed empirically. Simulated sizes of used areas (KDE95 and KDE50) sizes were very similar to the observed (Fig. 3, top and middle panel), except for the continuous forest, which approached similar values but could be 50 % smaller in some simulations. For the other lion tamarin groups, core areas were similar or slightly larger than the observed. Thus, it was no surprise to find slightly larger simulated daily path lengths, especially in the riparian forest (DPL, Fig. 3, bottom panel). This might have happened because lion tamarins in the model spent more time traveling and less time resting and consuming fruits (Fig. 4). Accordingly, the movement rate was also slightly overestimated (Fig. B1 in Suppl. Material 2), probably because of the constant displacement through the day. In turn, the model consistently reproduced the path twisting all areas except the riparian forest.

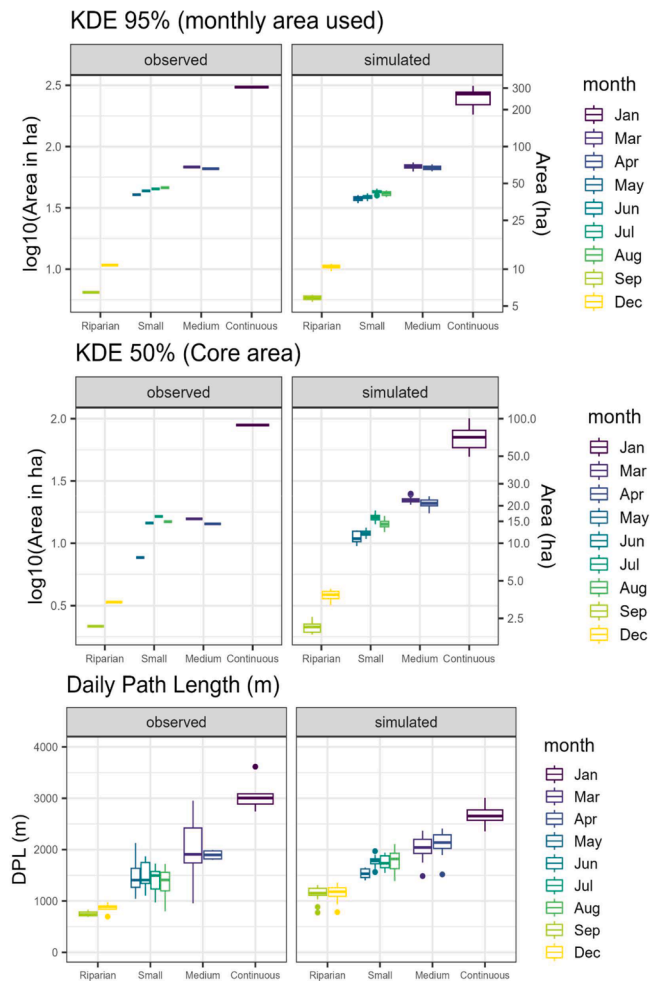


Fig. 3. Movement patterns of simulated and observed black lion tamarins. Each month represents 4 to 8 days of collected/simulated data. DPL = daily path length (in meters). Observed KDE values (left) have no replication, while DPL values represent different days. Simulated (right) has 20 replications (mean DPL of runs, 20 random seeds).

3.3. Seed dispersal

Seed dispersal distances were slightly overestimated (Fig. 5), following similar trends except for the medium fragment. Example runs showing the seed rain can be found in Fig. B2. Simulated dispersal events were aggregated or randomly distributed and with values ranging from 0.5 to 1.2, while empirical values were consistently lower (more clumped) (Fig. 6).

4. Discussion

Models are important tools to learn about the studied system, especially in the context of forest loss and fragmentation. Management decisions are more and more based on such models, although their applicability is so far rather limited. Hence our model explored the ability to generalize movement decisions of lion tamarins in several habitat sizes and shapes. This is an important step towards a general model of forest-specialist primate movement in unknown habitats and under habitat loss.

Following the pattern-oriented modelling (POM) approach (Grimm et al., 2014; Gallagher et al., 2021), here we extended a previously developed model to simulate the seed rain of four independent groups of a different primate species, within different environmental contexts (size, shape, and resource distributions). The model was able to

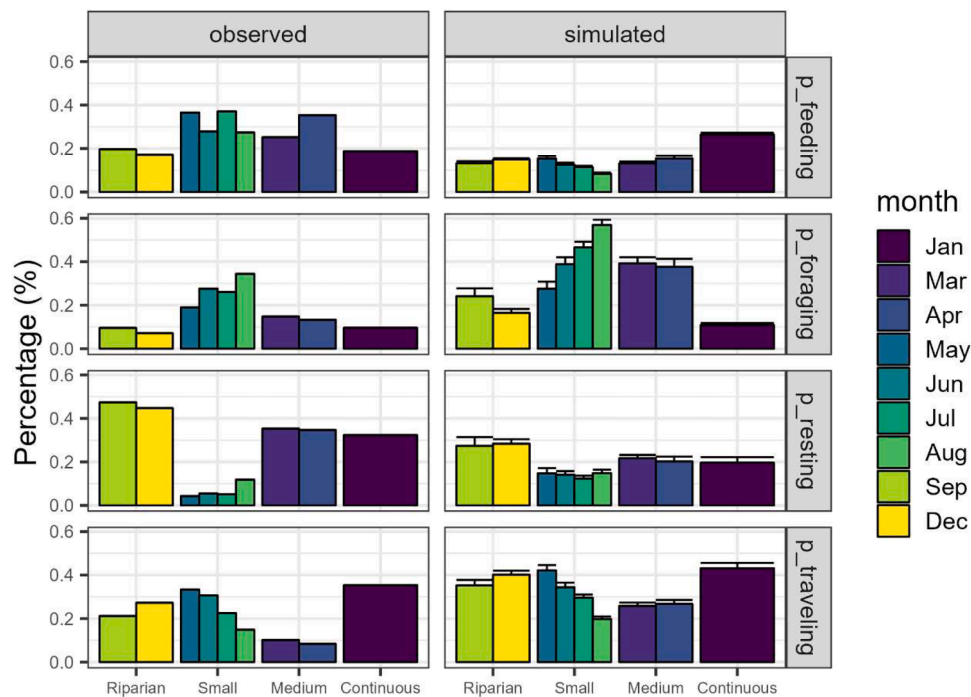


Fig. 4. Activity budget (percentage of each behaviour) of simulated and observed black lion tamarins. Mean + sd values are displayed. Observed values (left) have no replication. Simulated (right) has 20 replications (average of runs, 20 random seeds).

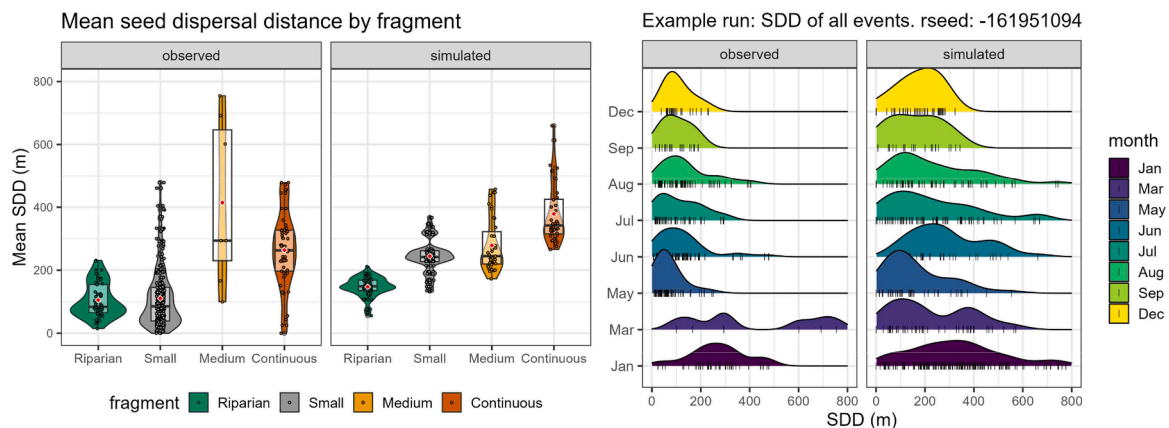


Fig. 5. Average seed dispersal distance (SDD) of four black lion tamarin groups (empirical and simulated). **A)** Violin plots with inset boxplots comparing average SDD by fragment. Observed values (left) have no replication (one point = one observed seed dispersal event, red diamond = observed mean). Simulated (right) have $n = 20$ replications (random seeds), where one point = mean SDD for each simulation, red diamond = average of means). **B)** Line ridge density plot for comparing observed SDD with single run (one random seed) of each time frame (group-month combination). Each dispersal event is represented as a tick on the horizontal line. Each fragment is represented by one tamarin group with 1 to 4 months with 3–8 days of collected/simulated data. We lack seed dispersal data for one time frame in the medium-sized forest (April). Densities were adjusted automatically by the bandwidth parameter in *ggridges* package (Wilke 2022).

reproduce well 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, path twisting and territorial defendability). Thus, our model might be applied for estimating ecosystem services by black lion tamarins and for conservation purposes, or further develop it to understand the interface of movement, fragmentation, and seed dispersal theoretically, from a forest specialist perspective.

While the original model simulated seed dispersal in tamarins (*Saguinus mystax* and *Leontocebus nigrifrons* [previously *Saguinus fuscicollis*]) inhabiting continuous Amazonian Forest (Bialozyt et al., 2014), here we focus on black lion tamarins within Atlantic Forest remnants. The model was re-parameterized using empirical data of four groups of lion tamarins inhabiting very different forest remnants at a fine temporal

and spatial scale. We improved the model by refining the movement rules and the choice of fruiting trees (guided by energy levels) and by including feeding bout, resting times and gut transit time parameterizations. With this approach, we identified that monitoring the borders of the home range is important to predict movement patterns in this species. This emphasizes that small tweaks in model design can result in more robust patterns matching (Millington et al., 2012). In accordance with previous research, we found that the inclusion of processes related to mutual avoidance can provide good insights into the system at hand (Potts and Börger, 2022; Theng et al., 2024; Zubiria Perez et al., 2021).

The calibration analysis resulted in parameter sets differing widely from each other between best fitted runs (Fig. C1). This might be happening because the model structure lacks a process (for example, the trade-off between consuming insects and fruits, which changes between

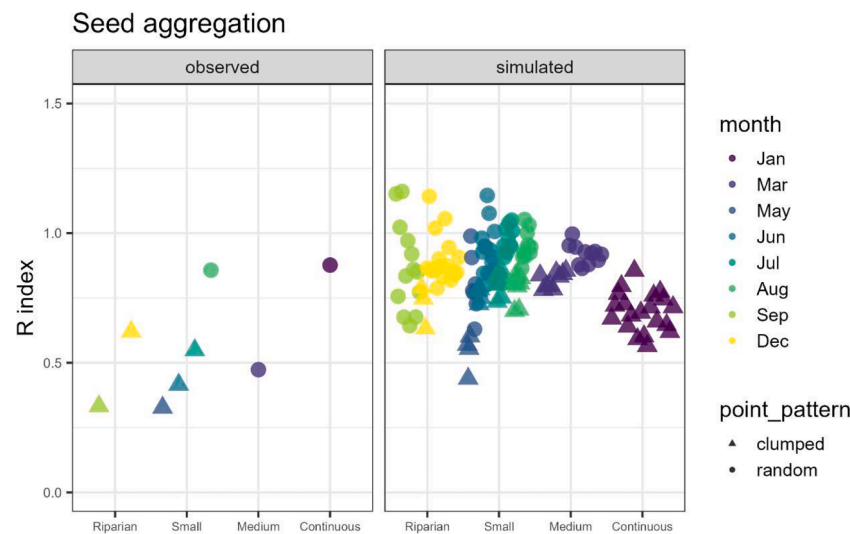


Fig. 6. Seed dispersal aggregation (measured from feces locations) of four black lion tamarin groups (empirical and simulated). The point pattern was defined as random or clumped based on Clark-Evans tests. Observed values have no replication, simulated has 20 replications or less, depending on agent survivability. We lack seed dispersal data for one time frame in the medium sized forest (April).

areas and months), or because it has a complex parameter landscape. A complex parameter landscape is likely, given the huge variation in primate activity budgets observed empirically (Carretero-Pinzón et al., 2016). This is in accordance with the results of the sensitivity analysis (Fig. 3), in which the main parameters affecting movement and seed dispersal patterns varied widely between areas and months. Previous mechanistic models of seed dispersal rarely performed sensitivity analyses (Morales and López, 2022). Here, we show that the set of parameters guiding variation in space use by a forest specialist primate is indeed variable (but see Dunbar, 2002). We suggest that studies investigating the seed dispersal on a fine scale of time and space should benefit from simulation models such as the one presented here and might provide further insight about the seed rain predictability. Lastly, using “educated guessed” parameter values (Table 2) has proved good enough for predicting most patterns of our interest, but it also suggests that our model might require a more complex approach of pattern-oriented calibration (Haythorne and Skabar, 2013; Hartig et al., 2014; Kang et al., 2022; Theng et al., 2024) to overcome the complex parameter landscape or, as we point out below, a better mechanistic understanding of the processes leading to lion tamarin ranging behaviour.

Recent ABMs have adopted multiple approaches to model primate movement behavior, with some applications to seed dispersal. Hopkins (2016) interfaced several movement models for howler monkeys’ feeding bouts in Barro Colorado Island, where resources were mapped in a 50-ha plot. The author concluded that the best model reproducing observed movement bouts of this howler monkey species (*Alouatta palliata*) 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 draw random values of step length and turning angle distributions) performed badly. Resonating Morales et al. (2013), Gavrilitchenko et al. (2022) have criticized pure step model approaches such as those used in Raghunathan et al. (2020) and Gazagne et al. (2020), which simulates the seed rain generated by *L. chrysomelas* and *Macaca leonina*, respectively. These two models depend strictly on data of a single group and draws steps (lengths and angles) randomly. Thus, they lack interfacing with the processes behind the movement decision and, therefore, they 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 and Kramer-Schadt, 2021), which we do in the

model here developed, thus providing a more robust simulation of the seed rain.

We argue that our model is a good candidate for predicting seed rain of unknown lion tamarin populations, given the attention to its premises and simplification. Although most models are developed to be as general as possible, we aimed at reproducing empirical patterns (“validation”) of multiple groups. Thus, our model required group specific parameterization, especially the ones related to movement patterns (speed and turning angles) and resting behaviour (see Evans et al. 2020 for a similar example). We argue that to avoid such groups-specific parameterizations it is preemptive to explore some processes related to environmental and social aspects on individuals’ internal state and, thus, their behavioural responses (how and when to move, Nathan et al., 2008; how fast to move, Wilson et al., 2015), such as landscape of fear and territoriality (Bonnell et al., 2013; Gaynor et al., 2019; Theng et al., 2024). One could shed light on how these responses occur with landscape-level studies sampling a gradient of fragment sizes, shapes and resource distributions. Below we discuss the model prediction capacity and explore further model extensions.

4.1. Movement patterns

The model reproduced the observed movement patterns of four distinct groups of lion tamarins in distinct environments, suggesting that our model is a good representation of the processes involved in lion tamarin movement and has good predictive power. The model also reproduces most quantitative patterns not initially assessed during the model development (MR, PT, DI). However, some mismatching cases are worth mentioning. First, concerning the activity budget, we found that simulated time spent traveling and foraging was higher, and frugivory and resting times were underestimated. This resulted in simulated lion tamarins having, in some cases, longer DPL. Discrepancies were less accentuated in the continuous forest. This may be due to the fact that the activity budget in the model is simplified to four behaviours (assessed through group scans) (Fig. B3), thus other behaviours such as social interactions and intergroup encounters (which are usually stationary) are dropped for simplification, leaving some timesteps in the model (up to 10 %) “free” for repeating the exclusive four implemented behaviours, which are mostly non-stationary (foraging and traveling).

A second mismatch that is worth noticing is the overestimation of MR and PT in the riparian forest group. It may be a direct consequence of the longer DPLs and the differences in activity budget discussed above.

This is further reflected in the DI (and in MI, an extension of DI that controls for territory border length), which was overestimated in the riparian forest, probably as a consequence of longer DPL and lower time spent resting (Fig. B7). This suggests that lion tamarins inhabiting riparian forests might be subjected to different motivations than lion tamarins inhabiting other forests.

Potts and Börger (2022) formalize how spatio-temporal patterns of movement can emerge from ABM modelling, comparing processes such as mutual avoidance, attraction to resources and central place attraction. While our model formally includes only attraction to resources, we partially circumvent the lack of these processes by restricting agent choices to the empirical resources (which resembles the empirical home range and thus a central place attraction) and by targeting trees at the border (a placeholder for mutual avoidance or territoriality). Because we lack a comprehensive understanding of lion tamarin territoriality, mutual avoidance between groups and its drivers on the individual level (but see Bury, 2022 and Ranc et al., 2020), we implemented only a simple rule of selecting a random “defended” tree at the home range border. Monitoring territory borders likely affect ranging and recursion movements (Berger-Tal and Bar-David, 2015; Watts and Mitani, 2001) and therefore, the area used (Potts and Borger, 2022) and resource visitation patterns (Theng et al., 2024; Bracis et al., 2018). We believe this was the main knowledge gap in our model, which likely drove the last two mismatches we discuss below.

We found an overall match between the empirical and simulated areas used (Fig. 3). It is interesting to note that, before implementing a territory border defense process by making lion tamarins to target trees at the border of the territory when satiated, simulated areas used were 50 % smaller on average. In a study on *L. chrysomelas*, Raboy and Dietz (2004) postulated that the search for fruiting trees and the low number of available sleeping sites may be factors driving this species’ ranging patterns. Comparably, our results show that searching for fruiting trees seems to be sufficient to reproduce most movement patterns of lion tamarins. However, by qualitatively looking at simulated trajectories, it is easily noticeable that the lion tamarin routes circumventing the home range border do not emerge as frequently as in empirical data, especially in the continuous forest (Fig. B1).

Regarding fruiting tree visitations, our model estimated that lion tamarins visited 10–50 % less trees than what was observed empirically (Fig. B9). Overall, these results suggest that, while territorial patrolling/border monitoring (i.e., defending resources at the border of the home range) is an important driver of lion tamarin ranging behaviour, this behaviour may be leading to a great proportion of trees not being visited. Exploring the cause of such divergence might provide important insights. For example, the degree of inter-group competition and space use between groups may shed light on this question. A global review, exploring space-use scaling and home range overlap in primates, found a negative relationship between home range size and animal density (Pearce et al., 2013). Similar tendencies have been confirmed for multiple primate species in fragmented landscapes (Ramsay et al., 2023). Regarding our study species, this implies that monitoring borders may drive used area size, especially when animal density is low, such as in the continuous forest. In line with the multiple central place foraging (Chapman, 1989), comparing the proportion of overlap of used areas between days (e.g., Rezende, 2022; Theng et al., 2024) could be an additional pattern to validate such patrolling behaviour.

4.2. Social vs ecological drivers

Whether social factors are as important as the resource distribution to drive lion tamarin ranging behaviour and thus seed dispersal (Karubian and Durães, 2009) is still a matter for future exploration. For instance, recent studies have compared the effect of resources and social factors in guiding group size, range dynamics and intergroup encounters in primates, finding greater effect of social than ecological factors (Ellis and Di Fiore, 2019; Thureau and Cords, 2024, but see Di Bitetti, 2001).

On the other hand, de Guinea et al. (2021) found that both social and environmental factors affected the travel bouts of howlers’ (*Alouatta pigra*).

A common suggestion in the literature is that primate movement is mostly guided by resource distribution and aggregation. While energy intake might limit black lion tamarin activity budgets (Kaisin et al., 2023), we emphasize that most fragments bear more than enough calories (Henry, 2011). Thus, instead of just feeding ecology and resource distributions, the ranging patterns of such small primate species might be also linked to often unaddressed factors such as territoriality (e.g., Theng et al., 2024), landscape of fear (predation pressure and diseases, Gaynor et al., 2019; Bonnell et al., 2013) and, ultimately, nutrition. These processes were not implemented in the model due to lack of data and of understanding of the system in hand as they often operate on a larger temporal scale (which we believe is far beyond the timestep of 5 min, Hansen et al., 2024; Kays et al., 2023) and might interact with energy expenditure and movement velocity (Wilson et al., 2015). Recent advances in movement ecology have identified fundamental units in movement patterns and how this affects simulation studies (Getz et al., 2024; Vissat et al., 2023). In the context of model simulations, modelling the processes guiding movement patterns above the scale we used (path-level resource selection functions *sensu* Zeller et al., 2016 and life history phases *sensu* Kays et al., 2023) is a promising next step for modelling frugivore ranging behaviour and their resulting seed dispersal services.

Despite focusing on the attraction to resources, our model did not rely on knowing all potential resource trees (i.e., sleeping sites or fruiting trees) in the study sites. Instead, it depended solely on observed used trees during a measured time frame. Other potential resources (e.g., fruiting trees of the same consumed species) are assumed to have been ignored while lion tamarins were traveling, meaning that lion tamarins do not exploit all available resources or fruiting patches on their routes. This suggests that other non-modelled factors might be playing a role on lion tamarins’ ranging patterns and resource targeting. In the ABM literature, however, only models with food availability in larger space and time scales and/or with general movement models (e.g., Carter et al., 2015; Crouse et al., 2022; Theng et al., 2024) have been successful in exploring the interplay between environmental and social/territorial dynamics *in silico*. Together with a more comprehensive understanding of how fragmentation and habitat loss affect the vegetation structure and fruit availability, more detailed information on energetic requirements might inform further model development, making it possible to test hypothesis about which factors governs lion tamarins (and other primates) ranging behaviour, distinguishing between sociological (e.g., group size, territoriality, food preference) and ecological factors (e.g., food availability and distribution).

4.3. Seed dispersal patterns

Here we show that the seed rain generated by lion tamarins is mostly aggregated, matching the observed patterns in nature and the overall expectation for vertebrates (Beckman et al., 2012; Muñoz-Lazo et al., 2011). However, simulated spatial patterns in our model were also frequently random. Furthermore, our model predicted slightly longer seed dispersal distances (SDD). Both discrepancies might happen because all seed dispersal events are accounted for in the simulation model, but not empirically, mainly due to two reasons: 1) empirical data collection is prone to observer specificity and error (Fig. B8) – e.g. it has been estimated that, when following another callitrichid species, about 86 % of defecation events are missed (Heymann EW, *pers. comm.*); 2) Because the criterion we used to assign empirical seed dispersal event relies on the exclusive consumption of one feeding tree species, the probability of identifying one seed dispersal event diminishes as gut passage time increases and the richness of consumed species decreases. Consequently, we are less likely to register long distance seed dispersal events empirically. In general, assigning the mother tree of dispersed

seeds *in-situ* is not a trivial task and may require molecular methods (Jordano, 2007; Gelmi-Candusso et al., 2019; Heymann et al., 2012). To increase model accuracy, we suggest that validation should be done on a more exhaustive set of dispersal events. Overall, despite these differences, we found that the model represented well the seed rain patterns in lion tamarins.

As the model does not depend on observer capabilities, nor on exclusive seed dispersal events and these methodological limitations will be hardly circumvented during empirical studies (see also Raghu-nathan et al., 2020), we suggest future comparisons to be made on the spatial level (Nearest neighbour distances or summary functions, Wie-gand and Moloney, 2013) with a virtual ecologist approach (Zurell et al., 2010) and not on the statistical level (e.g., R index), as the last depend heavily on the number of observations. We hope future studies with genetic methods applied in the field will help confirm the model prediction capability for seed dispersal (e.g., Gelmi-Candusso et al., 2019).

Lastly, in our model, we explored the movement patterns of lion tamarins at the group-level, without considering the number of individuals in each group. To acquire more realistic seed dispersal patterns, one possible implementation would be to simulate all the individuals in the group (Table 1) or to multiply the seed deposition locations by the number of individuals in the group and randomizing it by the mean group spread. However, group spread drivers are not well comprehended mechanistically (Bufalo F., *pers. comm*) and would potentially lead to one more group-specific, non-mechanistic, parameterization in the model.

4.4. Further model extensions

During model development, we identified three branches of inquiry that could improve the model prediction capabilities but would require further data collection and new development cycles. These would be useful to address new hypotheses regarding primate movement and seed dispersal studies, as well as potentially providing insights on long-term seed dispersal patterns, a promising venue of research as the full dispersal loop is inherently difficult to be assessed empirically given its time scale (Wang and Smith, 2002; Schupp et al., 2017).

4.4.1. Energy submodel

Recent simulation studies have been using empirically estimated caloric values to determine behaviour modes (Malishev and Kramer-Schadt, 2021; Chudzinska et al., 2021). As more ecophysiological and nutritional studies are conducted on lion tamarins (Rezende, 2022; Kaisin et al., 2023), we will be able to parameterize the model with real caloric acquisition and estimate satiation levels from energy intake and feeding bout duration. In turn, we partially circumvented this lack of information with the *step_revisit* parameter (a minimum revisitation period) which turned individual trees into “visited” resources and obliged simulated lion tamarins to visit a different tree, consequently varying their time spent feeding on each resource and virtually changing their caloric intake. This parameter can be made species-specific with empirical revisitation data or fine-tuned by the estimated fruit set and yielded energy, as done and discussed in other studies (Bonnell et al., 2013; Boyer et al., 2006; Boyer and Walsh, 2010; Hopkins, 2016; Janson and Byrne, 2007; Chudzinska et al., 2021; Ranc et al., 2022).

However, despite the high dependence on the energy levels, our model is still not parameterized with very detailed energy activity budgets (Malishev and Kramer-Schadt, 2021), neither with a digestion system for continuous energy acquirement (Warwick-Evans et al., 2018) nor grounded with calorimetry estimates. Instead, our model assigns a unique value of energy per timestep spent feeding on fruits, independent of specific fruit caloric content. This energy is then immediately available to the agent, which is not realistic considering empirical feeding bouts (Kaisin et al., 2023). Lastly, we used best-guessed parameters with a unitless scale that drifts away from energy expenditure estimates

(compare Table 2 energy parameters with e.g., recent black and golden lion tamarin estimates: 100.8 ± 5.9 and 83.4 to 94.5 kcal/individual/-day: Rezende, 2022 and Henry, 2011, respectively), which might be rescaled in future implementations.

Further insights can be gained from analyzing the model. First, the calibration resulted in an inconsistent set of parameters. Most of them were close to the min and max possible values (Fig. C1). Second, the sensitivity analysis (Fig. 2) indicated that the parameterization of the feeding bout was important in terms of reducing the non-linear and interactive effect of the parameters in the model (Figures B10-B17). This suggests that the model structure should benefit from more accurate energetic parameterization. Three possibilities of model extensions in this regard are: 1) Implementing metabolic rules derived from accelerometer data (Malishev and Kramer-Schadt, 2021), which might be a way of avoiding the highly variable *ad-hoc* estimates of energy expenditure and might make it possible to reproduce *in silico* the activity budgets (Warwick-Evans et al., 2018) and explore the energy expenditure generated by different movement modes (e.g., fast and slow travel; Sibly et al., 2013; Hölker and Breckling, 2002); 2) Using more realistic estimates of energy acquired by each fruit species (Henry, 2011), grounding the model to real calorimetric estimates; and, lastly, 3) including a continuous digesting process and acquisition rates (Warwick-Evans et al., 2018; Sibly et al., 2013; Chudzinska et al., 2021).

According to the optimal foraging theory, if animals spend more energy reaching a resource, they might heavily deplete it by exploiting it for longer times (Davis et al., 2022). Although we are certain that lion tamarins do not deplete much of the food patches they visit (see Henry, 2011), it has been shown that they may take longer foraging times in patches that provide less energy per time unit, such as fruits with low pulp to seed mass ratio, with consequences on the activity budget (Kaisin et al., 2023). This patch depletion intensity, which is linked to resource availability at the patch scale, is not represented in the model. Remarkably, different from other systems where resource availability and depletion can be estimated from remote sensing or other methods (e.g., seals: Chudzinska et al., 2021; ungulates: Ranc et al., 2022; polar bears: Klappstein et al., 2022; carnivores: Theng et al., 2024), the lack of good surrogates of resource availability and heterogeneity in forests impedes such modelling endeavours. Future empirical studies comparing feeding bouts and fruit intake in a spatially explicit context will shed light if the optimal energy theory is relevant for the studied system.

4.4.2. Cognition

Primates have special cognitive and heuristic abilities for traveling and finding resources (de Guinea et al., 2021; Urbani, 2023). There is no consensus on which primates use different maps for navigation and to what extent. However, it has been argued that Neotropical primates most likely use both Euclidian maps and route-based navigation, respectively in smaller and larger spatial scales (Urbani, 2023). In a study on capuchin monkeys (*Cebus capucinus*), Urbani (2023) considered larger scales when the tree target was not visible (>30 m). In our model, we implemented an Euclidean map-based navigation (i.e., agents know every tree location and travels to them using the shortest path). Constructing route-based maps is a challenging task as it may depend on unknown and complex landmarks in the landscape (Bufalo et al., 2024) that may also shape the movement of lion tamarins. Garber and Porter (2014) suggested that landmarks also play a role in route direction of *Leontocebus weddelli* (previously *Saguinus fuscicollis*), another callitrichid, in smaller scales (<60 m). Considering the type of navigation is important because both path recursion (i.e., returning to previously visited areas) and route-based navigation might result in higher route usage and, thus, higher density of dispersed seeds.

Primates usually know their resources and the speed at which they approach a given fruiting tree might be an indicator of its cognition and navigation map (Hopkins, 2016; de Guinea et al., 2019; Boyle et al., 2023). We do not model such a behaviour because agents in our model

have constant speed. Similarly, foraging sites might be located near fruiting trees (Garber and Porter, 2014). While this seems to be the case in the continuous forest group, where empirical routes clearly showed foraging before or after reaching a fruiting tree, this was harder to identify in the forest fragments. In our model, foraging for animal prey was implemented randomly during travels. Unraveling such feeding relationships might help grounding further model implementations.

Lastly, we saw some incongruent paths in the model which likely emerged from the model simple decision rule: in very sporadic 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 solved by implementing a cost estimation rule where agents know their distance to the target and decide to "stop by" another resource before proceeding to it or proceed to the target even with low energy. Furthermore, in very complex boundaries, our rules of movement showed one failure: agents could get stuck in equidistant boundaries (i. e., places where the agent could not reach an area with straight-line paths) in some simulations in the riparian forest. We tried our best to identify those runs and take them out from analysis. Implementations such as least-cost path (Chudzinska et al., 2021; Green et al., 2020) or A* solver (Caparrini, 2018) might solve this problem and should be considered for more complex fragment shapes.

4.4.3. Phenology cycles and longer simulation times

Plant phenology cycles were not considered in the model, mainly because our data collection periods were < 9 days. For larger temporal extents, phenology dynamics might be considered. To our knowledge, no ABM has implemented such fine-grained variation in phenology (Duriez et al., 2009; DeAngelis and Diaz, 2019). This would allow simulating longer periods of lion tamarin activity and seed rain (in the scale of months and years). How phenology cycles affect primate movement decisions, as they simultaneously interface both temporal and spatial processes of frugivory, is far from being understood (Albrecht et al., 2015). Further knowledge on how phenology synchrony and fruit availability spatially guide fruit consumption will make it possible to model available resources in the home range of each group and test how these affect the ranging behaviour, fruit selection and resource defense by forest-dependent frugivores.

5. Conclusions

Here we developed a fine scale, spatially explicit ABM for predicting black lion tamarin generated seed rain, which reproduced *in silico* most of the patterns of our interest, including those related to movement. The model was validated with four different lion tamarin groups inhabiting completely different forest fragments (small fragments to continuous and riparian forests), with few exceptions, especially after the implementation of a territoriality rule. Thus, the model has the potential to be applied to explore topics such as ecosystem services provision, home range dynamics and resource selection. However, we parameterized feeding behaviour of lion tamarins with empirical feeding bout durations and movement behaviour with velocities and resting times. These parameters are pretty much *ad-hoc*, varying profoundly with the environmental context (Malishev and Kramer-Schadt, 2021) which makes models less general (or "overfitted", Gallagher et al., 2021). Furthermore, we still lack a deep understanding of energetics and how it affects movement decisions. We encourage further research to search for more mechanistic rules (e.g., what leads to larger step lengths and home ranges: Szangolies et al., 2024; Pearce et al., 2013; tree resources selection, etc.) that will bypass such high level and location-specific parameterizations that result in overly phenomenological models, enhancing our understanding of the effect of fragmentation and habitat loss on the seed rain and forest regeneration. These rules should be grounded to the profound knowledge on lion tamarin natural history and its energetic relationships inside the frugivory loop.

CRedit authorship contribution statement

Eduardo M. Zanette: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ronald B. Bialozyt:** Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Mayara M. Santos:** Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Anne Sophie de Almeida e Silva:** Investigation, Data curation. **Felipe Bufalo:** Writing – review & editing, Investigation, Data curation. **Olivier Kaisin:** Writing – review & editing, Investigation, Data curation. **Yness Messaoudi:** Investigation, Data curation. **Mirela Alcolea:** Investigation, Data curation. **Eckhard W. Heymann:** Writing – original draft, Supervision, Investigation, Conceptualization. **Laurence Culot:** Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111093.

Data availability

<https://github.com/edimizac/predicting-seed-rain> (Data and code is provided on github:)

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