Individual Variation in Animal Movement and Effects on Seed Dispersal Distance

I don’t like this abstract. Revisit at the end…Seed dispersal is a fundamental process in plant ecology and due to its high importance in the ecosystem, various modelling approaches have been developed to understand seed movement and dispersal mechanisms. In particular, long-distance seed dispersal (LDD) plays a significant role in determining a population’s genetic diversity and range expansion. Animal-mediated seed dispersal is a key component of LDD events, as frugivores can travel long distances and transport seeds with them. In this study we seek to understand the implications of individual variation in animal movement and how these can impact estimates of long distance seed dispersal. We apply these methods to empirical data sets that contain locations for an araçari, *Pteroglossus pluricintus*, one of the primary frugivores for the Amazonian canopy tree *Virola flexuosa*. We combine animal movement data and gut retention time to simulate *Virola* seed dispersal. This approach showed that there is significant variation in individual araçari movement patterns which directly influence the estimated number of long-distance dispersal events for *Virola* seeds. We found that models that ignore this underlying variation in individual animal movement, underestimate the percentage of long-distance seed dispersal events and maximum seed dispersal distances.

# Introduction

A main goal of ecologists and evolutionary biologists is to document and predict the structure and dynamics of ecological systems. Although most of our current understanding of ecological systems is based on the average patterns observed in nature, understanding variability and its consequences in ecological processes has recently raised the interests of researchers (Benedetti-Cecchi 2003; Inouye 2005). Variation is now considered a property of ecological systems that might contain as much ecological information as do averages and regularities in nature (Benedetti-Cecchi 2003; Violle et al. 2012). Individual variation, i.e. the possibility for individuals within a population to present different ecological strategies or traits (Violle et al. 2012), has been widely discussed in ecology and evolutionary biology. In evolutionary biology the acknowledgement that individuals with different traits might vary in their fitness and survival under natural selection pressures dates back to Darwin’s seminal ideas (Darwin and others 1859). Today, it is widely recognized that individual variation plays a key role in the evolution of species and clades, and the relevance of individual variation in the performance of populations and species facing current threats (e.g. climate change, fragmentation and habitat loss) is a growing field of research (Forsman and Wennersten 2016). In ecology, individual variation is often mentioned as a mechanism for populations to reduce competition pressure (Bolnick et al. 2010; Araújo, Bolnick, and Layman 2011). Based on the niche complementarity principle, phenotypically different individuals will compete less strongly than more similar individuals (Bolnick et al. 2011), thus individual variation would act as a release from intra- and interspecific competition at a local scale. Despite the well recognized importance of individual variation in ecological and evolutionary processes, ecological theory has emphasized interspecific variation (Violle et al. 2012). Not surprisingly, the role of individual variability on the outcome of species interactions has also been poorly studied; most models of species interactions assume that all conspecific individuals are equivalent and interchangeable (Bolnick et al. 2011). Individuals, however, differ in several aspects that will affect their interactions with other species. This variability makes individuals non-interchangeable from the perspective of interacting patterns (Bolnick et al. 2003; González-Varo and Traveset 2016). The consequences of individual variability in interspecies interactions can even have cascading effects, going beyond from the species-species level to the community and ecosystem level (Post et al. 2008; Wolf and Weissing 2012).

Seed dispersal mutualisms may be a particularly attractive system to study the impacts of incorporating individual variation to understanding the importance of such variation to dispersal outcomes. Seed dispersal is one of the most critical stages in plant life history – it results in a spatial pattern of seed deposition which acts as a template that will define the distribution of plants and, consequently, community structure (Howe and Smallwood 1982; Nathan and Muller-Landau 2000; Russo, Portnoy, and Augspurger 2006). In seed dispersal mutualisms, animals provide the dispersal services while rewarding from fruit resources they consume. Plants produce fleshy fruits to attract and reward mutualist animals and rely on the behavior of the disperser to transport their propagules (Nathan and Muller-Landau 2000). The spatial patterns of seed deposited by disperser vectors will determine the probability of seed survival and recruitment, acting upon post-dispersal processes such as density-dependent survival and colonization (Howe and Miriti 2004). Therefore, at a local scale, seed dispersers will determine whether plant species escape from density-dependence processes (Comita et al. 2014), whereas at a larger scale, they can determine how quickly plants can cope with habitat and climate shifts (Ibáñez et al. 2006; Russo, Portnoy, and Augspurger 2006).

From the plant perspective, not all seed dispersers species provide with the same seed dispersal service, and often relatively few disperser species can have disproportionate effects on seed dispersal (Schupp 1993; Jordano et al. 2007; Schupp, Jordano, and Gómez 2010; Loayza and Rios 2014). Frugivores might differ on their selection of plants/fruits for consumption, in their treatment of seed while ingesting and manipulating the fruits, in their processing of seeds if ingested and in the distance where they will discard the seeds (Schupp 1993; Schupp, Jordano, and Gómez 2010; Côrtes and Uriarte 2013). Each one of these stages of the seed dispersal process will have strong consequences on the spatial seed shadow provided by each seed dispersal vector (Jordano et al. 2007; Carlo and Tewksbury 2014). Besides inter-specific differences among dispersal vectors, there is a recent recognition of the potential role of differences among individuals in the resulting seed dispersal they provide (Bolnick et al. 2003; González-Varo and Traveset 2016). Including individual variation in traits (morphological, behavioral and physiological) in seed dispersal studies, can provide new insights into the relative role of different dispersal vectors on seed deposition and ultimately, vegetation structure (González-Varo and Traveset 2016). In a recent review, Zwolak (Zwolak 2018) summarized the types of intraspecific variation in seed-dispersing animals that might affect the resulting seed dispersal service individuals provide, highlighting differences in sex, size or age (ontogenetic shifts), individual specialization and behavioral syndromes as the most important variation types. Incorporating these intrinsic traits into seed dispersal models may lead to more mechanistic understanding of seed dispersal, allow to build more accurate predictive frameworks of dispersal outcomes (Russo, Portnoy, and Augspurger 2006) and to identify links between characteristics of dispersal agents and the seed dispersal they provide (Zwolak 2018).

In this paper, we focus on the implications of intraspecific variation in animal movement for seed dispersal distances and seed aggregation across the landscape. To understand the consequences of this variation in movement, we developed a spatially-explicit individual-based model of the many-banded aracari, *Pteroglossus pluricinctus*, one of the primary frugivores of the Amazonian canopy tree *Virola flexuosa*. Also, previous studies focused on this system have shown that *P. pluricintus* is able to disperse seeds across long distances (K. M. Holbrook and Loiselle 2007; Holbrook and Loiselle 2009; Holbrook 2011), an important for plant population. Long distance dispersal (LDD) events are crucial to reaching suitable sites to germinate and establish and to colonize new habitats (Nathan 2006). Furthermore, rare events (often overlooked) are critical for dispersal and might have a large effect on resulting plant demography (Loayza and Rios 2014). Our first objective in this work was to study the differences of simulated seed shadows between models with and without underlying variability in animal movement. The second objective focused on quantifying the differences of LDD events reflected between seed shadows. Lastly, our third objective focused on the spatial spread between seeds, and how individual variation in animal movement affects seed aggregation. Identifying the implications of individual variation in animal movement over seed dispersal estimates can help us improve future models and understand the effects of frugivore traits on plant population dynamics.

# Methods

## Simulation description

To study the effects of individual variation in animal movement over final dispersal distances of foraged seeds, we developed a spatially-explicit individual-based model in a homogenous landscape consisting of a single source tree. We incorporated animal movement focusing on two characteristics, a movement distance (MD) sampled from a probability density distribution, and a movement angle (MA). In addition to this, we included gut retention time (GRT), the time that ingested seeds stay inside the frugivore until they are dropped. The animal was allowed to move freely within the landscape, and GRT determined when the animal would drop a seed. Once a seed was dropped, its location was recorded and seed dispersal distance was estimated as the distance from the origin to the seed’s location. The average seed dispersal distance for each simulation run was also estimated and used to for seed dispersion, calculated as the mean distance of each seed to the average location of all seeds in the run (Jones et al. 2017). For each simulation run, the simulation started at the source tree, an animal received a specific number of seeds and each seed was assigned a specific GRT sampled from a gamma distribution (Morales and Carlo 2006). The simulation was based on one minute time steps, where at each time step a movement distance (MD) and movement angle (MA) would determine the path for the animal to follow. For each seed, the location where it would get dropped was based on the animal’s location at the time it reached the GRT for each of the seeds. The total simulation time for each run was determined by the largest GRT sampled for that specific simulation run. Each simulation run focused on one individual animal dispersing seeds from one focus tree. Once all seeds in that run were dropped by the animal, the simulation run ended.

## Study design

To understand the consequences of individual variation in animal movement and how these influence seed dispersal distances, we simulated three different scenarios by varying the movement of individual animals. We used our first scenario as our null model, in which all the individuals from the simulation had the same average movement rate (), used as the parameter in the probability density function, and thus their movement distances per unit of time were sampled from the same probability distribution (). We chose this as our null model as it is the approach most commonly used in frugivore-generated seed dispersal kernels, where the movement rate for the frugivore population is determined and used either as a constant movement speed or to sample from a single distribution (EDIT citation, Will Tackenberg, 2008, constant rate, Jones 2017, exponential with different values for theoretical model, Levey bolker 2 papers lognormal). Our second scenario included individual variation in animal movement by incorporating different movement rates for each individual (), which meant that movement distances would be sampled from the same overall probability distribution, but with different parameters (). **Double check if these are the Erlang and hyperexponential distributions, not sure it is worth it to mention here though**. Considering that *Pteroglossus pluricinctus*, the focus frugivore in this paper, by belonging to social groups their movement patterns might be correlated, our third scenario ran simulations at the scale of family group variation in animal movement by assigning a different movement rate to each social group in the simulations, where the movement rate where considered as the average movement in meters per unit of time for all the tracking sessions for all individuals belonging to that social group.

## Parameterization

We focused our study on the many-banded araçari (*Pterglossus pluricinctus*), a small toucan, and its role as a frugivore of the *Virola flexuosa* tree. Previous studies by Holbrook (2011) collected radiotracking information for various dispersers over a period of four years, from 2001 to 2005, in the Ecuadorian Amazon rainforest. The methodology used at the time consisted of capturing and radio-tagging individuals from various toucan species, including *Pterglossus pluricinctus* and two larger Ramphastids, although data on the latter was scarce. Tracking periods lasted between four and six daylight hours, alternating morning and afternoons, attempting to record bird locations every 15 minutes, a time interval shown to represent the minimum seed retention time for *Virola flexuosa* seeds (K. M. Holbrook and Loiselle 2007). Out of the data collected, and following Holbrook (2011), we selected data from individuals with at least 40 recorded point locations. Even though location recordings were attempted every 15 minutes, this was not always possible, due to the individual being too far out from range or due to canopy cover, therefore point locations data is available every 15 minutes or multiples of 15 minutes, with the majority of point location recordings between 15 and 30 minutes (Holbrook 2011). Further details on field methods can be found in Holbrook (2011).

To take advantage of all the locations recorded for series of successive points, despite this variation in duration of time intervals, we calculated rates of movement, as the average number of meters moved per minute over the entire tracking period for that individual bird. These movement rates were later used in our simulation models as the parameter to describe the probability distribution of movement distances at each one minute time step for each simulation run. In the case of our null model, the movement rate was averaged across all individuals for all the tracking periods, and at the social group level we took the average number of meters moved per minute over the tracking periods for all individuals belonging to that group, with a total of 7 independent movement rates.

Parameter values for gut retention time were also based on empirically collected data from previous studies (K. M. Holbrook and Loiselle 2007), were passage trials were carried out with *Pteroglossus pluricinctus* individuals. However, these passage trials were not performed on every individual captured and some of the trials were also performed with captive birds, thus we could not explore individual variation in gut retention times for the individuals in the movement data set. These trials showed that the average gut retention time for *Pterglossus pluricinctus* was 28 minutes (K. M. Holbrook and Loiselle 2007), and presented a maximum retention time of over 100 minutes. The distribution of gut retention times is characteristically fat-tailed, thus we used a gamma distribution (shape = 4, scale = 5) with the appropriate shift to match our average retention time of 28 minutes (Morales and Carlo 2006; Levey et al. 2005), and used this distribution to sample gut retention times for each seed in our simulation runs.

*Include table in the supplement with the movement rates*

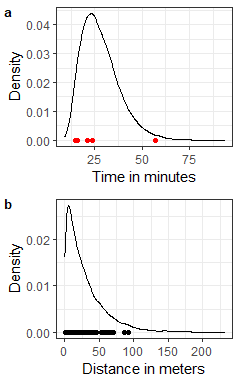
## Model processes

Each simulation run in our models consisted of one animal in a homogeneous landscape starting at the focus tree located at coordinates (0,0). We assume the landscape is in meters, as the sampling of movement distances for animal movement comes from estimates of meters moved per minute, the movement rates. Informed from field observations, *Pteroglossus pluricinctus* have a mean visit length of 4.0 minutes for each fruiting tree, consuming between 2 and 5 seeds during each visit, and not visiting another fruiting tree immediately after feeding (Holbrook’s dissertation and (Kimberly Mae Holbrook 2007)). Due to this underlying behavior, we decided to focus our simulations specifically to the events associated to feeding from one focus tree, and the animal movement occurring after foraging and before visiting another fruiting tree. Since one of the objectives for this paper is to explore the occurrence of long-distance dispersal events, we did not set boundaries for the landscape, as using the boundaries associated to the radiotracking sampling would limit animal movement and seed dispersal distances to only the scale sampled by previous researchers. *Pteroglossus pluricinctus* has shown maximum travel distances exceeding 3500m in a single 30 minute tracking interval, thus showing the potential to disperse *Virola* seeds at long ranges (Holbrook 2011).

At the beginning of each simulation run, the animal consumed five seeds at the focus tree location, and each of these seeds was assigned a gut retention time sampled from a gamma distribution (shape=4, scale=5, shift=8, Figure 1a). Once the animal in the simulation consumed the seeds, a movement distance was sampled from the assigned exponential distribution (Figure 1b), which varied depending on the underlying model such as the null, individual or family group model. A random direction from to degrees was used to determine the angle of movement, which with the movement distance would determine the animal’s position for the next time step, repeating this process for every time step and thus following an uncorrelated random walk with no directional tendency (*Edit references* Turchin 1998). Once the simulation run’s time matched the gut retention time for a seed, that seed would get dropped at the animal’s location at that specific time point, thus allowing us to record seed location in the landscape (Figure 2a). For each of our models we ran 10,000 simulation runs per individual or family group, depending on the model, and collected information on animal and seed locations at every time step.

#### Figure 1.

Density distributions from which we sample gut retention time (GRT) and movement distance (MD).



## Seed dispersal and aggregation metrics

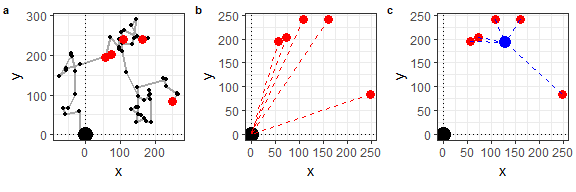
We calculated seed dispersal distance as the euclidean distance of each seed to the parent plant. Given that our models only considered one parent plant located at the origin per simmulation, we calculated seed dispersal distance (DD) as the distance from each seed’s location to the origin as follows:

where is the dispersal distance for seed in the simulation run and and are its xy coordinates in the landscape. We also used an aggregation metric to determine how evenly seeds would be dispersed across the landscape, and calculated seed dispersion (SD) as the average distance of each seed to the mean seed location in each simulation run (following methods in (Jones et al. 2017)):

where is the number of seeds for each simulation run (5), and and is the mean seed location in the simulation run. We obtained measures of seed dispersion for each simulation run, thus we calculated the average seed dispersion for each model as , where is the total number of simulation runs for the model being considered.The information on seed dispersal distance was used for the toucan-generated seed dispersal kernels for each one of our models (null, individual, and family group), and these seed dispersal distances were also classified as long distance dispersal events if they exceeded 500m (K. M. Holbrook and Loiselle 2007). The proportion of long-distance dispersal events, maximum dispersal distance, and average seed dispersion were used to compare seed dispersal between our three models of individual variation (Table1).

#### Figure 2.

Simulation example where animal movement determines location for seeds dropped. Calculations for seed dispersal distance from the parent tree and seed distance to the mean seed location as a measure of aggregation.



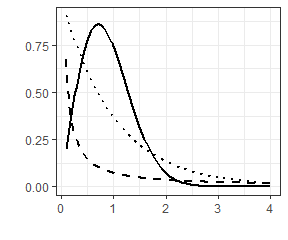
## Seed dispersal kernels

Seed dispersal kernels are functions used to describe the probability of a seed being dispersed or deposited at a specific distance away from its parent plant (Nathan and Muller-Landau 2000). The resulting data from our three simulation models provided a dispersal distance for each simulated seed, and thus we used this information to describe the seed dispersal kernels for each model (null, individual, and family). Dispersal kernels in nature tend to be leptokurtic, with a peak near the origin and long tails, therefore kernel shape can be summarized by its kurtosis (Morales and Carlo 2006). We quantified the dispersal kernels produced in our models by the sample statistics of mean and kurtosis to describe the overall shape and tail of distribution of seed dispersal distances. In addition to this, we also fit a Weibull distribution via maximum likelihood to obtain estimates of the shape and scale parameters in this distribution. This probability distribution is commonly used in dispersal ecology and has been shown to be flexible enough to accommodate variability in the tails and provide informative parameters associated to the mean dispersal distance and fatness of the tail (Morales and Carlo 2006). We fit the data associated to seed dispersal distances produced by each of the three models via Maximum Likelihood using the Weibull density function associated with the package ‘fitdistrplus’(Delignette-Muller and Dutang 2015):

Where the shape parameter determines the tail of the distribution, and is the scale parameter. It is worth mentioning that the standard parameterization of the Weibull in ‘R’ is different from the parameterization used in Morales and Carlo (2006), where the shape parameter remains the same, but the scale parameter is defined as , giving a density distribution function of . Since the shape parameter remains the same, we can note that for the distribution shows a tail with exponential decay, with values of the tail shows fast-decay, and when we can see a fat-tailed distribution (Fig 3.) We visually assessed the fit of the distributions via qqplots and used the Kolmogorov-Smirnov statistic to assess goodness of fit (Supplementary information).

#### Figure 3.

Variation in Weibull distributions determined by the value of the shape parameter. The scale parameter is defined as , and the shape parameters are defined as follows: solid line shows an exponential decay tail, dashed line shows a thin tail, and describes a fat tail with the dotted line.



Explain what are statistics of extremes and why they can be useful here. cite the GArcia 2017 paper, the Gaines and Denny 1993, Katz 2005. Coles 2001 for the theory or base knowledge. In our case, because we are looking at these simulated seed dispersal kernels, we use a peak over threshold (POT) approach, in which we find the threshold for the data and use an extreme value distribution to fit the tail. Describe the math probabilty density functions and the three laws that the extreme value distribution follows. For POT use a generalized pareto distribution.

* Based on Diagnostic plots, we used these values as the threshold for each of the models.

From extRemes package: “where shape = 0 gives rise to the exponential df (light tail), shape > 0 the Pareto df (heavy tail) and shape < 0 the Beta df (bounded upper tail at location - scale.u/shape). Theoretical justification supports the use of the GP df family for modeling excesses over a high threshold (i.e., y = x - threshold).”

# Results

## Seed dispersal distances and long distance dispersal

## Seed dispersion aggregation

The mean dispersal in the boxplots is not the same as the dispersal distances before. This mean dispersal is the distance from the origin to the mean seed location in each simulation run. The mean seed location is used to calculate dispersion, as the average distance of each seed to the mean seed location, as shown in Figure 1.

## Weibull seed dispersal kernel

## Extreme distributions to fit dispersal

Explain what are statistics of extremes and why they can be useful here. cite the GArcia 2017 paper, the Gaines and Denny 1993, Katz 2005. Coles 2001 for the theory or base knowledge. In our case, because we are looking at these simulated seed dispersal kernels, we use a peak over threshold (POT) approach, in which we find the threshold for the data and use an extreme value distribution to fit the tail. Describe the math probabilty density functions and the three laws that the extreme value distribution follows. For POT use a generalized pareto distribution.

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# Discussion

Even though LDD events are rare or infrequent, they have a disproportionately large effect on gene flow and the genetic pool of populations (Jordano 2017). In the case of well mixed populations, long-distance dispersal can cause random genetic loss through drift or have the opposite effect and maintain high genetic variance in populations that initially drifted (Bohrer, Nathan, and Volis 2005). This is important as in the long-term, these genetic consequences of dispersal can have significant effects for the survival of populations. From a metapopulation perspective, LDD events can have significant consequences for species persistence by enhancing genetic variability and as mechanism for survival in spatially and temporally heterogenous environments. In particular, long-distance dispersal events have a higher probability of reaching isolated populations and therefore establishing a connection and maintaining unrelated populations. It is of special interest to focus in highly heterogenous habitats with rapid change in spatial structure where local extinctions are high, since long-distance dispersal can allow persistence of a metapopulation with immigration and emigration based on long distance dispersal. From a more evolutionary perspective, long-distance dispersal can allow for a species to colonize distant habitats and expand its range, which can also lead to differentiation and speciation (Ronce 2007). We have shown that individual differences in frugivore movement can have significant consequences on the number of long-distance seed dispersal events and it remains to be explored how these individual differences can influence population dynamics in the long term and at larger spatial scales.

# Conclusion

# Acknowledgements

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