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 (Holbrook and Loiselle 2007, 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 within 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 calculated and used to estimate 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 two different scenarios by varying the movement of individual animals in each of those scenarios. 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 (). 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 probability distributions with different parameters (). Considering that not all individuals are independent of each other, and that by belonging to social groups their movement patterns might be correlated, we also 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.

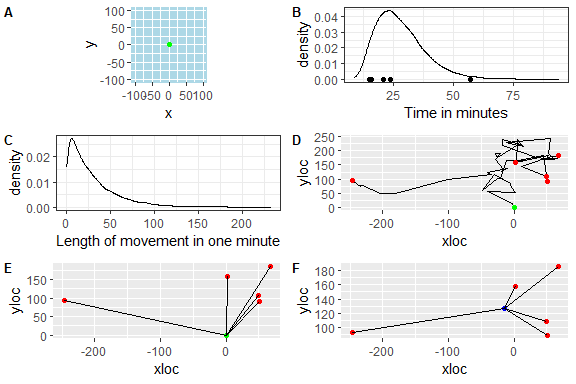
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## Note: As of version 1.0.0, cowplot does not change the

## default ggplot2 theme anymore. To recover the previous

## behavior, execute:  
## theme\_set(theme\_cowplot())

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## Parameterization

Where is the data coming from? What is a movement rate and how are we calculating it? Why are we using that (uneven time intervals)? Why are we using an exponential distribution and what type of movement is this? It is an uncorrelated random walk, but the step size is different.

We give randomly between 3-5 seeds, because that’s what’s observed in the field. We are simulating here the trajectory and fate of seeds after only one event of frugivory to make things simpler.

We have a maximum landscape area, based on the home range size of the individuals, we chose a grid, and it’s modled as a torus so that there is no edge effect.? But do I want this if we want to explore long distance?

Gut retention time based on data and using a gamma distribution from morales paper.

## Seed dispersal distance and agregation metrics

How we calculated these distances, the averages and SD, and then how we calculated the dispersion, long distance dispersal events.

## Seed dispersal kernel fitting

Look into this, but probably use a Weibull distribution like morales and carlo, and then compare the parameters to describe them. An alternative approach would be to use an extreme distribution like the garcia paper to describe this.

# Results

## Seed dispersal distances and long distance dispersal

## Seed dispersion aggregation

## Extreme distributions to fit dispersal

# Discussion

# Conclusion

# Acknowledgements

# References

Araújo, Márcio S., Daniel I. Bolnick, and Craig A. Layman. 2011. “The Ecological Causes of Individual Specialisation.” *Ecology Letters* 14 (9): 948–58. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>.

Benedetti-Cecchi, Lisandro. 2003. “The Importance of the Variance Around the Mean Effect Size of Ecological Processes.” *Ecology* 84 (9): 2335–46. <https://doi.org/10.1890/02-8011>.

Bolnick, Daniel I., Priyanga Amarasekare, Márcio S. Araújo, Reinhard Bürger, Jonathan M. Levine, Mark Novak, Volker H. W. Rudolf, Sebastian J. Schreiber, Mark C. Urban, and David A. Vasseur. 2011. “Why Intraspecific Trait Variation Matters in Community Ecology.” *Trends in Ecology & Evolution* 26 (4): 183–92. <https://doi.org/10.1016/j.tree.2011.01.009>.

Bolnick, Daniel I., Travis Ingram, William E. Stutz, Lisa K. Snowberg, On Lee Lau, and Jeff S. Paull. 2010. “Ecological Release from Interspecific Competition Leads to Decoupled Changes in Population and Individual Niche Width.” *Proceedings of the Royal Society B: Biological Sciences* 277 (1689): 1789–97. <https://doi.org/10.1098/rspb.2010.0018>.

Bolnick, Daniel I., Richard Svanbäck, James A. Fordyce, Louie H. Yang, Jeremy M. Davis, C. Darrin Hulsey, and Matthew L. Forister. 2003. “The Ecology of Individuals: Incidence and Implications of Individual Specialization.” *The American Naturalist* 161 (1): 1–28. <https://doi.org/10.1086/343878>.

Carlo, Tomas A, and Joshua J Tewksbury. 2014. “Directness and Tempo of Avian Seed Dispersal Increases Emergence of Wild Chiltepins in Desert Grasslands.” *Journal of Ecology* 102 (1): 248–55.

Comita, Liza S, Simon A Queenborough, Stephen J Murphy, Jenalle L Eck, Kaiyang Xu, Meghna Krishnadas, Noelle Beckman, and Yan Zhu. 2014. “Testing Predictions of the Janzen–Connell Hypothesis: A Meta-Analysis of Experimental Evidence for Distance-and Density-Dependent Seed and Seedling Survival.” *Journal of Ecology* 102 (4): 845–56.

Côrtes, Marina Corrêa, and María Uriarte. 2013. “Integrating Frugivory and Animal Movement: A Review of the Evidence and Implications for Scaling Seed Dispersal.” *Biological Reviews* 88 (2): 255–72. <https://doi.org/10.1111/j.1469-185X.2012.00250.x>.

Darwin, Charles, and others. 1859. *The Origin of Species by Means of Natural Selection*. Collin’s Clear-Type Press.

Forsman, Anders, and Lena Wennersten. 2016. “Inter-Individual Variation Promotes Ecological Success of Populations and Species: Evidence from Experimental and Comparative Studies.” *Ecography* 39 (7): 630–48. <https://doi.org/10.1111/ecog.01357>.

González-Varo, Juan P., and Anna Traveset. 2016. “The Labile Limits of Forbidden Interactions.” *Trends in Ecology & Evolution* 31 (9): 700–710. <https://doi.org/10.1016/j.tree.2016.06.009>.

Holbrook, Kimberly M. 2011. “Home Range and Movement Patterns of Toucans: Implications for Seed Dispersal.” *Biotropica* 43 (3): 357–64. <https://doi.org/10.1111/j.1744-7429.2010.00710.x>.

Holbrook, K. M., and B. A. Loiselle. 2007. “Using Toucan-Generated Dispersal Models to Estimate Seed Dispersal in Amazonian Ecuador.” In *Seed Dispersal: Theory and Its Application in a Changing World*, 300–321. CAB International, Wallingford.

———. 2009. “Dispersal in a Neotropical Tree, Virola Flexuosa (Myristicaceae): Does Hunting of Large Vertebrates Limit Seed Removal?” *Ecology* 90 (6): 1449–55. <https://doi.org/10.1890/08-1332.1>.

Howe, Henry F, and Maria N Miriti. 2004. “When Seed Dispersal Matters.” *BioScience* 54 (7): 651–60.

Howe, Henry F, and Judith Smallwood. 1982. “Ecology of Seed Dispersal.” *Annual Review of Ecology and Systematics* 13 (1): 201–28.

Ibáñez, Inés, James S Clark, Michael C Dietze, Ken Feeley, Michelle Hersh, Shannon LaDeau, Allen McBride, Nathan E Welch, and Michael S Wolosin. 2006. “Predicting Biodiversity Change: Outside the Climate Envelope, Beyond the Species–Area Curve.” *Ecology* 87 (8): 1896–1906.

Inouye, Brian D. 2005. “The Importance of the Variance Around the Mean Effect Size of Ecological Processes: Comment.” *Ecology* 86 (1): 262–65. <https://www.jstor.org/stable/3451006>.

Jones, Landon R., Scott M. Duke‐Sylvester, Paul L. Leberg, and Derek M. Johnson. 2017. “Closing the Gaps for Animal Seed Dispersal: Separating the Effects of Habitat Loss on Dispersal Distances and Seed Aggregation.” *Ecology and Evolution* 7 (14): 5410–25. <https://doi.org/10.1002/ece3.3113>.

Jordano, Pedro, Coralith Garcı́a, José A Godoy, and Juan Luis Garcı́a-Castaño. 2007. “Differential Contribution of Frugivores to Complex Seed Dispersal Patterns.” *Proceedings of the National Academy of Sciences* 104 (9): 3278–82.

Loayza, Andrea P, and Rodrigo S Rios. 2014. “Seed-Swallowing Toucans Are Less Effective Dispersers of Guettarda Viburnoides (Rubiaceae) Than Pulp-Feeding Jays.” *Biotropica* 46 (1): 69–77.

Morales, Juan Manuel, and Tomás A. Carlo. 2006. “The Effects of Plant Distribution and Frugivore Density on the Scale and Shape of Dispersal Kernels.” *Ecology* 87 (6): 1489–96. [https://doi.org/10.1890/0012-9658(2006)87[1489:TEOPDA]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87%5B1489:TEOPDA%5D2.0.CO;2).

Nathan, Ran. 2006. “Long-Distance Dispersal of Plants.” *Science* 313 (5788): 786–88.

Nathan, Ran, and Helene C. Muller-Landau. 2000. “Spatial Patterns of Seed Dispersal, Their Determinants and Consequences for Recruitment.” *Trends in Ecology & Evolution* 15 (7): 278–85. <https://doi.org/10.1016/S0169-5347(00)01874-7>.

Post, David M., Eric P. Palkovacs, Erika G. Schielke, and Stanley I. Dodson. 2008. “Intraspecific Variation in a Predator Affects Community Structure and Cascading Trophic Interactions.” *Ecology* 89 (7): 2019–32. <https://doi.org/10.1890/07-1216.1>.

Russo, Sabrina E., Stephen Portnoy, and Carol K. Augspurger. 2006. “Incorporating Animal Behavior into Seed Dispersal Models: Implications for Seed Shadows.” *Ecology* 87 (12): 3160–74. [https://doi.org/10.1890/0012-9658(2006)87[3160:IABISD]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87%5B3160:IABISD%5D2.0.CO;2).

Schupp, Eugene W. 1993. “Quantity, Quality and the Effectiveness of Seed Dispersal by Animals.” *Vegetatio* 107 (1): 15–29.

Schupp, Eugene W., Pedro Jordano, and José María Gómez. 2010. “Seed Dispersal Effectiveness Revisited: A Conceptual Review.” *New Phytologist* 188 (2): 333–53. <https://doi.org/10.1111/j.1469-8137.2010.03402.x>.

Violle, Cyrille, Brian J. Enquist, Brian J. McGill, Lin Jiang, Cécile H. Albert, Catherine Hulshof, Vincent Jung, and Julie Messier. 2012. “The Return of the Variance: Intraspecific Variability in Community Ecology.” *Trends in Ecology & Evolution* 27 (4): 244–52. <https://doi.org/10.1016/j.tree.2011.11.014>.

Wolf, Max, and Franz J. Weissing. 2012. “Animal Personalities: Consequences for Ecology and Evolution.” *Trends in Ecology & Evolution* 27 (8): 452–61. <https://doi.org/10.1016/j.tree.2012.05.001>.

Zwolak, Rafał. 2018. “How Intraspecific Variation in Seed-Dispersing Animals Matters for Plants.” *Biological Reviews* 93 (2): 897–913. <https://doi.org/10.1111/brv.12377>.