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

## Model 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 a seed would get dispersed. 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.

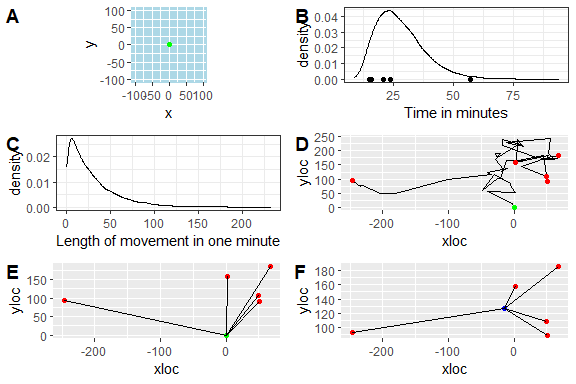
##   
## \*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*

## 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())

## \*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*\*



In order to analyze the effect of differences in animal movement over final dispersal distances of foraged seeds we developed a spatially-explicit individual-based model in a homogeneous landscape that incorporated animal movement distances and seed gut retention time (GRT). Our landscape consisted of a single source tree at the origin, our simulation time steps were based on one minute intervals, and each simulation started at the source tree (0,0), where each individual bird was given five seeds and was allowed to move freely in the landscape until the simulation ended once all seeds were dropped, Figure1. Each seed’s gut retention time was determined at the start of each simulation run, being randomly sampled from a Gamma distribution (shape = 4, scale = 5, shift = 8) (Morales and Carlo 2006) so that the average gut retention time was 28 minutes(Holbrook and Loiselle 2009, 2007). For each simulation run, the total simulation time was determined by the largest gut retention time sampled for the five seeds, therefore, once the last seed was dropped, the simulation ended. We calculated the Euclidean distance from the source tree to each of the dropped seeds to determine their seed dispersal distance. We simulated animal movement using a memoryless process, a random walk with a uniformly distributed angular direction and a random step size chosen from a probability distribution. The probability distribution chosen to simulate step size varied according to the different models we propose in Table1.

Caption for figure 1. Simulation example. The simulation proceeded as follows: an individual bird starts the simulation at time zero and location zero zero. That bird is given five different seeds, with gut retention time (GRT\_I), where GRT is gamma distributed. The animal is allowed to move freely across the landscape where at each time point T\_i, a movement angle is sampled ~uniform(360) (think of greek letter) and a step size is randomly selected d\_i, where D ~ f(x), where f(x) is the probability density function of one of the models we’ve selected. The movement process is repeated and at T\_i == GRT\_i a seed is dropped at the bird’s location (x\_i, y\_i) and therefore that seed’s final locations is (x\_i, y\_i). The simualation ends at T\_i = max(GRT\_1:5), and seed dispersal distances are calculated from the origin (0,0) to each seed’s location (x\_i, y\_i).

# Simulations at different organizational levels

Our main hypothesis is about the incorporation of variation in animal movement at different organizational levels, meaning how are the differences in individual animal movement affecting population level estimates of seed dispersal. How does the underlying variation in individual animal movement impact our estimates of long distance seed dispersal. We explored the effects of individual differences in movement by modifying our base simulation, described above, in which the probability density function used to sample step sizes was different between population, individual, or family level simulations. What we consider as population level simulations are those where all birds share the same probability density to sample step sizes from, while for individual and family level simulations we use the same overall pdf, but allow for variation in the parameters specified for such function, where each set of parameters corresponds to a specific individual or family group. We also performed simulations in which we allowed for variation not only of parameters, but also of the overall structure of the pdf for sampling step sizes, this means that each individual or family group was allowed to have it’s own pdf and its own set of parameters (Box 1 or table 1 with description of models, either the movement or simulation). We used four different probability density functions for sampling the animal movement step size, these included an exponential distribution (Jones et al. 2017), gamma distribution [citation], Weibull distribution[citation], and lognormal distribution (Levey, Tewksbury, and Bolker 2008). These four distributions are leptokurtic, and they vary in the fatness of their tails, thus allowing for different levels of variation in step size. **should add number of runs? or mention that that is in appendix B**

# 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. A subset of animal movement data collected in a previous study (Holbrook 2011) was selected and used towards our models and simulations. In this previous study, araçari home ranges, average movement distances, patterns and movement rates were estimated for tracked birds over a period of four years, from 2001 to 2005, in the Ecuadorian Amazon rainforest. Further details on field methods can be found in Holbrook (2011). Although this previous study included two larger Ramphastids as well, we used data only from the many-banded araçari, because a higher number of recorded locations were available. In addition to this, the home range of this species was found to be the largest for all the species studied, and therefore it was better suited to study long-distance seed dispersal events.

### Animal movement probability distributions

What data am I using for this parameterization? It is radiotracking data, and the information on continuous trajectories for each tracked bird, to scale those distances into number of meters moved per minute for each tracking segment. I consider a tracking segment as the distance moved between two continuous radio tracking detections. (Check Kimberly’s paper), because here we are taking advantage of all the tracking data since there are different tracking interval times. Then, we used that data to fit the four models described above, and did it at the different organizational levels. We considered population level data, as all the data pooled from all individuals tracked, and fit the four distributions to that data to estimate parameters. At the individual level, we fit the four pdfs for the data in respect to each individual. For the family level data, we used only a subset of the total data set to include only individuals for which family level information existed. Because these are social individuals, they tend to move with their group and so we their movements may be correlated. We wanted to explore if there were any differences at the family group levels. We fit the four pdfs to the subset of this data, as the subset population level, and then fit each distribution to the data associated to each of the family groups. We used the parameters estimated from these fits to sample step sizes for our simulation models. We also evaluated the fit of each of these distributions visually through qq plots (found in appendix A), and further details on data organization and model fitting can be found in the online repository.

### Model selection? for the step size

# Statistics associated to the simulations

We analyzed simulation outputs and had seed dispersal distance as our main focus. We calculated summary statistics for each of the dispersal distances, and estimated the percentage of long distance dispersal events. Using the 500 meter threshold which was determined in previous work.

## Results

### Animal movement rate models

We compared the fit of the different probability distributions to animal movement rate data with Akaike’s Information Criteria(AIC) and it’s corrected version for small sample sizes (AICc), we also used the Bayesian Information Criteria (BIC) to compare these model fittings. At the population level, all information criteria concur and show that the lognormal model fits the data for movement rates the best, with the weibull model next, see table 1. However, as we visually assessed fit of these models with QQ plots and goodness-of-fit statistics (see the supplemet), the lognormal distribution model greatly overestimates the data towards the tail, whereas all the other models are significantly more conservative and tend to underestimate the data.

At the individual level, we observed similar outcomes, where the lognormal distribution consistently overestimated the data, whereas the other distributions considered did not. When comparing across distribution models at the individual level, AIC and AICc showed the lognormal fit as the best one followed by the exponential model, whereas the BIC had the exponential as the best model followed by the lognormal.

When comparing the population level models with the ones at the individual level, we found that information criteria differed. In the case of AIC and AICc, these consistently categorized the individual level models as best fitting when compared to their equivalent distribution model at the population level. However, BIC values show that only when we consider the exponential distribution model does the individual level do a better fitting than the population, with all other models having higher BIC values for the models that include individual heterogeneity.

The mixed/heterogeneous model considered the best fitting distribution for each individual, and then selected given distribution to be included in the general model that includes movement for all the individuals and calculates the information criteria value. Using different information criteria yielded different best fitting models (see supplement) for each individual, which changed the distributions included on the overall model, therefore producing two different mixed/heterogeneous modelsd with individual variation, one associated to the AIC/AICc target distributions and a different one for BIC. However, all information criteria agreed on nine out of twelve individual models. In the case of AIC and AICc four individuals were better described by an exponential distribution, three by a Weibull distribution and five by a lognormal distribution. When using BIC as the model selection tool, seven individuals were described by an exponential distribution, four by a lognormal and one by the Weibull distribution. The overall AIC, AICc and BIC values were calculated for each of the mixed/heterogenous model and compared to the previous fits, where the first five results are shown in the following table (the rest can be seen in the supplement). This shows that only the lognormal model at the population level is better than the mixed/heterogeneous model by <2 BIC units.

### Seed Dispersal Distances

We analyzed the seed dispersal distances produced by the simulation runs and there were clear differences between the simulation models. These differences clear between models that used different distributions for movement rates, whether or not they consider individual variation, the seed dispersal distances under the lognormal distribution were extremely high with several outliers for dispersal distance. The exponential, Gamma and Weibull models for movement rates produced similar seed dispersal distance distributions at the population level. All the simulations showed that models that included individual variation in animal movement rates had a higher number of long distance dispersal events.

## Discussion

added Oct 2020: call for the need for more complex animal movement models when running seed dispersal simulations. Even the posibility of mixed distribution models, where not only we allow for each individual or fmailiy group to have it’s own model, but also use multiple distributions for each. The short movements performed by these animals may be better described by a different distribution than those performed at longer intervals.

Considering animal movement in this simple framework of movement rates allows us to easily compare between individuals and how including intraspecific variation can change our estimates and fits of different models. It is known that because of this individual variation, no one distribution will fit all individuals, and therefore approaches with mixed distributions or that select different distributions for each individual are important if we want to understand the relationship between frugivore movement and seed dispersal (Russo, Portnoy, and Augspurger 2006). Previous research has focused on exploring the effects of lanscape fragmentation, heterogeneity (Jones et al. 2017, @levey\_modelling\_2008) or plant aggregation (Pegman, Perry, and Clout 2017). However, focus on intraspecific variation in frugivores and their effect on seed dispersal has only recently been studied more closely(Snell et al. 2019). The models we have used in this study show that individual variation between individual movement rates exist. There is clear evidence for heterogeneity across individuals with respect to which distribution explains the data best with both, the AIC and the BIC, regardless of whether these information criteria match. We need to move towards developing better animal movement models that incorporate this type of heterogeneity, where we don’t just pool tracking data for all individuals, but where we consider the tail end distributions of their movement.

We have also shown that including individual variation in type of distribution for movement rates produces one of the best fitting models to the data. Although in our direct comparisson between mixed models and single distribution models, the lognormal distribution at the population level was the best fitting one, the difference of 1.900455 BIC points is too small for us to reject our mixed model that states heterogeneity across individuals. This small difference points at perhaps how small sample sizes per individual can have an effect on the fits.Using BIC, a difference of approximately 4 BIC points is equivalent to stating significant difference at an 0.05 alpha level, therefore the difference of <2 BIC points is not sufficient for us to reject our mixed models with individual variation. All other models that follow are over 10 BIC units from out mixed/heterogeneous model.

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

# 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.

Levey, Douglas J., Joshua J. Tewksbury, and Benjamin M. Bolker. 2008. “Modelling Long-Distance Seed Dispersal in Heterogeneous Landscapes.” *Journal of Ecology* 96 (4): 599–608. <https://doi.org/10.1111/j.1365-2745.2008.01401.x>.

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>.

Pegman, Andrew P. McKenzie, George L. W. Perry, and Mick N. Clout. 2017. “Exploring the Interaction of Avian Frugivory and Plant Spatial Heterogeneity and Its Effect on Seed Dispersal Kernels Using a Simulation Model.” *Ecography* 40 (9): 1098–1109. <https://doi.org/10.1111/ecog.02191>.

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>.

Snell, Rebecca S., Noelle G. Beckman, Evan Fricke, Bette A. Loiselle, Carolina S. Carvalho, Landon R. Jones, Nathanael I. Lichti, et al. 2019. “Consequences of Intraspecific Variation in Seed Dispersal for Plant Demography, Communities, Evolution and Global Change.” *AoB PLANTS* 11 (4). <https://doi.org/10.1093/aobpla/plz016>.

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>.