

Abstract

Seed dispersal is a fundamental process in plant ecology and due to its importance in shaping plant distribution and communities, various modelling approaches have been developed to predict seed movement and dispersal processes. Frugivore-generated seed dispersal patterns are largely influenced by animal movements, and the intraspecific variation in animal movement and behaviors. In particular, long-distance seed dispersal (LDD) plays a significant role in determining genetic diversity and range expansion in plants. As frugivores can travel long distances and transport seeds with them, animal-mediated seed dispersal is a key component of LDD events. In this study we seek to understand the implications of individual variation in animal movement rates and how these can impact estimates of long-distance seed dispersal by changing the heaviness of tails in dispersal kernels. We use a simulation approach to explore the effects of intraspecific variation estimating parameters from empirical data for the araçari, *Pteroglossus pluricinctus*, 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 with an individual-based model on a homogeneous unbounded landscape. This approach showed that variation in individual araçari movement rates directly influences the shape of estimated seed dispersal kernels and the number of long-distance dispersal events for *Virola* seeds. Additionally, to infer the tail behavior of generated seed dispersal kernels under varying levels of disperser heterogeneity, we include an approach using statistics of extremes, which is rarely used to explore species interactions in the ecological field. We found that models ignoring underlying variation in animal movement rates are unable to predict seeds

reaching distant locations (beyond 5km) and underestimate the variance of dispersal kernels and percentage of long-distance seed dispersal events. We suggest that the modeling approaches described in this paper can be a simple method to incorporate intraspecific variation of animal movement in future frugivore-generated seed dispersal kernels.

CHAPTER 2 CONSEQUENCES OF INCORPORATING HETEROGENEITY IN ANIMAL MOVEMENT RATES INTO MODELS OF SEED DISPERSAL

The importance of the variance in community ecology has started to resurface. Despite being recognized as a major driver of diversity in the 1970s, intraspecific variation has largely been ignored in community ecology over the last few decades (Violle et al. 2012; Holyoak & Wetzel 2020). Variation, or heterogeneity, has long been considered a property of ecological systems that might contain as much ecological information as do averages and regularities in nature (Pielou 1969). However, ecological models typically focus on trait means and assume that individuals within a species are interchangeable (Bolnick et al. 2003, 2011), an assumption that can mislead our understanding of ecological dynamics or create bias in ecological estimates (González-Varo & Traveset 2016). Ignoring individual variation can significantly impact the way we understand species interactions and connectedness (Poisot et al. 2015), or the way individuals respond to fluctuating climatic conditions (Lewis & King 2017). In particular, ignoring individual heterogeneity may affect predictions of rare interactions or occurrence of extreme events, which are determined by variation around the mean and not a population's average (Gaines & Denny 1993; Nathan et al. 2008; Denny 2017). The impact of more frequent extreme events in ecological processes has also been demonstrated in population dynamics modeling; when individual heterogeneity is phrased as demographic stochasticity it shapes extreme events and as a consequence, quasi-extinction dynamics (Ferguson & Ponciano 2015).

Seed dispersal mutualisms may be a particularly attractive system to study the effects of individual heterogeneity on species interactions, as reliance on species averages is a current limitation in the study of plant-seed disperser mutualisms (Schupp

et al. 2017; Zwolak 2018). 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 & Smallwood 1982; Terborgh & Wright 1994; Nathan & Muller-Landau 2000). In seed dispersal mutualisms, frugivore behavior, physiological traits, and movement patterns largely influence the spatial deposition of the seeds they carry (Côtés & Uriarte 2013). Several studies have explored how fragmenting landscapes (Levey et al. 2005; Damschen et al. 2008; Jones et al. 2017), varying levels of plant aggregation (Morales & Carlo 2006; Pegman et al. 2017), or frugivore behavior (Russo & Augspurger 2004; Westcott et al. 2005; Russo et al. 2006; Karubian & Durães 2009; Sasal & Morales 2013) impact seed deposition patterns. Recent work has also emphasized the importance of considering seed disperser communities or assemblages, as the contributions to seed dispersal across species vary significantly (Jordano et al. 2007; Schupp et al. 2010; Rehm et al. 2018). However, less attention has been devoted to understanding how complex animal behavior, movement, or individual heterogeneity in frugivores may impact seed dispersal distances and deposition patterns (Côtés & Uriarte 2013; Snell et al. 2019; Zwolak & Sih 2020).

Of particular importance, understanding the effects of individual variation in frugivore movement on long-distance seed dispersal can inform models of community assembly at larger scales. Long-distance dispersal events are a key process in shaping landscape-level characteristics such as population spread, gene flow between populations, establishment in new micro-habitats (Ouborg et al. 1999; Nathan & Muller-Landau 2000; Jordano 2017), and they can also determine a plant population's ability to

adapt to a rapidly changing climate (Kremer et al. 2012; González-Varo & Traveset 2016). Even though it has been suggested that different frugivore species may contribute disproportionately to long-distance dispersal events (Jordano et al. 2007), and that individuals differ in how far they move and disperse seeds (Lenz et al. 2011), little work has been done to understand how individual heterogeneity might contribute to long-distance seed dispersal.

In this paper, we focus on the consequences of incorporating intraspecific variation in animal movement rates over seed dispersal distances and patterns. Specifically, we developed a spatially-explicit individual-based model to explore how differences in animal movement rates could influence seed dispersal deposition and the parameters of distribution functions associated to dispersal distances. Individual-based models are commonly used to understand the maintenance and generation of diversity (Levi et al. 2019), and in the seed dispersal literature they are used to develop a mechanistic understanding of the plant-seed disperser mutualism across changing landscapes, or disperser behaviors (Russo & Augspurger 2004; Levey et al. 2005; Morales & Carlo 2006; Will & Tackenberg 2008; Jones et al. 2017; Pegman et al. 2017; Holbrook & Smith 2000; Bialozyt et al. 2014). Using a simple simulation model, we explore how to incorporate this individual heterogeneity via pooling approaches (Langrock et al. 2012), using previously collected data from the the many-banded araçari, *Pteroglossus pluricinctus*, one of the primary frugivores of the Amazonian canopy tree *Virola flexuosa* (Holbrook & Loiselle 2007, 2009). We consider three different pooling levels to incorporate no variation in movement rates, variation constrained by social groups, and variation at the individual level. Our findings show

that incorporating individual heterogeneity in disperser movement rates can be recognized in the outcomes of simulation models through differences in the number of long-distance seed dispersal events, greater variance and heavier tails in the distribution of seed dispersal distances. Our research also demonstrates the importance of framing the study of rare events in seed dispersal ecology within the context of extreme value theory in statistics to better predict the changes in probabilities of seeds dispersing extreme distances.

Methods

Simulation Approach: An Overview

To study the effects of individual variation in animal movement on final dispersal distances of foraged seeds, we developed a stochastic, spatially-explicit and individual-based modeling framework in a homogenous landscape consisting of a single source tree. After “consuming” five seeds from the source tree, our model animals would move and deposit the seeds at random. To parameterize and run the model using realistic values (see “Study Design and Model Parameterization” section below) we used empirical movement metrics obtained from a radio-tagging study of various toucan species, including *Pteroglossus pluricinctus* (Holbrook 2011). We also used available estimates of the seed retention times for toucans that ingested tagged seeds of *Virola flexuosa*, a tropical plant belonging to the nutmeg family (Holbrook & Loiselle 2007; Holbrook 2011).

Here, a simulation approach is useful in as much as it represents an effort to understand the factors that contribute to variation in seed shadows, which are the spatial distribution of seeds dispersed from a single plant. Seed shadows are studied using Seed Dispersal Kernels (SDKs heretofore), which are probability models used to

describe the chances that a seed is dispersed or deposited at a specific distance away from its parent plant (Nathan & Muller-Landau 2000). Dispersal kernels in nature tend to be leptokurtic, with a peak near the origin and long tails (Morales & Carlo 2006).

Although the seed dispersal process could be conceptualized/summarized using a long series of complex steps, here we hypothesized that any given SDK is the result of three key components: 1) the accumulation of a series of movement bouts per unit time (one minute in our case) of an animal after ingesting a seed, 2) the movement angle accompanying each movement bout of the animal, and 3) the gut retention time (GRT, the time that ingested seeds stay inside the frugivore until they are dropped). As we describe below, we modeled all three components as random variables, and used a stochastic simulation to generate seed shadows using the *Pretoglossus pluricinctus* and *Virola flexuosa* system. A single simulation run of our model consisted of a virtual animal (a bird) ingesting five seeds, then allowing it to move at random through the landscape in one-minute bouts until it had “dropped” all five seeds. Our program recorded each animal’s trajectory as well as the seed dropping locations (Figure 1A). We used our simulation program to calculate dispersal and dispersion measures (Figure 1, panels B and C), and estimated parameter values for seed dispersal kernels (Figure 1, panel D). We used this information to test the hypothesis that individual variation in the movement distance rate per unit time ultimately resulted in highly leptokurtic and long tailed SDKs as opposed to the SDKs obtained under the assumption of homogeneity in animal movement rates. Specifically, we evaluated the differences in the SDKs resulting from assuming i) that all virtual toucans in a large flock feeding from a single source tree had identical movement rates per minute, ii) movement rates of

virtual toucans would be bound by the average movement rate of their social group, as these toucans often forage with their social group, or iii) that each individual toucan had its own movement rate different from others.

Study Design and Model Parameterization

To estimate movement rates and gut retention times, we focused on available empirical data on the many-banded araçari (*Pteroglossus 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 consisted of capturing and radio-tagging individuals from various toucan species, including *Pteroglossus pluricinctus* and two larger Ramphastids, although data on the latter were scarce. Location recordings were attempted every 15 minutes, but due to field conditions, this time frame wasn't always possible, leading to location recordings at uneven time intervals. To manage this heterogeneity in time between locations, we estimated movement rates, which are described as the average number of meters moved per minute over the entire tracking period for each tracked individual (Holbrook 2011). We used a threshold of 30 movement bouts, to estimate an individual's movement rate, for which we had data on 12 individuals. A movement bout is the movement between two consecutive point locations. Because *Pteroglossus pluricinctus* individuals tend to forage in social groups, we also calculated movement rates at the social group level by averaging the movement rates of the individuals belonging to a given social group (Table 2-1).

We simulated three different scenarios by varying the movement rate of individual animals. We considered different pooling approaches, meaning that the data

used to estimate the movement rate were grouped at different levels with each scenario (Langrock et al. 2012). The first scenario consisted of a 'complete pooling' approach, in which a single movement rate is used for all individuals. The second scenario followed 'partial pooling', where movement rates for individuals were constrained by the distribution of movement rates within social groups. The final scenario incorporated individual variation with a 'no pooling' approach, where each individual had its own movement rate (See Figure 2-2). The movement rate is the inverse of the average distance moved in one minute, and thus it is used as the parameter in an exponential distribution to sample an animal's movement distance at every time step in the simulation run (See simulation description below).

The movement rates calculated from the data were used to run our simulations in the following manner. 1) We fitted a lognormal distribution to the movement rates for the twelve individuals to describe what we consider the population's distribution of movement rates (Figure 2-2). 2) For the complete pooling scenario, we calculated the expected value of the fitted lognormal distribution and used it as the single movement rate for those simulations. 3) In the case of the partial pooling, due to the low number of individuals per social group, we used the social group's movement rate as the μ parameter in a lognormal distribution and used the variance (σ^2) of the fitted distribution in step 1 to describe the distribution of movement rates for a given social group (Figure 2-2). 4) From each of the seven movement rate distributions associated for each social group, we sampled six movement rate values, and used them as the members of each social group in the partial pooling scenario. 5) Finally, for the no pooling scenario, we

sampled 30 individual movement rates from the lognormal distribution fitted in step 1 (Figure 2-2).

Parameter values for gut retention time were also based on empirically collected data from previous passage trials carried out with *Pteroglossus pluricinctus* individuals (Holbrook & Loiselle 2007). These passage trials were performed on four individuals captured in the field, held for two days, and fed *Virola flexuosa* seeds, which were marked with cotton threads and placed inside papaya cubes. Gut retention times were calculated based on seed ingestion and regurgitation times of tagged seeds. The distribution of gut retention times is best described with a fat-tailed distribution (Morales & Carlo 2006), thus we fit a gamma distribution to the field data on gut retention times, and estimated the gamma parameters, assessing goodness of fit visually using QQplots. We used this gamma distribution to later sample gut retention times for each seed in our simulation runs (Figure 2-3).

Simulation Description

Each simulation run started with the animal at the origin with the source tree, at location (0,0). At the beginning of the simulation run, the animal received five seeds, each seed with an associated gut retention time randomly sampled from the gamma distribution described in Figure 2-3. The simulation ran at one-minute intervals, and at every time step, a movement distance and movement angle determined the animal's movement path (grey path in Figure 2-1). Movement distances were randomly sampled from an exponential distribution, using as a parameter, the inverse of the movement rate selected for that specific simulated animal. Movement rates were randomly sampled according to the scenario being simulated as shown in Figure 2-2. Movement angles were sampled at each time step from a random uniform distribution, thus the

simulated movement path had no specific directionality. Each simulation run allowed for the five seeds to be dropped at the animal's location when the simulation reached each one of the gut retention times associated to each seed. The simulation run ended once all five seeds were dropped. We ran 100,000 simulation runs for each of the three pooling scenarios (complete, partial, and no pooling), with the number of simulations distributed evenly among the number of individuals for that particular scenario (42 in partial pooling and 30 in no pooling).

Average Seed Dispersal and Aggregation Metrics

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

$$DD_i = \sqrt{(0 - x_i)^2 + (0 - y_i)^2} \quad (1-1)$$

where DD_i is the dispersal distance for seed i in the simulation run, and x_i and y_i are that seed's location coordinates in the landscape. As described above, every simulation run consisted of five seeds being dispersed by the virtual animal, each with 100,000 simulation runs per pooling scenario, this meant we had 500,000 seeds dispersed for each pooling scenario. We calculated the average seed location per run, out of the five seeds dispersed in each run, and estimated the dispersal distance per run as the distance from the origin to the average seed location. We also used an aggregation metric to determine how evenly seeds would be dispersed across the landscape in each simulation run. We calculated seed dispersion as the average distance of each seed to

the mean seed location in each simulation run following methods in previous studies (Jones et al. 2017):

$$SD_j = \frac{\sum \sqrt{(x_{mj} - x_{ij})^2 + (y_{mj} - y_{ij})^2}}{n} \quad (1-2)$$

where n is the number of seeds for each simulation run (5 seeds), and x_{mj} and y_{mj} are the mean seed locations in the j simulation run. Thus, for each pooling scenario we had 100,000 values of average dispersal and seed dispersion. Given that seed dispersion is a measure of distances away from a spatial mean, an increase in seed dispersion for our study is equivalent to having seeds be deposited more evenly (Jones et al. 2017). We calculated mean and standard deviation for these metrics across all simulation runs for each pooling scenario to compare across models.

Seed Dispersal Kernel Estimation

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 the model of each pooling scenario. 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 three models by calculating the mean and standard deviation, kurtosis, maximum dispersal distance, and percentage of long-distance dispersal events for each of the pooling scenarios. To classify dispersal distances as long-distance events, we used a threshold of 500m based on previous work associated to this specific system (Holbrook & Loiselle 2007). In addition to this,

we also fit a Weibull probability distribution, commonly used in dispersal ecology as it is flexible enough to accommodate variability in the tails and provide informative parameters associated to the mean dispersal distance and heaviness of the tail (Morales & Carlo 2006). Given that we had a large number of simulated seeds, we fit Weibull distributions to random Monte Carlo subsamples in each scenario. This means that for each pooling scenario, we sampled 100 seeds and fitted a Weibull distribution to their distance from the origin. We repeated this process 1000 times for each pooling scenario and compared the distribution of shape and scale parameters across pooling scenarios using the non-parametric kernel density estimation from the `kde1d` package in R (Nagler & Vatter 2020) and calculating their mean and 95% confidence intervals. To fit the data associated to seed dispersal distances via Maximum Likelihood we used the function 'fitdist()' from the package 'fitdistrplus' (Delignette-Muller & Dutang 2015) in R using the following probability density function:

$$W(x) = \left(\frac{a}{b}\right) \left(\frac{x}{b}\right)^{a-1} \exp[-(x/b)^a] \quad (1-3)$$

The estimated shape and scale parameters determine the tail of the distribution, and the location of the peak of the distribution respectively. It is worth noting that the standard parameterization of the Weibull distribution in 'R' is different from the parameterization used in Morales and Carlo (2006), where the shape parameter $a = \nu$ remains the same, but the scale parameter is defined as $\kappa = b^{-\nu}$, giving a density distribution function of $W(r) = \kappa \nu r^{\nu-1} \exp[-\kappa r^\nu]$. We can note that for $a = \nu = 1$ the distribution shows a tail with exponential decay, with values of $\nu > 1$ the tail shows fast-decay or thin tail, and when $\nu < 1$ we can see a fat-tailed distribution (Morales and Carlo 2006).

More recently, statistics of extremes have been used to model extended dispersal kernels of seeds and pollen (García and Borda-de-Água 2017) and in particular have been proposed to understand long-distance dispersal events (Rogers et al. 2019). In our particular case, we evaluated how an approach using statistics of extremes could help us fit the tail of the frugivore-generated seed dispersal kernels for each of the models we simulated. We used a peak over threshold (POT) approach, in which we filtered the dispersal distances above a given threshold and fit a Generalized Pareto (GP) distribution to those values (readers interested in more technical details associated to statistics of extremes should consult Coles 2013 for a general overview, or García & Borda-de-Água 2017 for a seed dispersal specific text). The advantage of using an extreme value distribution approach lies in the fact that seed dispersal distances that are too far from the mean might be considered as outliers with more conventional approaches, and thus their frequency not accurately predicted with commonly used dispersal kernels. However, we know that extreme long-distance dispersal events are not as rare, but their frequency is low when using conventional sampling approaches such as seed traps (Nathan & Muller-Landau 2000; Levey et al. 2008). Therefore, a statistics of extremes approach for long-distance seed dispersal events can give us a better prediction of these events without underestimating their frequency.

Initially, we defined long-distance dispersal events as any dispersal event over 500m from the parent tree in order to compare our results to previous studies in this same ecological system (Holbrook & Loiselle 2007, 2009). We used this threshold to calculate the percentage of long-distance seed dispersal events. To select the threshold

for a POT approach, we used mean excess and diagnostic plots fitting the data to a sequence of thresholds, with the goal of finding the lowest threshold providing similar parameter values with the lowest variation around those estimated parameters. This is a useful quantitative approach to define long-distance dispersal events based on a specific biological system's data (García & Borda-de-Água 2017). There still exists a lot of variation in methodologies to define what long-distance dispersal is, and this varies within biological systems as well (Jordano 2017). Thus, providing a method using data to establish the threshold is useful to compare the number or distribution of long-distance dispersal events across studies in the future. To fit the Generalized Pareto distribution, we randomly sampled 10,000 seed distances from each of the pooling scenarios, and selected the appropriate thresholds using mean excess plots. We estimated shape and scale parameters for each dataset using the previously selected threshold. In the case of the Generalized Pareto, shape parameters below zero indicate a thin-tailed distribution with an upper limit, a shape parameter greater than zero corresponds to a heavy-tailed distribution with no upper limit, and shape parameters equal to zero follow exponential tails. Using the estimated parameter values for each of the three simulated data sets, we calculated conditional probabilities of seeds dispersing over 200, 500, 1000, and 5000 meters under the three pooling scenarios. We performed these analyses and fit Generalized Pareto distributions to the data via maximum likelihood using the package `extRemes` in R (Gilleland & Katz 2016).

Results

Average Seed Location and Dispersion Per Simulation Run

Dispersal per run was calculated as the distance from the origin to the average seed location in each simulation run and average dispersal per run was highest in the

CP scenario at 175m (SD = 82.1m), followed by the NP scenario at 157m (SD = 95.3m), and last with the PP scenario at 141m (SD = 89.4m). The overall distribution of average dispersal per run across all three scenarios was similar (Figure 2-4), however, the density of outliers and maximum average dispersal distances was highest in the NP scenario, followed by the PP scenario. In the case of seed dispersion, higher values of seed dispersion indicate a more even seed deposition for each simulation run. When comparing the three pooling scenarios, we observe that the overall distribution of seed dispersion values is comparatively similar, with boxplot whiskers all falling under 200m of dispersion (Figure 2-4). Some differences are observed when focusing on the outliers, where the PP and CP scenarios have the largest dispersion values per run (614 and 602 respectively), although the NP scenario shows a higher density of values over 400m. A two-dimensional representation of these results is observed in Figure 2-4, where we observe the average seed locations per run for each of the three scenarios, all of them with a higher density of seed deposition close to the origin, and the NP scenario with the highest number of average seed locations falling outside the 500m LDD threshold from the origin.

Estimated Seed Dispersal Kernel Functions

We estimated parameter values of a Weibull distribution for 1000 random samples of 100 seeds from each of the simulation models corresponding to each pooling scenario and generated the seed dispersal kernel curves shown in Figure 2-5. When focusing on the tail of the distributions (Figure 2-5), we observe differences between the dispersal kernels generated under the three pooling scenarios, with the NP scenario having a higher number of kernels with heavier tails. The shape and scale parameters estimated for the dispersal kernels varied between pooling scenarios

(Figure 2-5), with the PP scenario having the lowest values for the estimated shape parameter, followed by the NP scenario. Although variation existed between the estimated shape parameters for the Weibull kernels, no shape parameters were smaller than 1, a value indicating a heavy tail. The estimated mean dispersal distance from the kernels showed the CP scenario having the highest values, followed by the NP scenario, and PP scenario last (Figure 2-5). The distribution of variance values estimated for each of the dispersal kernels was similar across pooling scenarios, however there was considerable variation in the outliers, with the NP scenario having the highest estimated variances.

Seed dispersal distances generated by the simulations under the three pooling scenarios showed differences in kurtosis, with the NP and PP scenarios having higher kurtosis than the CP scenario (Table 2-2), alluding to a higher number of outliers or extremes in the scenarios incorporating levels of individual variation. Although the highest mean dispersal distance was found in the CP scenario, the maximum dispersal distance for an individual seed occurred in the NP scenario, which also had the highest percentage of seed dispersal events over 500 meters (Table 2-2).

Analyzing Seed Dispersal Kernel Tails with A Statistics of Extremes Approach

We selected thresholds specific for each of the pooling scenarios based on the distribution of the data, a subsample of 10,000 seed distances for each scenario. The threshold values selected from the mean excess plots are listed on Table 2-3, with the NP scenario having the highest threshold, followed by the CP scenario. Estimated shape and scale parameters followed the same pattern as did the Weibull parameters in the previous sections, with CP having the largest scale parameter, followed by NP, and PP last. However, in the case of the shape parameter, both CP and PP had shape

parameters smaller than zero, with the NP scenario's shape parameter being greater than zero. The heavier tail estimated for the NP scenario is also represented when considering the conditional probabilities of a seed dispersal distance being over 1000 or 5000 meters (Table 2-3). When focusing on the probability that a seed will be dispersed over 1000 meters from its parent plant, there is a difference of one order of magnitude between the three scenarios, with the NP scenario having the highest probability of depositing seeds over 1000 meters. When observing the most extreme case of seeds being deposited over 5000 meters from the parent plant, both the CP and PP scenarios have a zero probability of doing so under the Generalized Pareto tail fit, whereas the NP scenario has a very small, but nonzero, probability.

Discussion

Spatial patterns of seed dispersal are largely influenced by plant-specific traits, frugivore characteristics and behaviors, and interactions with the landscape (Schupp & Fuentes 1995; Nathan & Muller-Landau 2000). Frugivore-generated seed dispersal kernels have been used to estimate seed dispersal distances in multiple studies (Levey *et al.* 2005, 2008; Morales & Carlo 2006; Russo *et al.* 2006; Will & Tackenberg 2008; Jones *et al.* 2017), often with the goal of understanding how incorporating animal movement and behavior will impact seed dispersal distances. Usually, the focus tends to be on seed dispersal and how spatial patterns of seed aggregation can change in response to animal behavior or landscape heterogeneity. However, fewer studies have emphasized the role of intraspecific variation in animal movement over generated seed dispersal patterns, or even the relative importance that different disperser species may have in carrying seeds and contributing to seed dispersal patterns (Rehm *et al.* 2018; Zwolak 2018). Various modeling and simulation approaches have been developed to

understand how the interactions between landscape heterogeneity and frugivore characteristics affect seed deposition patterns (Levey *et al.* 2005; Russo *et al.* 2006; Jones *et al.* 2017), and others, like Levi *et al.* (Levi *et al.* 2019) have implemented mechanism-free simulations that highlight the importance of rare and long-distance seed dispersal events like the ones we have modeled here. Additionally, there is a lack of focus in the literature on the complexity of animal movement and how it influences seed dispersal and plant population dynamics across multiple scales (Côtés & Uriarte 2013). We found that by incorporating different levels of movement heterogeneity across individual frugivores, seed dispersal and aggregation metrics changed. Overall, our simulated seed dispersal kernels showed that an increase in variation of animal movement rates markedly influenced the heaviness of the tail in dispersal kernels: the greater the heterogeneity, the more relevant long-dispersal events are. Additionally, by increasing the level of variation in animal movement rates, we observed increases in the kurtosis and estimated variance of dispersal kernels, having direct implications for the number of predicted long-distance dispersal events. Using a statistics of extremes approach, our results show that predicting extreme seed dispersal events is more likely under scenarios that incorporate individual variation in animal movement rates. Understanding the consequences of individual variation in animal movement is a critical step to incorporate our local scale predictions on regional and community level models of population dynamics. Although extreme value theory has long been used in other areas of biology to better understand the maintenance and generation of genetic (virus) variants (Orr 2005), its use in modeling the ecological processes related to seed dispersal is still in its infancy.

The Effect of Variation in Animal Movement Over Seed Deposition Patterns

Average seed locations for simulations across all three pooling scenarios were between 140 and 175 meters, with standard deviations of over 100 meters, generating significant overlap in the average distribution of seed dispersal measures for the three pooling scenarios (Figure 2-4). Previous studies on this system have found that the majority of dispersed seeds are dispersed beyond 100 meters of the parent plant (Holbrook & Loiselle 2007). However, a focus on the seed dispersal data points beyond the upper quartile shows differences between the pooling scenarios, with the NP scenario having a higher density and larger extent of average dispersal per run. A similar result was found when comparing seed dispersion, a metric of spatial aggregation, which at higher levels represents a more even distribution of seeds (Jones *et al.* 2017). The overall distribution of the dispersion points per simulation run was comparable across scenarios. This result might be explained by the fact that we used a simple uncorrelated random walk for animal movement, in a homogeneous unbounded landscape, thus leading to a highly even pattern of radial seed deposition. When focusing on seed dispersion data points beyond the upper quartiles, it is unclear if differences across simulation scenarios persist. In addition to gut retention time, seed aggregation is also determined by landscape characteristics such as fragmentation (Levey *et al.* 2005; Morales & Carlo 2006; Carlo & Morales 2008a; Jones *et al.* 2017). In our frugivore-plant system, however, the forested landscape was intact and no anthropogenic barriers to animal movement were present.

Implications of Animal Movement Heterogeneity Over Seed Dispersal Kernels

Dispersal kernel shape and scale parameters have significant implications for ecological and evolutionary processes (Nathan & Muller-Landau 2000; Nathan 2007). Specifically, dispersal kernel shape can largely determine the extent to which seeds will get dispersed, thus predicting the probability of LDD events (Morales & Carlo 2006; García & Borda-de-Água 2017). The simulation scenarios that included variation in animal movement rates had larger percentages of dispersal events beyond 500m (Table 2-2) as well as higher kurtosis than the CP scenario, which had a single movement rate for the simulations. We observed this finding again as the NP scenario also holds the largest seed dispersal distance for an individual seed, despite the average seed dispersal distance for this scenario, not being the largest one. By incorporating individual variation in movement rates of frugivores, we obtain highly leptokurtic dispersal kernels, an increasing in the number of outliers and also an increasing in the number of predicted long-distance dispersal events. This qualitative difference between scenarios was replicated in the distribution of the shape parameters, which largely determine the heaviness of the tail for the dispersal kernels (Figure 2-5). Although none of the shape parameters fell below 1, a threshold that determines a heavy tail, shape parameters for the PP and NP scenarios have lower values, leading to heavier tails when compared to the CP scenario. This difference becomes more evident as we analyze the estimated mean and variances generated from these dispersal kernels (Figure 2-5). Although the estimated mean for dispersal kernels under the CP scenario is larger than the estimates under the PP and NP scenarios, the estimated variance is larger for the dispersal kernels generated by models incorporating varying levels of individual heterogeneity in frugivore movement. This individual variation in

movement has a noticeable effect on higher moments (variance and kurtosis) at the seed dispersal scale, which is not noticeable when we are focusing on just the mean.

When analyzing the tail of the distributions with the statistics of extremes approach, this difference becomes clearer. The NP scenario is the only one with an estimated shape parameter greater than 0, indicating a Generalized Pareto heavy tail. This result becomes more evident with the predicted probabilities of seed dispersal beyond 1000 and 5000m (Table 2-3). Even though these probabilities are small, they are not unreasonable, as under these predictions 1 in every 1000 seeds will fall beyond 1km over the estimated threshold for the NP scenario, 2 in every 10,000 seeds for the PP scenario, and 4 in every 100,000 seeds for the CP scenario. These predictions also show that no seeds are expected to be deposited over 5km for both the CP and PP scenario, however 7 in 10^{12} seeds are predicted to be deposited beyond this distance for the scenario including individual heterogeneity in disperser movement rates.

Variation in Animal Movement Effects Over Community Dynamics

The importance of long-distance dispersal for plant community genetic variation and recolonization is broadly recognized (Cain *et al.* 2000; Levey *et al.* 2008; Jordano 2017), and understanding how we can better model and predict these rare events can guide future efforts in restoration and conservation biology. Previous studies have also recognized the need to carefully address the complexities of animal behavior and movement patterns (Russo *et al.* 2006; Côrtes & Uriarte 2013; Zwolak 2018; Nield *et al.* 2019, 2020), as the variation in disperser traits can directly impact seed dispersal patterns. It is also necessary to consider that seed dispersal mutualisms do not occur in closed environments, and multiple disperser species will benefit multiple plants through seed dispersal services; considering how these multiple species interact and differ in

their movement patterns is an important focus for further study (Rehm *et al.* 2018, 2019).

Although novel network approaches can be a path forward to model disperser communities, the question remains of how individual heterogeneity will influence long-distance seed dispersal events. In particular, incorporating complexity and variation in disperser movement and behavior is necessary to be able to account for the disproportionate influence that some frugivores may have on the number of long-distance dispersal events and consequently on the effect over plant population dynamics and gene flow (Jordano *et al.* 2007). Novel network approaches or modeling techniques in the seed dispersal literature need to explicitly consider rare events and incorporate statistics of extremes to truly understand these ecological processes vary across scales. In our simulation study, the hierarchy of the CP, PP, and NP levels of variation in movement rates are distinguishable across the generated seed dispersal kernels. The effects of individual variation in movement needs to be extended to models of spatial community dynamics, where it is expected that rare events will lead to different outcomes.

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. These extreme dispersal events create a link between local and regional dynamics that are yet to be explored. Incorporating individual variation in animal movement models is an active area in the movement ecology field, with various approaches being developed to incorporate this

heterogeneity in hierarchical frameworks (Börger & Fryxell 2012; Bastille-Rousseau *et al.* 2016). By not including disperser individual heterogeneity effects over seed dispersal, we might be missing part of how these different ecological scales are connected.

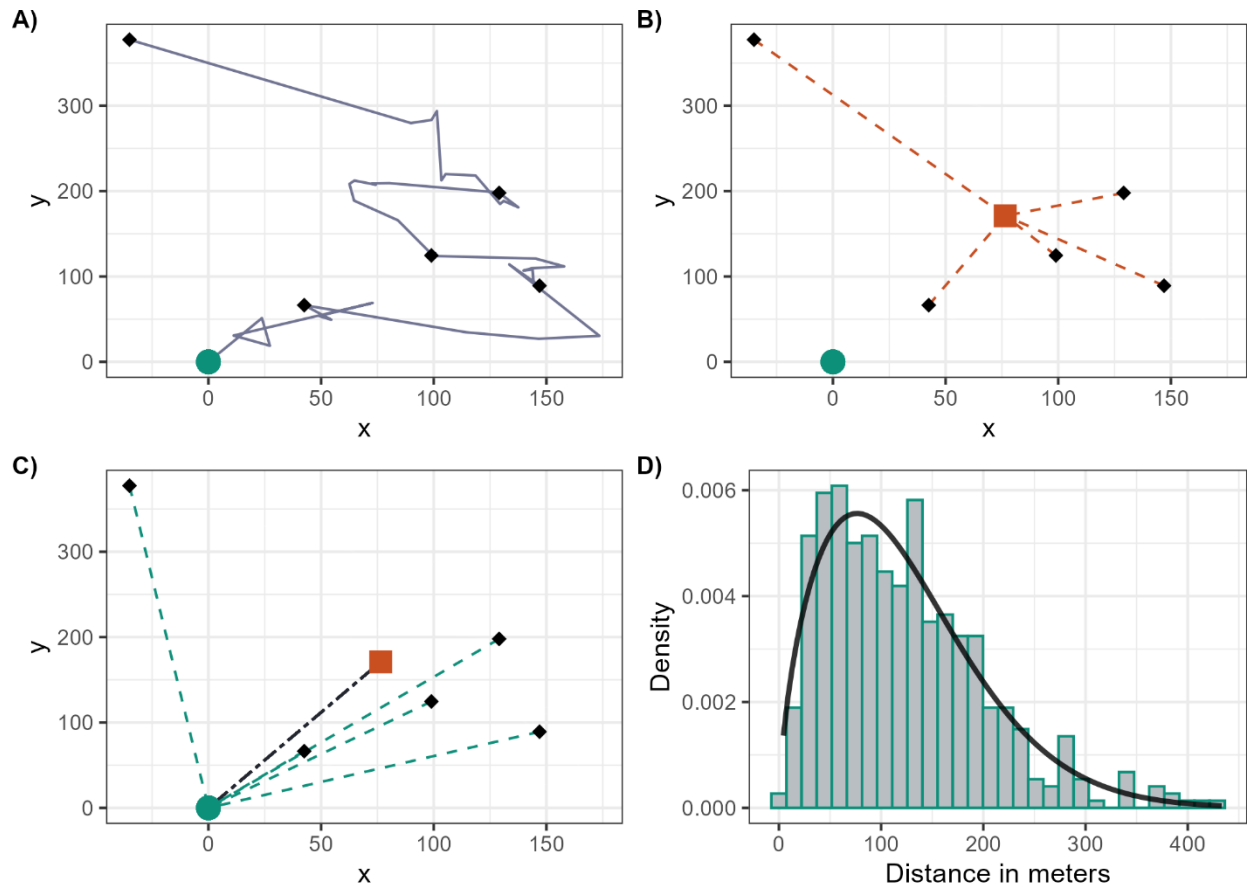


Figure 2-1. Simulation process overview and seed dispersal measures. Panels A through C represent one simulation run, whereas panel D shows the results from 100 simulation runs. A) An animal starts at the origin (coordinates (0,0) represented by the teal dot) where it ingests five seeds. The animal moves in the landscape (grey trajectory path) and drops seeds (black diamonds) as it reaches their gut retention time. B) The mean seed location per run is calculated and shown in the orange square. The distance of each seed to the mean location is used to calculate seed dispersal as described in the main text. C) Average seed dispersal per run (black dashed line) is calculated as the distance from the origin (teal dot) to the mean seed location (orange square). Seed dispersal distance for each seed (teal dashed lines) are calculated as the distance of each seed from the origin. D) Seed dispersal distances for each seed in 100 simulation runs are used to generate a seed dispersal distance histogram. A Weibull distribution is fit to the data to describe the seed dispersal kernel.

Table 2-1. Movement rates for the twelve tagged individuals from data collected by Holbrook (2011). Movement rate for individuals is calculated as the distance moved in meters per minute for every movement bout, averaged across all observations during the tracking period. In the case of social groups, the movement rate is calculated as the average for all movement bouts across all individuals belonging to that social group. Movement rate units are in meters displaced per minute.

Tag ID	n. observations	Movement rate	Social group	Movement rate
1	42	30	f1	40.1
3	76	41.9		
5	42	47.1		
7	68	25	f2	25
13	58	31.2	f3	29.4
19	53	27.3		
22	43	27.8	f4	27.8
28	38	17.9	f5	17.9
49	84	20.2	f6	26.1
84	80	32.2		
29	32	20.9	f7	16.5
30	48	13.6		

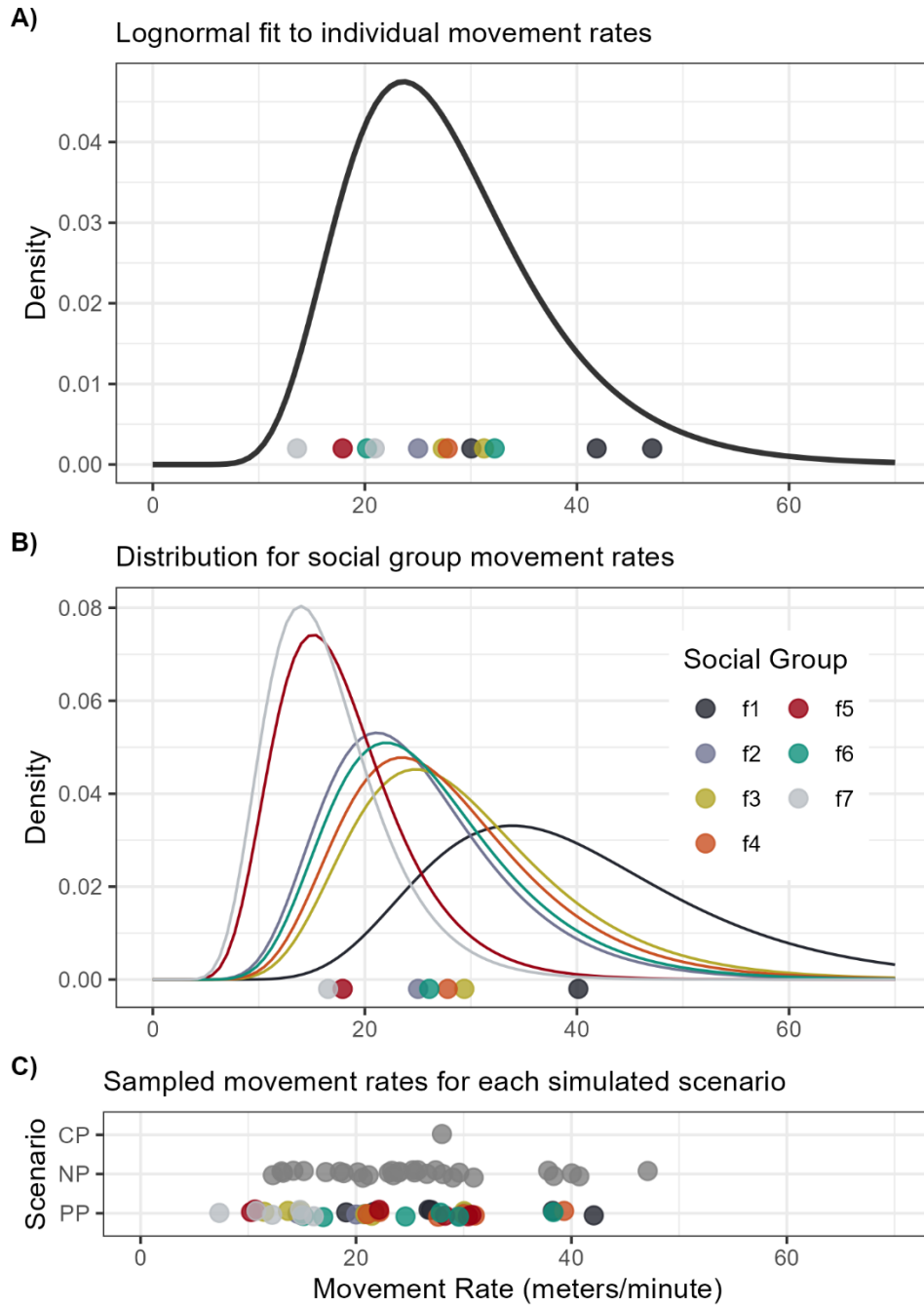


Figure 2-2. Fitted distributions to movement rate data from estimated from radiotracking. A) lognormal distribution fitted to the twelve data points of movement rate. B) Lognormal distributions for each social group. C) movement rates used for each of the pooling scenarios.

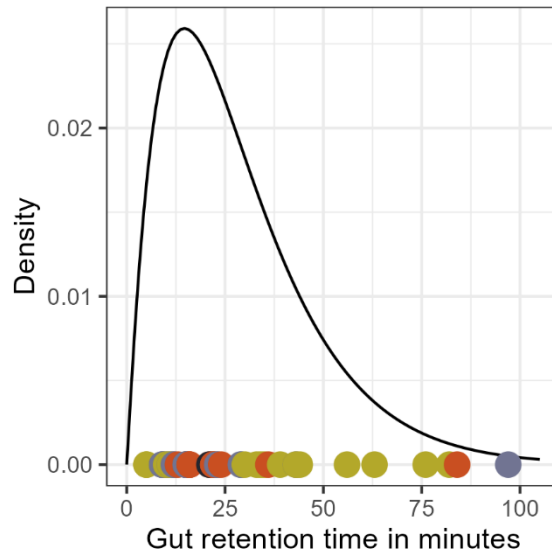


Figure 2-3. Description of gut retention times using field data for four individuals, shown by each dot along the x axis. The density curve fitted corresponds to a gamma distribution with parameters shape = 2.0562 and scale = 13.8688. This gamma distribution is later used to sample gut retention times for simulations.

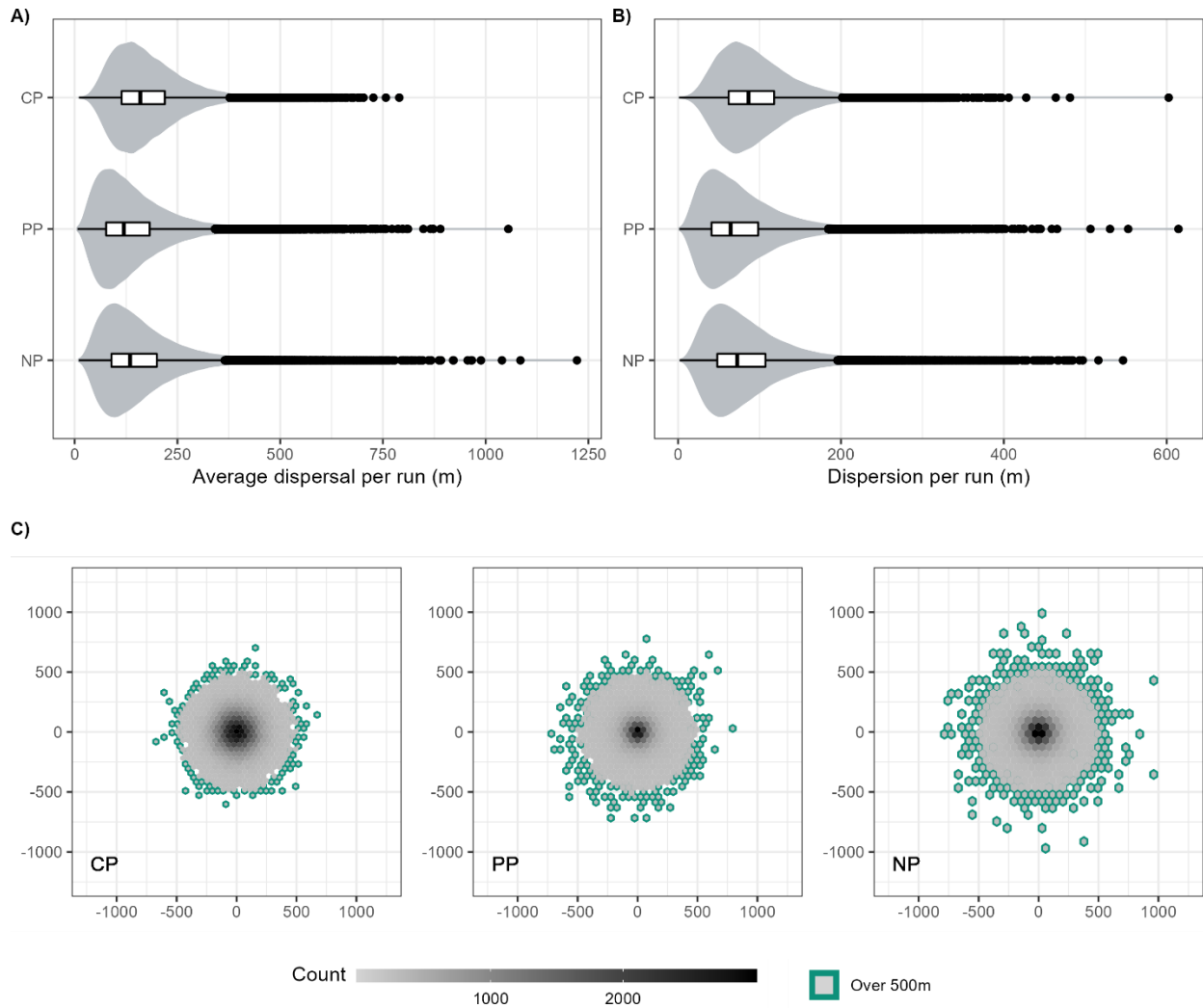


Figure 2-4. Average dispersal and dispersion for simulation runs. A) Dispersal per run is calculated as the distance from the origin to the average location of the 5 seeds in that run. The average seed location is then used to calculate dispersion as the distance of each seed to the average seed location in that run. Overall distribution of average dispersal is similar across scenarios, with differences in the density and location of outliers, with the furthest average dispersal at 1222m in the NP scenario. B) Seed dispersion per run in the three pooling scenarios. Higher values of dispersion represent more even distribution of seeds per simulation run. The overall distribution of dispersion data points is comparable across scenarios. When we focus on outliers, we observe a higher density of points past 400m of dispersion in the NP scenario, however the most extreme outliers belong to the PP, and CP scenarios. C) Average seed locations per simulation run.

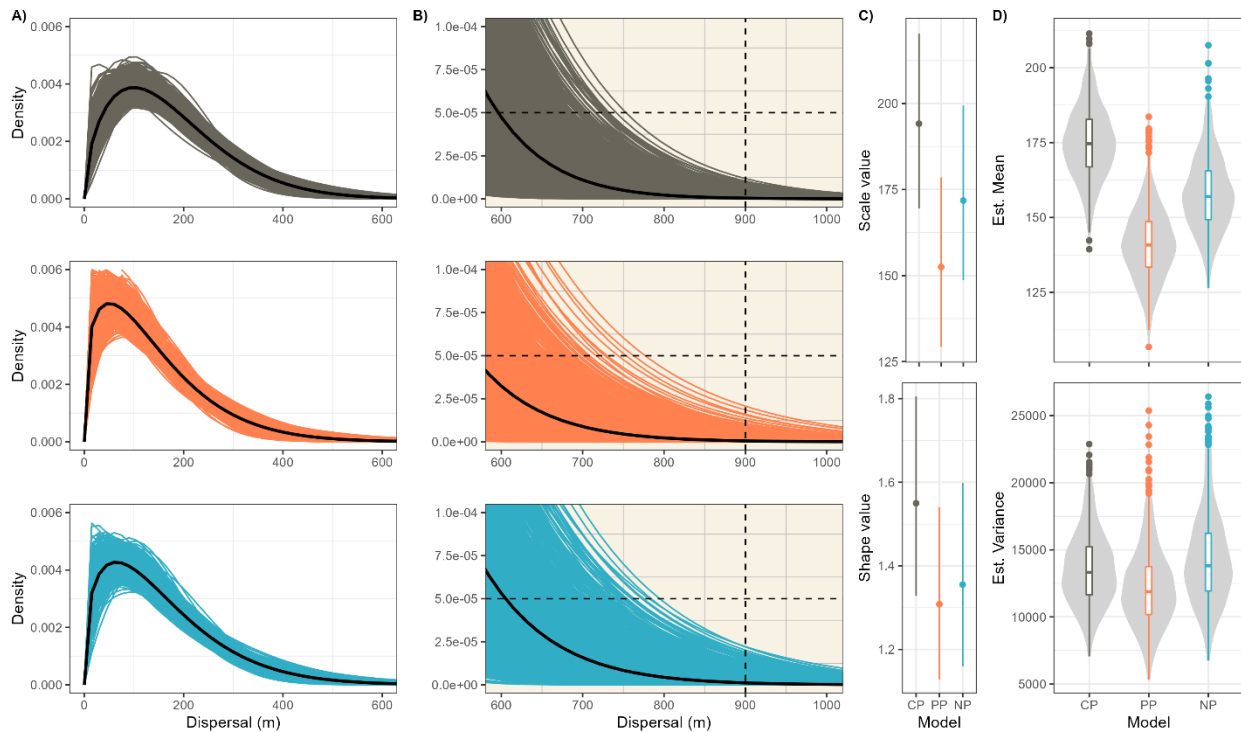


Figure 2-5. Estimated seed dispersal kernels and distribution of parameter values for the three pooling scenarios. A) Seed dispersal kernel curves for 1000 random samples of 100 seeds for each of the pooling scenarios based on fitting a Weibull probability density function to the data. B) Focus on the tails of the dispersal kernels, where the dashed lines are used for guiding purposes only. The NP scenario (blue) has a higher density of heavy tailed kernels, when compared to the other two scenarios. C) Each dispersal kernel is modeled using a Weibull distribution where estimated parameter values are obtained for each of the 1000 random samples. For the shape and scale parameters, we calculate the mean and their 95% confidence intervals generated from a non-parametric kernel density estimation to the 1000 parameter values obtained from the 1000 Weibull fits. D) Calculated expected value (mean) and variance for each of the kernel density curves using the scale and shape parameters obtained from the Weibull distribution fits. Overall distribution of variance for the three scenarios is similar, with the number and extent of outliers for the NP scenario being relatively higher.

Table 2-2. Summary table on seed dispersal distances for each of the pooling scenarios. For each of the scenarios, the metrics reported in this table are based on the 500,000 seeds deposited under each of the simulated scenarios.

Model	Mean Dispersal Distance (SD)	Kurtosis	Maximum Dispersal Distance	Percent Dispersal events over 500 m.
CP	174.5(120)m	5.53	1344	1.878%
PP	140.8(120)m	8.74	1606	1.586%
NP	156.8(130)m	8.87	1716	2.23%

Table 2-3. Estimated parameter values and standard errors associated with those estimates after fitting a Generalized Pareto Distribution to dispersal distances falling above a given threshold (v) for each of the three simulated pooling scenarios. A random sample of 10,000 seed dispersal distances was selected from each simulated data set to estimate the Generalized Pareto Parameters. From the fitted distributions, we calculated conditional probability of seeds dispersing beyond 200, 500, 1000, and 5000 m.

Model	Scale	Shape	Pr($X \geq 200m$)	Pr($X \geq 500m$)	Pr($X \geq 1km$)	Pr($X \geq 5km$)
CP ($v = 119$)	131.97 ± 2.07	-0.087 \pm 0.009	0.53	0.036	4.73×10^{-5}	0.00
PP ($v = 99$)	113.77 ± 2.19	-0.012 \pm 0.014	0.41	0.027	2.46×10^{-4}	0.00
NP ($v = 156$)	118.70 ± 2.70	0.034 \pm 0.016	0.69	0.063	1.70×10^{-3}	7.23×10^{-12}

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