

## Article

# Effects of Landscape Heterogeneity and Disperser Movement on Seed Dispersal

Michael G. Just <sup>1,\*</sup>, Wade A. Wall <sup>1</sup>, Stacy D. Huskins <sup>2</sup> and Matthew G. Hohmann <sup>1</sup>

<sup>1</sup> U.S. Army Corps of Engineers, Engineer Research and Development Center, P.O. Box 9005, Champaign, IL 61826, USA

<sup>2</sup> Endangered Species Branch, Bldg 0-9125 McKellors Road, Fort Liberty, NC 28310, USA

\* Correspondence: michael.g.just@usace.army.mil

**Abstract:** The primacy of endozoochory for the maintenance and expansion of many woody plant populations is well known, but seed dispersal is not well understood for most species. This is especially true for rare species, where small population size and low fruit production can limit field- or observation-based experiments. Additionally, the effect of environmental heterogeneity on disperser movement is rarely investigated but has been shown to improve estimates of plant population spatial patterns and dynamics. We used simulation experiments to explore the effects of environmental heterogeneity and disperser movement on *Lindera subcoriacea* seed dispersal, a rare shrub from the southeastern United States with avian-dispersed seeds. Our experiments incorporated environmental heterogeneity and simulated disperser movement for five bird species, based on either landscape permeability or straight path rules. We anticipated that permeability-based movement would result in greater dispersal distances and seed dispersal effectiveness, which characterizes both quantity and quality. Generally, we did not find differences in seed dispersal between permeability and straight path experiments. However, we did find that permeability-based experiments had greater deposition into suitable habitat during flight (23 vs. 1%). These rare but longer distance depositions may be especially important for plants that are influenced by gap or interpopulation dynamics. We also found consistently greater dispersal into high quality habitats regardless of disperser species in permeability experiments, implying that incorporating species-specific assessments of landscape utilization (occupancy) could influence the effectiveness of seed dispersal. Our study suggests that including environmental heterogeneity in seed dispersal models can provide additional insights not provided by avian parameters (e.g., gut capacity, seed retention time, and flight speed) commonly used to inform dispersal models.

**Keywords:** bog spicebush; habitat suitability; landscape permeability; *Lindera subcoriacea*; long-distance dispersal; seed dispersal effectiveness



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## 1. Introduction

Seed dispersal is a key ecological phenomenon that contributes to many ecological processes, including individual fitness, population demography, metapopulation dynamics, gene flow, biodiversity maintenance, and community development [1,2]. Our understanding of seed dispersal for most plants is not well-resolved, due to difficulties in tracking individual seeds before, during, and after dispersal [3,4]. While endozoochory is a well-studied plant–animal interaction, it remains an active research area because of the marked variation in dispersers and environmental conditions that can affect the ecological processes linked to seed dispersal [5–9]. Simulation experiments, in particular, have been used successfully to overcome the limitations of field-based experiments imposed by this variation and other factors [10,11].

Estimating how many and where seeds are likely to be dispersed is key to understanding the ecological processes affected by seed dispersal [12]. Dispersal kernels are the

probability distributions of dispersal distances [13] and characterize how likely is it that a seed is dispersed a given distance. Kernel scale and shape are the statistical properties that are of ecological interest [13,14]. The scale of the kernel is determined by the mean and variance of the dispersal distance, whereas the shape describes the tail of the kernel and is estimated from the dispersal distance kurtosis. In addition to dispersal distance, probability estimates of dispersal to suitable habitats are also important for understanding processes affected by seed dispersal.

This information can be used to estimate the seed dispersal effectiveness (SDE) of a disperser, which is the product of the quantity ( $SDE_Q$ ; number of seeds dispersed) and quality ( $SDE_D$ ; the probability a dispersed seed produces a new adult) components of seed dispersal, and is useful for understanding the dispersal services that a plant receives [15–17]. Thus, a better understanding of seed dispersal can be achieved by exploring the effects of disperser identity and environmental heterogeneity. For example, estimates of dispersal kernels and SDE can help determine the likelihood and quality of long-distance dispersal (LDD) events, which are important for metapopulation processes and may provide conservation insight [18,19].

For seeds dispersed through endozoochory, dispersal patterns (i.e., seed rain) are affected by disperser identity and behavior, environmental heterogeneity, and their interactions [20–22]. Disperser identity is important, because some inter- and intra-specific characteristics may affect the seed dispersal kernel and SDE differently among dispersers [21,23,24]. For example, the length of time from seed consumption until digestive passage or regurgitation (seed retention time [SRT]) varies among species and is an important predictor of dispersal kernel properties [8,25,26]. The size, movement, and habitat preferences of animals have all been shown to contribute to SDE [25,27,28]. Disperser movement, behavior, and seed retention times provide necessary inputs to estimate seed dispersal kernels [29–35].

The movement of animals between locations is likely better characterized as directed rather than random walks [36,37]; that is, movement decisions (direction, route, and speed) are affected by the distance between locations and landscape environmental heterogeneity. Accordingly, incorporating environmental heterogeneity into animal movement better approximates reality [38], and the interactive effect of dispersers and the environment on seed dispersal is an area of active research [22,39,40]. Environmental heterogeneity may include characteristics of vegetation physiognomy, topography, and landscape fruit availability, among others. A suite of these characteristics can be used to estimate the likelihood that a given disperser would occupy a given area [41,42]. Occupancy likelihood has been promoted as a tool to identify potential least-cost pathways/corridors for conservation [43,44], and habitat suitability and use, from which occupancy is modeled, have been used to characterize avian movement pathways [45–48]. Thus, occupancy provides a way to identify potential routes and distances a disperser may travel between locations.

There is vast temporal and spatial variation in the many intrinsic (i.e., variation in traits of individual plants) and extrinsic (i.e., variation in ecological context) drivers that can affect multiple (sub)components of SDE [49]. Considering this variation, we developed a model to describe seed dispersal for one of the largest aggregations of the rare wetland shrub, *Lindera subcoriacea* Wofford (Lauraceae; bog spicebush) [50], by five generalist, avian frugivores. The species is relatively unknown, but is considered vulnerable due to factors like poor recruitment, recent population extirpations, and population growth rates near unity [50,51].

To test whether animal movement rules, environmental heterogeneity, and disperser identity can explain dispersal kernel estimates and SDE of *L. subcoriacea*, we conducted a series of simulation experiments. We compared the differences in seed dispersal when disperser movement was determined by straight path- or landscape permeability-based rules [20,45,52]. The use of permeability-based movement rules for dispersers, using occupancy likelihoods and other factors, may be beneficial in describing seed dispersal and may differ from straight path movement between locations, but we are unaware of a quantitative comparison of these movement methods. Our expectations for experiments

using permeability-based movement were that dispersers would accrue longer travel distances and thus have more dispersal during flight. For bird species that are more likely to occupy upland habitat that is unsuitable for *L. subcoriacea* recruitment, the permeability-based movement method would result in lower SDE. We evaluated the potential usefulness of this more nuanced simulated disperser movement, as there are few published examples of models that incorporate both animal movement and environmental heterogeneity to describe seed dispersal [24,29,53,54]. We also conducted experiments comparing dispersal when disperser species were parameterized with distinct vs. the same physiological parameters to parse the effects of physiology (e.g., gut capacity, SRT, and flight speed) versus environmental heterogeneity on seed dispersal. Our expectations for these experiments were that SDE would differ, but  $SDE_D$  would not, due to the effects of environmental heterogeneity on disperser movement. Lastly, to assess the conservation implications of our results for this vulnerable species [3], we evaluated our dispersal estimates in relation to several metrics that characterize inter-population connectivity, including nearest neighbor distance, Hanski's connectivity [55], and the number of individuals in *L. subcoriacea* populations.

## 2. Materials and Methods

### 2.1. Study System and Species

Fort Liberty (previously known as Fort Bragg; 35°07' N, 79°10' W), a U.S. Army installation located within the Sand Hills ecoregion of the southeastern U.S. [56], served as the location for our field-based and simulation efforts. Fort Liberty hosts one of the largest remaining intact areas of the longleaf pine (*Pinus palustris* Mill.) ecosystem and includes multiple high-quality natural communities that are under active fire-based management [57]. Longleaf pine–wiregrass (*Aristida stricta* Michx.) savanna (xeric Sandhill scrub) is the dominant vegetation community [57], though numerous wetlands (e.g., stream-head pocosin, sandhill seep) are interspersed throughout the landscape [58].

*Lindera subcoriacea* is a rare, dioecious, avian-dispersed [59] shrub that inhabits several wooded wetland communities of the southeastern U.S. [51]. Small, isolated populations of *L. subcoriacea* have been identified in seven southeastern states [50]. Fruits (drupe) contain a single ovoid seed ( $7.02 \pm 0.29$  mm long and  $4.0 \pm 0.2$  mm wide; [51]). As compared to other *Lindera* spp. in the southeastern U.S. (e.g., *L. benzoin* (L.) Blume [northern spicebush], *L. melissifolia* Blume [pondberry]), relatively little is known about *L. subcoriacea*. However, recent work has revealed that the species has low and uneven fruit production (maturing in early August) among individuals, poor recruitment into larger size classes, and an estimated population growth rate near unity [51,60]. Given what is known about *L. subcoriacea* and its populations, the species has been classified with a global range rank of G3 (vulnerable) [61]. Moreover, it is currently under review by the U.S. Fish and Wildlife Service for listing under the Endangered Species Act [62].

Fort Liberty hosts at least 100 bird species, although the duration and seasonality of residency varies by species [63]. During the post-breeding period, which overlaps with peak dispersal/removal of mature *L. subcoriacea* fruit [59], a total of 22 seasonally-frugivorous bird species were observed on Fort Liberty (authors' unpublished data). A subset ( $n = 18$ ) of the observed species had sufficient observations to develop species occupancy models [64]. We performed simulation experiments to characterize *L. subcoriacea* dispersal, using five generalist bird species to represent the frugivore community: *Turdus migratorius* L. (American Robin), *Cyanocitta cristata* L. (Blue Jay), *Sialia sialis* L. (Eastern Bluebird), *Melanerpes erythrocephalus* L. (Red-headed Woodpecker), and *Vireo griseus* Boddaert (White-eyed Vireo). These dispersers spanned a range of body masses (~11–88 g) and exhibited varying landscape occupancy patterns. For plant species dispersed by generalists, like *L. subcoriacea*, understanding the dispersal characteristics of a complement of likely dispersers should provide a good summary of dispersal [65]. Our evaluation of this assumption for our study species is summarized in Tables S1 and S2; see the Supporting Information for this article.

## 2.2. Model Design

We developed an agent-based, spatially-explicit, stochastic, and event-driven model to simulate seed dispersal for one of the largest aggregations of *L. subcoriacea*. The purpose of our model is to describe how disperser characteristics, key environmental conditions, and their interactions affect *L. subcoriacea* seed dispersal patterns. The model shares fundamental elements used in other woody plant seed dispersal simulation experiments [22,30,66]. Our model and supporting analyses were conducted in R [67], and the agent-based framework was implemented with the package NetLogoR (0.3.7) [68]. A thorough description of the model that follows the ODD (overview, design concepts, and details) protocol of Grimm et al. [69,70] is included in Appendix S1.

Briefly, our model represented the movement of individual birds of a given species across the Fort Liberty landscape as they visited and foraged upon *L. subcoriacea* or visited other locations (Figure S1). Movement and foraging decisions varied by species as a function of pertinent bird and environmental parameters (Table 1). Birds selected locations to forage and/or visit based on their fruit availability and distance to other locations; the product of these two components determined the attractiveness of the potential destinations (Figure S1B,C). Attractiveness varied by species (Appendix S1). We used these characteristics for attractiveness as previous work has identified negative relationships between frugivory and distance to fruit resources, and positive relationships between frugivory and fruit resource availability [8,71]. Upon arrival at a new location, birds were assigned a perching time, drawn from a Gamma distribution, based on multi-species estimates used in other avian seed dispersal simulations [22,24,66]. When the perching time elapsed, birds moved to a new location if they were still active for the day. Birds were active for four hours per day, based on anticipated and observed patterns of peak avian activity at our study site [72,73]. Birds flew at constant speeds (Table 1), derived allometrically [74], between locations. Because *L. subcoriacea* has no specialist avian frugivores, and for modeling simplicity, the probability of moving to a *L. subcoriacea* location was generically set at 25%, and at 75% for a non-*Lindera* location (Appendix S1). While perched at *L. subcoriacea*, birds could have one or no foraging events; this was dependent on fruit availability and gut capacity (Figure S1B). Birds did not forage at non-*Lindera* locations in the model. In general, birds are thought to eat as much as their current capacity allows [75] and in our model the quantity consumed followed a type II functional response [76,77], but did not exceed gut capacity (Table 1). For modeling simplicity, the same SRT, drawn from a Gamma distribution (allometrically-derived parameters vary by species (Table 1)), was assigned to all seeds consumed during a foraging event. Once the SRT elapsed for a given foraging event, all seeds from that event were dispersed (i.e., deposited via defecation or regurgitation), whether perched or flying. Additionally, at the end of each day any remaining seeds were dispersed at the final perching location, where the bird remained until the following day.

**Table 1.** Parameters for the five avian disperser species used in our experiments. Maximum fruit is the maximum number of *L. subcoriacea* fruits an individual could consume during a foraging event. Gut capacity is the number of *L. subcoriacea* fruits a bird can digestively process at a given time. Flight speed (meters/minute). Mean seed retention time (SRT) and standard deviation (minutes).

Species	Body Mass (g)	Maximum Fruit	Gut Capacity	SRT (SD) (min)	Flight Speed (m/min)
<i>C. cristata</i>	88.0	10	15	35.8 (17.92)	695.6
<i>M. erythrocephalus</i>	69.5	8	12	28.51 (14.27)	674.5
<i>S. sialis</i>	27.5	4	6	11.96 (5.99)	597.9
<i>T. migratorius</i>	78.5	9	14	32.05 (16.04)	685.3
<i>V. griseus</i>	11.4	3	4	5.62 (2.81)	533.3

Flight speed [74] and SRT [78] were determined with body mass [79] based allometry.

### 2.3. Modelling Landscape

The modelling landscape consisted of cells that represented an area of  $30 \times 30$  m, emulating the spatial extent of Fort Liberty at the same resolution. We chose this cell size to match the resolution of remotely-sensed and derivative data used in this effort. Landscape cells were characterized by their location, occupancy likelihood (per bird species), and fruit availability ( $\text{kg ha}^{-1}$ ). The locations of *L. subcoriacea* within the modelling landscape were based on previously reported spatial coordinates of all known female individuals ( $n = 88$ ) [50,51]. We located individuals at the nearest landscape cell centroid. We set the initial fruit availability for each *L. subcoriacea* cell (LISU) as the maximum number of fruits reported for the plant over nine annual surveys conducted from 2011–2019 [50,51]. Each LISU cell was considered to be one plant. For any cells that would have hosted multiple observed individuals, we summed their fruits and used the value as the initial fruit availability for that cell. LISU cells ( $n = 75$ ) had a mean of  $130.5 \pm 33.5$  (SE) and a median of 3 fruits. All fruits were considered mature (ripe) throughout modelling and no additional fruits were produced within the model; this summarized our field observations of fruit maturation trends [59]. Non-LISU locations varied within and among bird species and were a subset ( $n = 100$ ) of the remaining cells in the landscape; their fruit availability was representative of their vegetation type and season (see Appendix S1).

### 2.4. Simulation Experiments

We performed simulation experiments using the model described above. We varied movement method (landscape permeability, straight path) and bird physiological parameter set (distinct, same), and used their pairs as the basis for our experiments. Experiments using the same bird physiological parameters used *T. migratorius* parameters for all species, as it was moderately sized among the five. We did not use mean parameter values, because we could not assume that a  $\sim 55$  g frugivorous bird was ecologically viable when considering scale-dependent resource availability constraints [80,81]. Complete experiment descriptions are described in our Appendix S1. For each of the four experiments, we executed 30 replicates, each lasting for 7 simulation days, representing the mean duration of ripe fruit dispersal/removal [59]. Each bird species ( $n = 5$ ) had their own set of experiments. Each bird ( $n = 5$ ) continuously foraged, perched, or moved for 240 min per day. There were no direct interactions of the conspecific individuals in the model, aside from preventing each other from occupying the same location and, as fruit was depleted, birds may have travelled greater distances to forage. Birds started each replicate at a pseudo-randomly selected, weighted by occupancy probability, LISU cell. The spatial arrangement and starting fruit availability of LISU cells and other locations did not vary between replicates or bird species. For each replicate, we recorded LISU cell fruit availability, seed starting and ending location, distance dispersed, and habitat suitability of dispersal location. Seeds were recorded as dispersed when they were deposited at a non-origin location (Appendix S1: Section 1.3: Process overview and scheduling). For birds, we recorded the number of fruits eaten, number of seeds dispersed, and distance travelled (i.e., route distance) (Figure S1D; see Appendix S1: Section 3.1-Submodels).

We varied the movement method to evaluate the utility of the more demanding permeability-based approach, as there is a dearth of models that include both animal movement and environmental heterogeneity to describe seed dispersal. Our expectation was that this nuance would identify SDE differences for *L. subcoriacea* based on disperser identity. Experiments that used *T. migratorius* physiological parameters for all species investigated the effects of bird parameters versus environmental conditions as revealed by  $\text{SDE}_Q$ ,  $\text{SDE}_D$ , and SDE values. Results from these experiments are found in the Tables S3–S10.

### 2.5. Analyses

#### 2.5.1. Seed Dispersal Effectiveness

We estimated SDE as the product of  $\text{SDE}_Q$  and  $\text{SDE}_D$ . For  $\text{SDE}_Q$ , we first summed the number of dispersed seeds (i.e., consumed seeds deposited at a non-origin location) for each

experimental replicate. Given the resolution of our modelling landscape, this represents the minimum distance needed to move into a different cell. We then used the mean number of dispersed seeds per experiment to characterize  $SDE_Q$ . The quality component of SDE,  $SDE_D$ , was similarly aggregated and is recorded as the mean proportion of seeds that were dispersed to suitable locations. *Lindera subcoriacea* habitat suitability was represented by the values reported for a species distribution model [82]. This model estimated habitat suitability with MaxEnt [83] using *L. subcoriacea* presence data from 126 populations and climatic, edaphic, vegetation, topographic, and fire history data. Hohmann and Wall [82] set a threshold of 0.73 for suitable habitat, as this value represented the lower limit of most known *L. subcoriacea* populations. Given the possibility that the species recruitment niche might differ from its persistence niche [51], we chose to not overinterpret the habitat suitability values and instead used a binary approach where landscape cells with a value  $\geq 0.73$  were considered suitable habitat. We compared the mean  $SDE_Q$  and  $SDE_D$  components between bird species or movement methods with the Wilcoxon–Mann–Whitney (base::wilcox.test) or Kruskal–Wallis tests (base::kruskal.test).

### 2.5.2. Seed Dispersal Kernels

For dispersal kernel analyses, we considered the movement of each dispersed seed and combined the results of the five birds across instances and recorded the mean distance of all dispersal events. For each experiment by bird species, we fitted a Weibull probability density function (Equation (1)) using MASS::fitdistr [84] to the dispersal distance data, using the function described in Austerlitz et al. [85] to estimate the dispersal kernel.

$$f(x | \alpha, \beta) = \frac{\beta}{2\pi\alpha^2} x^{\beta-2} \exp\left(-\frac{x^\beta}{\alpha^\beta}\right) \quad (1)$$

Here,  $\alpha$  is the scale parameter and  $\beta$  the shape parameter. The Weibull distribution has been used in other studies to describe seed dispersal kernels and has generally outperformed other density functions for endozoochory [22,66,86]. The scale of the Weibull distribution is used to estimate mean seed dispersal distance and the shape parameter, which determines the shape (slope) of the curve [86], is used to estimate kurtosis. We estimated the mean and standard error of the dispersal kernel parameters using the maximum likelihood solution for the Hessian matrix with numDeriv::hessian [87]. We also estimated the mean dispersal distance and kurtosis [85].

### 2.5.3. Population Size, Nearest Neighbor Distance and Connectivity

To assess the conservation implications of our results, we evaluated our dispersal estimates in relation to several metrics that characterize inter-population connectivity, including nearest neighbor distance (NND), Hanski's connectivity [55], and the number of individuals in *L. subcoriacea* populations [50]. All three of these metrics are expected to influence seed rain and potentially promote emigration/immigration, thereby enhancing gene flow, population rescue, and dioecious species mate assurance [3,88]. We calculated the perimeter to perimeter NND for the 62 distinct subpopulations (*sensu* subelement occurrences [89,90]) of *L. subcoriacea* (hereafter populations) on Fort Liberty using meta-cap::patch\_config [91]. We estimated the connectivity for each population (patch) using the following formula (Equation (2)).

$$S_i = \sum_{j \neq i}^R \exp(-\alpha d_{ij}) p_j A_j \quad (2)$$

Here,  $\alpha$  is a distance decay parameter,  $d$  is the distance (m) from patch  $i$  to patch  $j$ ,  $p$  is patch occupancy, and  $A$  is the area ( $m^2$ ) of the patch  $j$  [55]. We set  $\alpha$  to 0.0076, which is the inverse of the average dispersal distance estimated by our simulations.

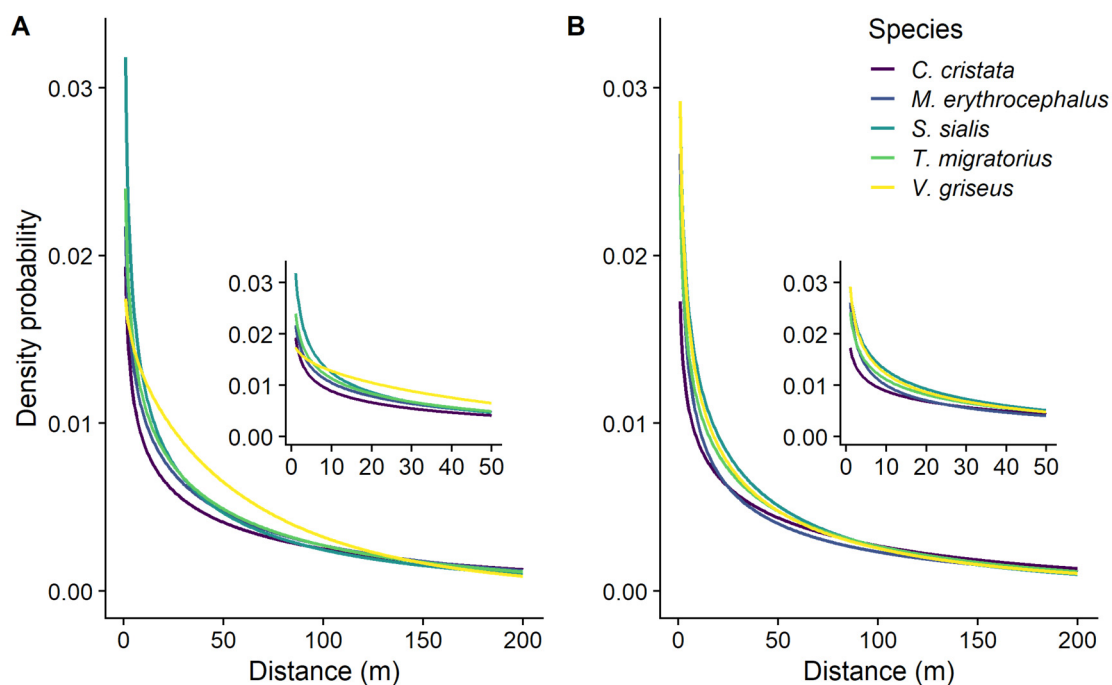
### 3. Results

#### 3.1. Seed Dispersal Kernels

For landscape permeability experiments, the mean kernel shape ranged from  $0.93 \pm 0.07$  to  $0.67 \pm 0.03$  across the five bird species, all of which describe a decreased likelihood of dispersal with increased distance from the source (Table 2; Figure 1A). The mean scale of the permeability-based dispersal kernels ranged from  $71.1 \pm 9.07$  to  $152.0 \pm 10.35$  m; these are the distances within which an estimated 63.2% of the seeds would be dispersed. We found a similar range of values,  $78.9 \pm 8.77$  to  $141.6 \pm 9.25$  m, for the straight path experiments (Table 2; Figure 1B).

**Table 2.** Seed dispersal kernels for avian disperser species based on landscape permeability or straight path-based movements. Means of 30 simulations are shown with standard errors in parentheses for each species by movement method. Dispersal kernels were fit with a two-parameter (scale, shape) Weibull distribution. The standard errors of the parameters were estimated using a Hessian matrix and maximum likelihood procedures [85]. Kurtosis was estimated using the kernel parameters and the method described by [85].

Movement	Species	Scale (m)	Shape	Kurtosis
Permeability	<i>C. cristata</i>	152.0 (10.35)	0.71 (0.02)	19.3 (2.1)
	<i>M. erythrocephalus</i>	111.4 (8.08)	0.74 (0.02)	16.5 (1.95)
	<i>S. sialis</i>	86.4 (10.1)	0.67 (0.03)	23.8 (4.2)
	<i>T. migratorius</i>	98.1 (6.47)	0.74 (0.02)	16.7 (1.77)
	<i>V. griseus</i>	71.1 (9.07)	0.93 (0.07)	7.7 (1.88)
Straight path	<i>C. cristata</i>	141.6 (9.25)	0.76 (0.02)	15.3 (1.61)
	<i>M. erythrocephalus</i>	134.6 (11.21)	0.65 (0.02)	27.8 (3.56)
	<i>S. sialis</i>	78.9 (8.77)	0.73 (0.03)	17.8 (3.09)
	<i>T. migratorius</i>	102.1 (6.77)	0.73 (0.02)	17.8 (1.89)
	<i>V. griseus</i>	88.6 (14.94)	0.70 (0.05)	20.8 (5.26)



**Figure 1.** Seed dispersal density probability plots (seed dispersal kernels) using a Weibull distribution with parameters estimated from experiments using (A) landscape permeability or (B) straight path movement rules. Different colored lines represent different avian disperser species.

3.2. Seed Disperser Effectiveness

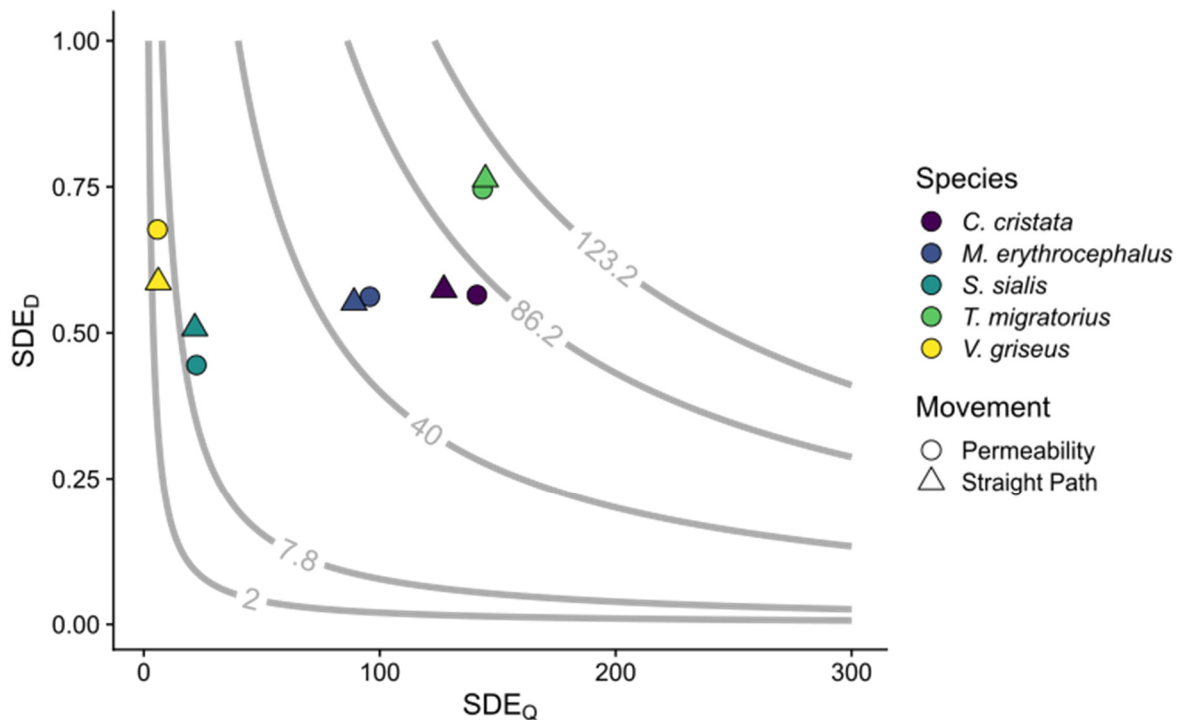
3.2.1. SDE<sub>Q</sub> and Proportion Dispersed

Within movement methods, the mean SDE<sub>Q</sub> varied among species (permeability:  $p < 0.001$ ,  $\chi^2_4 = 123.84$ ; straight path:  $p < 0.001$ ,  $\chi^2_4 = 123.51$ ). For landscape permeability experiments, SDE<sub>Q</sub> varied among species, ranging from  $5.7 \pm 0.57$  to  $141.4 \pm 5.95$  for *V. griseus* and *T. migratorius*, respectively (Table 3; Figure 2). For landscape permeability experiments, SDE<sub>Q</sub> for *C. cristata* and *T. migratorius* did not differ. For straight path experiments, the mean number of seeds dispersed did not differ between *C. cristata* and *T. migratorius*, nor between *C. cristata* and *M. erythrocephalus* (Table 3).

**Table 3.** Mean number of seeds dispersed (SDE<sub>Q</sub>) and mean relative percentage of total seeds dispersed (across experiments for all species; % Disp.) for the five study species; standard error of the mean is presented within parentheses. Results depict thirty experiments per species by movement method.

Species	Permeability	Straight Path	U	Permeability	Straight Path	U
	SDE <sub>Q</sub>	SDE <sub>Q</sub>		% Disp.	% Disp.	
<i>C. cristata</i>	135.4 (8.36) a	122.4 (6.93) ab	519	33.73 (1.57) a	32.09 (1.49) a	492 <sup>NS</sup>
<i>M. erythrocephalus</i>	93.3 (4.91) b	87.1 (4.24) a	520.5	23.65 (1.16) b	23.17 (1.08) b	475 <sup>NS</sup>
<i>S. sialis</i>	22.1 (1.29) c	21.4 (1.72) c	471	5.56 (0.27) c	5.59 (0.42) c	447.5 <sup>NS</sup>
<i>T. migratorius</i>	141.4 (5.95) a	143 (7.05) b	469.5	35.59 (1.25) a	37.58 (1.47) a	403 <sup>NS</sup>
<i>V. griseus</i>	5.7 (0.57) d	6 (0.55) d	416.5	1.46 (0.16) d	1.57 (0.14) d	402 <sup>NS</sup>

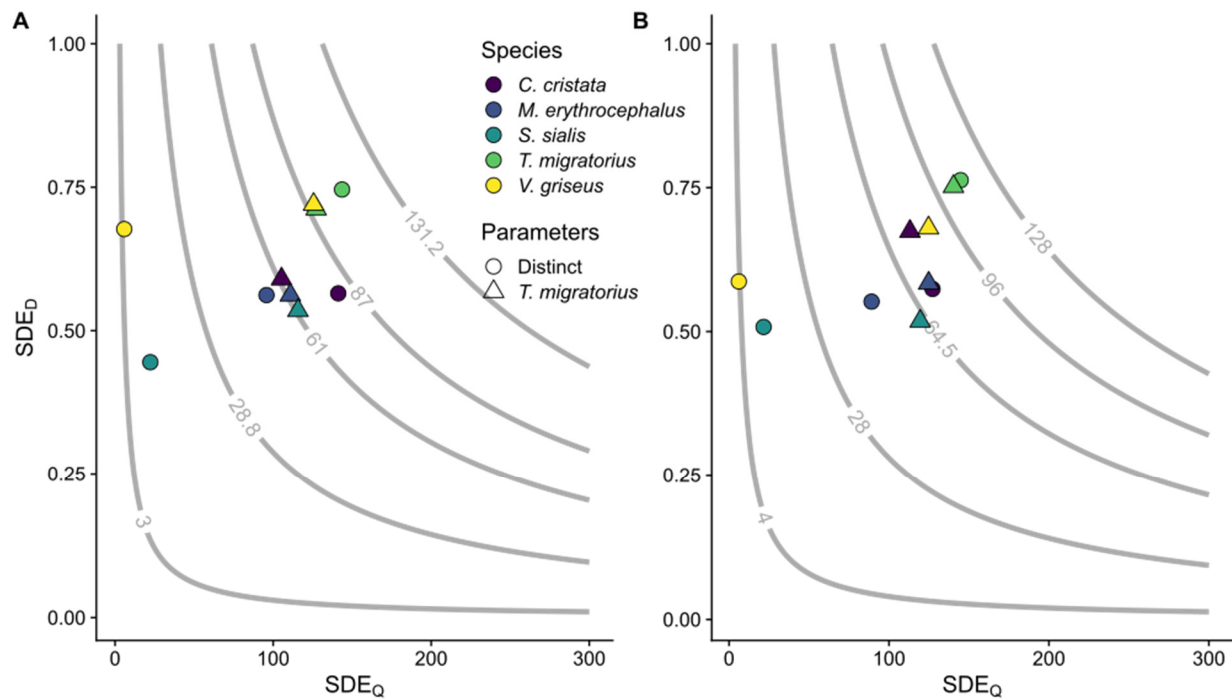
Results of Wilcoxon–Mann–Whitney tests (U) comparing SDE<sub>Q</sub> or proportion dispersed permeability and straight path movement experiments for each bird species (<sup>NS</sup> not significant;  $p \geq 0.05$ ). Different letters within movement methods represent species’ differences using Dunn’s Test post hoc comparisons ( $\alpha = 0.05$ ) on Kruskal–Wallis analysis of the given variable between species.



**Figure 2.** Seed dispersal effectiveness (SDE). Each point represents the mean SDE value for a given disperser species (color) by movement type (shape); 30 experiments per species per movement method. SDE is estimated as the product of SDE<sub>Q</sub> (mean number of seeds dispersed) and SDE<sub>D</sub> (mean proportion of seeds deposited in suitable locations). The grey lines and values are isoclines for the 5th, 25th, 50th, 75th, and 95th percentiles of SDE as averaged across all experiments.



Considering all species and comparing within movement methods,  $SDE_Q$  differed between experiments using distinct or *T. migratorius* parameters (Table S9, Figure 3). *Sialis sialis* and *V. griseus*  $SDE_Q$  differed between movement methods (Table S10).



**Figure 3.** Seed dispersal effectiveness (SDE). Each point represents the mean SDE value for a given disperser species (color) by movement method experiment using distinct or *T. migratorius* physiological parameters (shape). Panel (A) displays landscape permeability and Panel (B) straight path experiments. SDE is estimated as the product of  $SDE_D$  and  $SDE_Q$ . The grey lines and values are isoclines for the 5th, 25th, 50th, 75th, and 95th percentiles of SDE as averaged across all experiments for the given movement method; 30 experiments per species per movement method per physiological parameter set.

Within movement methods, the mean relative percentage of seeds dispersed varied among species (landscape permeability:  $p < 0.001$ ,  $\chi^2_4 = 125.64$ ; straight path:  $p < 0.001$ ,  $\chi^2_4 = 126.30$ ). Across permeability experiments, *T. migratorius* dispersed, on average,  $35.59 \pm 1.25\%$  of all dispersed seeds, whereas *V. griseus* dispersed  $1.46 \pm 0.16\%$  (Table 3). We found a similar range of values for the straight path experiments, where *T. migratorius* dispersed, on average,  $37.58 \pm 1.47\%$  of all dispersed seeds, whereas *V. griseus* dispersed  $1.57 \pm 0.14\%$  (Table 3). Within species, neither the  $SDE_Q$ , nor the proportion of seeds dispersed, differed between movement methods (Table 3). Similarly, across species, both  $SDE_Q$  ( $H_1 = 0.30$ ,  $p = 0.56$ ) and the proportion of seeds dispersed ( $H_1 = 0.002$ ,  $p = 0.97$ ) did not differ between movement methods.

### 3.2.2. $SDE_D$

For permeability experiments, the mean proportion of seeds dispersed to suitable locations ( $SDE_D$ ) varied between species ( $p < 0.001$ ,  $\chi^2_4 = 40.58$ ) and ranged from  $0.44 \pm 0.03$  to  $0.75 \pm 0.02$  for *S. sialis* and *T. migratorius*, respectively (Table 4; Figure 2). For straight path experiments,  $SDE_D$  also varied among species ( $p < 0.001$ ,  $\chi^2_4 = 26.11$ ) with a range of  $0.51 \pm 0.04$  to  $0.76 \pm 0.02$  for *S. sialis* and *T. migratorius*, respectively (Table 4). *Turdus migratorius* differed from the other four species, which did not differ. Within (Table 4) or across ( $H_1 = 0.09$ ,  $p = 0.76$ ) species,  $SDE_D$  did not differ between movement methods. We found no differences in  $SDE_D$ , across species and within movement methods between experiments using distinct or *T. migratorius* physiological parameters (Table S9, Figure 3).

**Table 4.** Mean proportion of seeds deposited in suitable *L. subcoriacea* habitat (SDE<sub>D</sub>) for the five study species by movement method; standard error of the mean is presented within parentheses. Results depict thirty experiments per species by movement method.

Species	Permeability	Straight Path	U
	SDE <sub>D</sub>	SDE <sub>D</sub>	
<i>C. cristata</i>	0.57 (0.03) ab	0.57 (0.04) a	431 <sup>NS</sup>
<i>M. erythrocephalus</i>	0.56 (0.03) ab	0.55 (0.03) a	471 <sup>NS</sup>
<i>S. sialis</i>	0.44 (0.03) a	0.51 (0.04) a	339.5 <sup>NS</sup>
<i>T. migratorius</i>	0.75 (0.02) c	0.76 (0.02) b	403 <sup>NS</sup>
<i>V. griseus</i>	0.68 (0.06) bc	0.59 (0.07) a	512 <sup>NS</sup>

Results of Wilcoxon–Mann–Whitney tests (U) comparing SDE<sub>D</sub> between landscape permeability and straight path movement experiments for each bird species (<sup>NS</sup> not significant;  $p \geq 0.05$ ). SDE<sub>D</sub> is presented as the mean value with standard error of the mean in parentheses. Different letters within movement methods represent species' differences using Dunn's Test post hoc comparisons ( $\alpha = 0.05$ ) on Kruskal–Wallis analysis of SDE<sub>D</sub> between species.

### 3.2.3. SDE

Within movement methods, the mean seed dispersal effectiveness (SDE; the product of SDE<sub>Q</sub> and SDE<sub>D</sub>) varied between species (permeability:  $p < 0.001$ ,  $\chi_4^2 = 124.00$ ; straight path:  $p < 0.001$ ,  $\chi_4^2 = 44.12$ ; Figure 2). For both movement methods, *T. migratorius* had the greatest SDE, while *V. griseus* had the lowest (Table 5). Within (Table 5) and across ( $H_1 = 0.03$ ,  $p = 0.85$ ) species, SDE did not differ between movement methods. Like SDE<sub>Q</sub>, SDE also varied between experiments, across species within movement methods, and when parametrized with distinct or *T. migratorius* parameters (Table S9, Figure 3). *Sialis sialis* and *V. griseus* differed between experiments in both movement methods for SDE (Table S10).

**Table 5.** The product (SDE) of the mean number of dispersed seeds (SDE<sub>Q</sub>) and the mean proportion of seeds dispersed to suitable locations (SDE<sub>D</sub>), for the five study species for experiments by movement method; standard error of the mean is presented within parentheses. Results depict thirty experiments per species per movement method.

Species	Permeability	Straight Path	U
	SDE	SDE	
<i>C. cristata</i>	76.6 (6.06) ab	73 (6.55) ab	474.5 <sup>NS</sup>
<i>M. erythrocephalus</i>	53.7 (4.21) a	49.8 (4.29) a	511 <sup>NS</sup>
<i>S. sialis</i>	9.7 (0.75) c	10.8 (1.19) c	430 <sup>NS</sup>
<i>T. migratorius</i>	104.2 (4.5) b	107 (4.79) b	435 <sup>NS</sup>
<i>V. griseus</i>	3.8 (0.49) c	3.7 (0.46) c	443.5 <sup>NS</sup>

Results of Wilcoxon–Mann–Whitney tests (U) comparing SDE between landscape permeability and straight path movement experiments for each bird species (<sup>NS</sup> not significant;  $p \geq 0.05$ ). SDE is presented as the mean value with standard error of the mean in parentheses. Different letters within movement methods represent species' differences using Dunn's Test post hoc comparisons ( $\alpha = 0.05$ ) on Kruskal–Wallis analysis of SDE between species.

### 3.3. Route and Seed Dispersal Distances

Within movement methods, mean route distances varied between bird species (permeability:  $p < 0.001$ ,  $\chi_4^2 = 31.2$ ; straight path:  $p < 0.001$ ,  $\chi_4^2 = 42.2$ ). When comparing species pairwise, *V. griseus* had the shortest mean route distance ( $92.4 \pm 17.82$  m) and was different than the other species for permeability experiments, while straight path experiments had idiosyncratic post hoc differences among dispersers (Table 6). Within or across species, route distances did not differ between the two movement methods.

Within movement methods, mean seed dispersal distances varied among species (permeability:  $p < 0.001$ ,  $\chi_4^2 = 41.3$ ; straight path:  $p < 0.001$ ,  $\chi_4^2 = 48.0$ ). Pairwise species comparisons revealed idiosyncratic post hoc groupings for both movement methods (Table 6). Within species, dispersal distances did not differ between the two movement methods, except for *M. erythrocephalus* (Table 6). Across species, dispersal distances did not differ between the two movement methods.

**Table 6.** Mean route and seed dispersal distances (m) for the five study species by movement method and mean percentage of foraged seeds not dispersed (Not Disp.) and seeds dispersed during flight (Flight) for the five study species by movement method. Standard error of the mean is presented within parentheses. Results depict thirty experiments per species per movement method.

Species	Permeability	Straight Path	U	Permeability	Straight Path	U
	Route Dist. (m)	Route Dist. (m)		Disp. Dist. (m)	Disp. Dist. (m)	
<i>C. cristata</i>	320.9 (51.8) a	270.9 (40.9) ab	508	242.3 (29.97) a	217.8 (28.66) ab	509 <sup>NS</sup>
<i>M. erythrocephalus</i>	230.2 (41.08) a	302.2 (40.77) a	333	200.5 (34.93) ab	288.1 (39.42) a	299 <sup>*</sup>
<i>S. sialis</i>	278.9 (60.45) a	233.1 (77.15) cd	558	161.7 (34.15) bc	135.8 (33.13) cd	494 <sup>NS</sup>
<i>T. migratorius</i>	272.6 (43.73) a	179.3 (34.14) bc	563	165.8 (18.47) ab	159.7 (25.72) bc	499 <sup>NS</sup>
<i>V. griseus</i>	92.4 (17.82) b	158.3 (62.08) d	439.5	74.4 (14.61) c	127.5 (43.08) d	410.5 <sup>NS</sup>
Species	% Not Disp.	% Not Disp.	U	% Flight	% Flight	U
<i>C. cristata</i>	84.3 (0.62) a	85.8 (0.58) a	330	1.28 (0.51) a	1.28 (0.48) a	406 <sup>NS</sup>
<i>M. erythrocephalus</i>	88.8 (0.49) b	88.8 (0.53) a	427	0.82 (0.34) a	0.84 (0.38) a	460 <sup>NS</sup>
<i>S. sialis</i>	95.3 (0.25) c	95.6 (0.35) b	412	3.16 (0.8) a	3.11 (1.38) a	504.5 <sup>NS</sup>
<i>T. migratorius</i>	86.6 (0.53) ab	86.9 (0.54) a	421	1.13 (0.38) a	0.4 (0.22) a	538.5 <sup>NS</sup>
<i>V. griseus</i>	98.3 (0.16) d	98.4 (0.14) b	444.5	3.5 (1.99) a	0.88 (0.66) a	468 <sup>NS</sup>

Results of Wilcoxon–Mann–Whitney tests (U) comparing route or dispersal distance, or percentage of seeds not dispersed or dispersed during flight between landscape permeability and straight path movement experiments for each bird species (<sup>NS</sup> not significant;  $p \geq 0.05$ ,  $* p < 0.05$ ). Route and dispersal distance (m) and the percentage of seeds not dispersed and dispersed during flight (%) are presented as the mean value with standard error of the mean in parentheses. Different letters within movement methods represent species’ differences using Dunn’s Test post hoc comparisons ( $\alpha = 0.05$ ) on Kruskal–Wallis analysis of the given variable between species.

### 3.4. Seed Deposition

For landscape permeability experiments, the percentage of seeds (of those consumed) that were deposited at the same location as where they were eaten differed ( $p < 0.001$ ,  $\chi^2_4 = 121.6$ ) between species and ranged from  $84.3 \pm 0.62\%$  to  $98.3 \pm 0.16\%$  for *C. cristata* and *V. griseus*, respectively. By design, all dispersal events were  $>15$  m. Again, we found a similar range of values for the percentage of seeds not dispersed for the straight path experiments, from  $84.8 \pm 0.58\%$  to  $98.4 \pm 0.14\%$  for *C. cristata* and *V. griseus*, respectively (Table 6).

Within and across species, the mean percentage of dispersed seeds deposited in flight did not differ between permeability and straight path experiments (2.0% vs. 1.3%), and no species had a mean greater than 3.5% (Table 6). Species did not differ in the percentage of seeds deposited in flight. The mean dispersal distance and number of seeds deposited in suitable or unsuitable *L. subcoriacea* sites during flight or while perched is presented in Table 7.

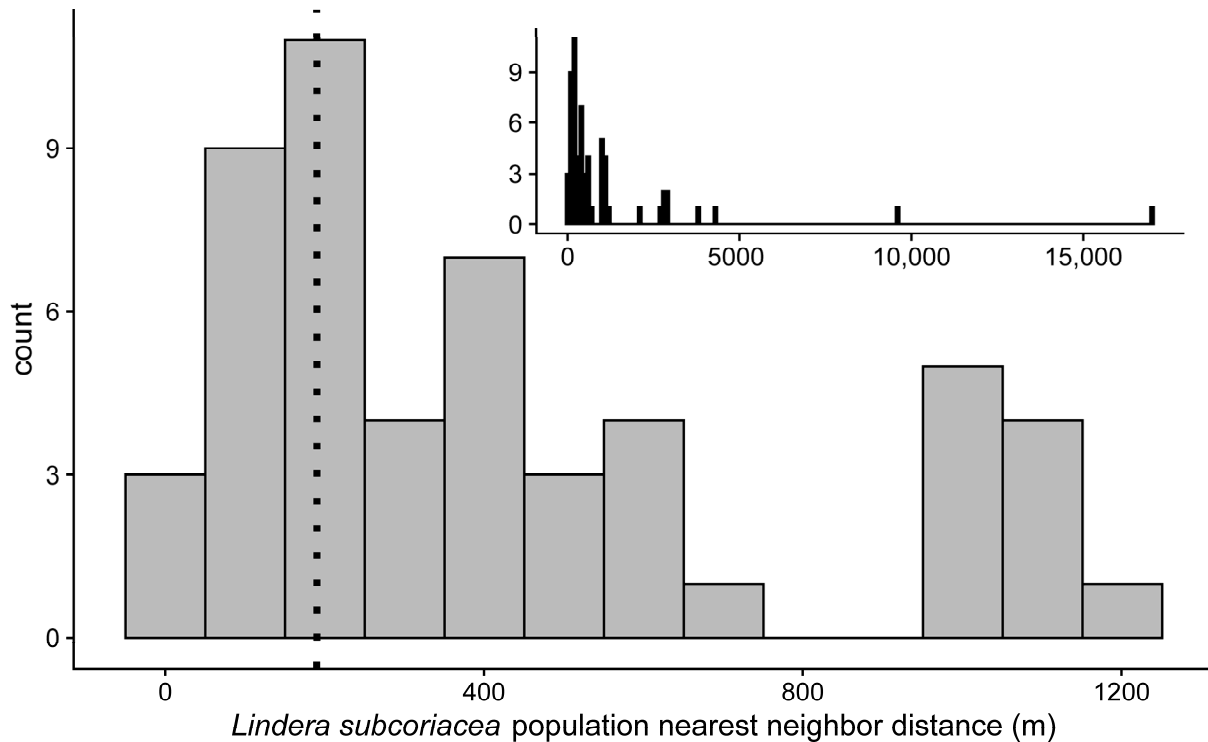
**Table 7.** Mean dispersal distance and number of depositions by *L. subcoriacea* habitat suitability across all species by movement method. Dispersal is parsed between flight and perched. Standard errors of the mean are presented in parentheses.

Dispersal/Movement	Not Suitable		Suitable		Total	
	n	Distance (m)	n	Distance (m)	n	Distance (m)
Flight						
Permeability	117	1735.4 (164.5)	35	1070.0 (85.4)	152	1582.1 (130.0)
Straight Path	94	1594.9 (144.6)	1	4626.2	95	1626.8 (146.6)
Perched						
Permeability	4386	218.6 (9.9)	7403	155.6 (7.8)	11,789	179.0 (6.1)
Straight Path	3974	302.6 (19.1)	7329	136.1 (6.9)	11,303	194.6 (8.1)

### 3.5. Population Size, Nearest Neighbor Distance, and Connectivity

Eighteen of the 62 (29.0%) *L. subcoriacea* populations on Fort Liberty had a NND  $\leq 190$  m (Table S11, Figure 4), the distance within which 90% of dispersed seeds were deposited.

Populations had a mean connectivity of  $389.6 \pm 118.6$ ; individual values ranged from 0–5388.4. There also was a positive relationship between the number of individuals within populations and  $(\log_{10} + 1)$  population connectivity ( $y = 2.42 + 5.09x$ , adj.  $R^2 = 0.21$ ,  $p < 0.01$ ; Table S11, Figure S2).



**Figure 4.** Histogram of the nearest neighbor distance for *L. subcoriacea* populations  $\leq 2$  km ( $n = 52$ ). Ninety percent of dispersed seeds were deposited at a distance  $\leq 190$  m (vertical dotted line). Inset histogram also includes populations with nearest neighbor distances  $\geq 2$  km ( $n = 62$ ).

#### 4. Discussion

We used simulation experiments to investigate how environmental heterogeneity (i.e., fruit availability, distance, and occupancy) and disperser movement, using landscape permeability- or straight path-based rules, affected the seed dispersal of *L. subcoriacea*, as characterized by the seed dispersal kernel and SDE. We conducted experiments with five generalist disperser species that likely interact with the heterogeneous environment differently (unpublished data). However, for this effort, we are not particularly interested in any given species' effect on dispersal. Instead, our discussion emphasizes across-species results, as this aggregation is more relevant to our objective to compare environmental heterogeneity and disperser movement methods on the overall dispersal of *L. subcoriacea*. In general, we did not find differences between the landscape permeability and straight path movement experiments. This first comparison of these two movement methods suggests that use of the less computationally intensive straight path model may be a suitable and preferable methodology. However, we acknowledge that there may be cases where permeability-based movement may be more appropriate (see below). Our unique approach using species-specific occupancy models and avian parameters for dispersers also provided an opportunity to evaluate how their interactions affect seed dispersal. Indeed, we observed differences in  $SDE_D$  between species that were attributable to environmental heterogeneity, distinct from avian parameters (Table S10). Additionally, 29.0% of *L. subcoriacea* populations on Fort Liberty had a NND  $\leq 190$  m; 90% of seeds were dispersed within this distance. Our experiments have provided important insights about how aspects of seed dispersal might affect *L. subcoriacea* inter-population connectivity.

Importantly, for our case study, our simulation was different than many simulations with complete or near-complete in silico landscapes [22,30,66]. Our landscape and its features that determined disperser occupancy probability, which influenced disperser movement distance and travel route, were confined to reality (as abstracted to a  $30 \times 30$  m cell for a static time point) in terms of *L. subcoriacea* location, seasonally-specific landscape fruit availability, features affecting occupancy, etc. Therefore, we did not find that it would be useful to evaluate a 'full range' of landscape values as the majority of the values included would not align with reasonably, ecologically expected conditions for our study site. Moreover, there are a number of seed dispersal simulations that do not include a full range of values in their analyses [20,24,32,92]. For some studies, including ours, this is because the study design inherently explored the varied effects of different parameters of interest. For example, our use of the five bird species, each with specific parameters, allowed us to examine the response of our dispersal metrics to the varied parameters (i.e., gut capacity, seed retention time, and flight speed; the state variables related to perching time, seed retention time, the number of fruits consumed, and the selection of next locations and background fruit loss were probabilistic, not static/single values). These parameters are pertinent to seed dispersal and provided an ecologically reasonable opportunity to evaluate how our model responded to key disperser variations.

We found SDE did not differ between movement methods within our five disperser species or when all species were considered together (Table 5; Figure 2). Our expectation that SDE would differ between experiments using landscape permeability- or straight path-based movement was not met. Instead, for our study system and parameters that varied between experiments, our findings suggest that using straight path movement can be as useful as using landscape permeability rules for describing seed dispersal from simulations. Moreover, since experiments utilizing straight path movement need fewer input data and are less computationally intensive, they could be the preferred method for simulating disperser movement. For plants dispersed by many disperser species, the preference for straight path experiments could be ever stronger for these same reasons. However, there may be scenarios when modelers might want to consider the use of permeability-based movement. For example, we anticipate permeability-based movement would be preferred when (1) there is marked spatial variation in the occupancy of a disperser (i.e., patchy habitat usage) and the size and isolation of habitat patches is coarse (i.e., large interpatch distances) relative to the movement distances of the disperser [93,94], or (2) when there is strong correlation between disperser occupancy and suitable habitat for recruitment.

Our experiments using *T. migratorius* parameters for all disperser species, but still using species-specific occupancy models, were conducted to evaluate the variation in seed dispersal, specifically SDE, due to environmental heterogeneity or avian parameters. Looking at species collectively, both SDE and  $SDE_Q$  differed between experiments using distinct or *T. migratorius* physiological parameters (Table S9). These results could have been expected, as *T. migratorius* was the second largest species after *C. cristata*, and increasing the capacity to eat more fruit and fly at a faster speed for the remaining species should increase  $SDE_Q$  and subsequently SDE values (Table S9; Figure 3). However, perhaps more interesting and important for modelling seed dispersal is that  $SDE_D$  did not differ between the experiments across species (Table S9). This finding aligns with our expectations and suggests that using species-based estimates of heterogeneous landscape utilization (occupancy) can affect the quality of seed dispersal.

*Lindera subcoriacea* seeds were not dispersed great distances in our experiments. For example, the scale of the dispersal kernel was less than 152 m across species and movement methods. Unlike the scale of the dispersal kernel, the shape did not differ among species; all shape values were less than one (Table 2); thus, the probability of seed dispersal decreases with distance [95]. Most consumed seeds (~84–98%) were not dispersed, and these proportions did not differ between movement methods (Table 6). This limited dispersal distance agrees with observational findings for other large-seeded drupes in the region [96]. We recognize that disperser movement among individual *L. subcoriacea* or other perches

within a  $30 \times 30$  m area is expected behavior, but such movements are at a finer resolution than our experiments. While capturing movement within cells may have increased the numbers of dispersed seeds, it seems unlikely that this would have resulted in different conclusions from our findings, which were focused on increasing our understanding of potential inter-population connectivity. For example, although we occasionally observe *L. subcoriacea* seedlings near maternal plants, we anticipate low  $SDE_D$  at short dispersal distances due to conspecific negative density/distance dependence (CNDD) effects on seedling recruitment, as has been documented for *L. benzoin* [97,98].

For rare species, especially those within dynamic, fragmented, or heterogeneous landscapes (as has been described for *L. subcoriacea*; [51]), LDD events have been recognized as important for inter-population processes, which affect gene flow, and population persistence and expansion [18,99,100]. If *L. subcoriacea* inter-population processes rely on long dispersal distances, then LDD events would be those of greater importance. There is not a standard definition for LDD, but it is generally characterized as an extremely far dispersal distance that occurs at an extremely low frequency [18,101,102]. Across our experiments only a small proportion ( $\sim 0.02$ – $0.16$ ) of consumed seeds were dispersed and approximately 90% of dispersed seeds were deposited within 190 m of their starting location. While this result and the observed NND of populations suggest some demographic connectivity may exist among 29% of *L. subcoriacea* populations, LDD events are needed to facilitate inter-population processes for the majority of populations in our system. Although infrequent, with a mean percentage of only 1.6% of dispersed seeds, seeds dispersed during flight may enable LDD (Table 6). For example, considering all disperser species, the mean dispersal distance for seeds dispersed during flight was  $1582.1 \pm 130.0$  m ( $n = 152$ ) or  $1626.8 \pm 146.6$  m ( $n = 95$ ) for permeability or straight path experiments, respectively (Table 7). In contrast the mean dispersal distance for seeds deposited at perches was  $179.0 \pm 6.1$  m ( $n = 11,789$ ) or  $194.6 \pm 8.1$  m ( $n = 11,303$ ) for permeability or straight path experiments, respectively. Although in-flight distances were very similar between permeability and straight path experiments, we found that  $\sim 23\%$  (35/152) were dispersed into suitable habitat from permeability and  $\sim 1\%$  (1/95) from straight path experiments (Table 7), suggesting permeability experiments may provide an improved understanding of  $SDE_D$ . For example, quality of deposition may contribute to the observed positive relationship between population connectivity and number of individuals within *L. subcoriacea* populations.

The importance of dispersal for *L. subcoriacea* inter-population dynamics is expected to be magnified for several reasons related to the species sexual system, single-seed fruit, seed longevity, seed production, and seedling recruitment. As a dioecious species, *L. subcoriacea* is subject to both Baker's law and the seed shadow handicap. Baker's law states that self-incompatible species are less likely to establish a sexually reproducing colony after LDD than self-compatible species because only the latter can do so with a single individual [103–106]. Thus, (re)colonization, a key inter-population process, is expected to be negatively affected due to the lack of reproductive assurance in dioecious species. Although high fecundity, seed dormancy, high immigration (i.e., SDE), and perenniality can reduce population extinction rates and increase the proportion of occupied sites across a landscape [88,107], *L. subcoriacea* has low seed production, low seedling survivorship, and presumably no seed bank [108,109]. For example, *L. subcoriacea* has an average survival rate of 1% at one year post-dispersal [51]. This suggests that dispersal and/or perenniality may be largely responsible for maintaining *L. subcoriacea* occupancy across our study landscape. While rare and infrequent, over time LDD can provide important demographic and genetic connectivity among populations of long-lived plants [99,110,111]. Additionally, large avian species capable of consuming many *L. subcoriacea* fruits may deposit multiple seeds in the same location during an LDD event, increasing the likelihood that individuals of both sexes recruit into isolated locations [112,113]. For example, in our results, 85.7% of LDD events (dispersal > 190 m) resulted in the deposition of multiple seeds at the same location. However, variation in SRT for multiple seeds consumed during the same event would

likely reduce the number of seeds anticipated to be dispersed to the same location, reducing the potential for reproductive assurance during these LDD events.

The seed shadow handicap, which describes the smaller seed shadow, higher spatial aggregation, and greater intra-specific competition anticipated for the offspring of dioecious species relative to self-compatible, cosexual species [106], is also affected by dispersal. A general expectation of having separate sexes is that females of dioecious species need to produce at least twice as many seeds as self-compatible individuals in order to compensate for males. However, all else being equal, these seeds will originate from half as many locations and be dispersed at twice the density to half the area than the seeds of self-compatible species. To compensate for the seed shadow handicap, dioecious species require greater dispersal ability and/or reduced CNDD effects [106,114]. However, if the mean dispersal distance is much greater than the spatial scale over which CNDD effects occur, the seed shadow handicap is expected to disappear [106]. Indeed, our estimated mean dispersal distance of 177 m is much greater than the 15–20 m maximum distance over which CNDD effects are typically expected to occur [115]. On the other hand, the majority (~84–98%) of seeds eaten in our simulations were deposited in the same cell in which they were eaten. Although no information about the magnitude of CNDD effects for *L. subcoriacea* are available, it is interesting that among 29 co-occurring woody species, the lowest CNDD effect (~0.55) on seedling recruitment was reported for the closely related dioecious *L. benzoin* [98].

## 5. Conclusions

There are still additional considerations to be addressed when modeling *L. subcoriacea* seed dispersal, including various intrinsic and extrinsic drivers, and use of allometrically estimated versus observed avian parameters. For example, Hohmann et al. [59] found that understory cover affected the magnitude of pre-dispersal seed predation and individual height affected *L. subcoriacea*  $SDE_Q$ , but neither of these drivers were captured within our current model. The effects of vegetation management, such as prescribed fire, can also affect the availability of *L. subcoriacea* and other fleshy fruits in time and space [51, 116] and influence *L. subcoriacea*  $SDE_Q$  [59], but this variation was not included in our experiments. Finally, more nuanced, empirical information on dispersers (e.g., fruit-specific SRT, or perching times) could be incorporated into our model to potentially improve our understanding of *L. subcoriacea* seed dispersal [117,118].

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/ecologies5020013/s1>, Appendix S1: Model description (Overview, Design concepts, and Details [ODD] protocol); Table S1: Seasonal avian frugivores on Fort Liberty, NC; Table S2: Wilcoxon rank sum tests for Quasi-SDE and subcomponents; Table S3: Seed dispersal kernels for avian disperser species; Table S4: Mean number of seeds dispersed and mean relative percentage of total seeds dispersed; *T. migratorius* physiological parameters; Table S5: Mean proportion of seeds deposited in suitable *L. subcoriacea* habitat by movement method; Table S6: SDE by movement method; Table S7: Mean route and seed dispersal distances by movement method; Table S8: Mean percentage of foraged seeds not dispersed and seeds dispersed during flight by movement method; Table S9: Comparison of seed dispersal effectiveness subcomponents between experiments (across species) using distinct or *T. migratorius* physiological parameters by movement method; Table S10: Comparison of seed dispersal effectiveness subcomponents between experiments within species using distinct or *T. migratorius* physiological parameters by movement method; Table S11: Nearest neighbor distance and connectivity for the *L. subcoriacea* sub-element occurrences; Figure S1: Seed dispersal simulation conceptual diagram; Figure S2: Number of *L. subcoriacea* individuals within populations versus the connectivity of those populations.

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