Appendix S1: Model description

The model description that follows is based on the ODD (Overview, Design concepts, and Details) protocol for describing individual- and agent-based models [1], as updated by Grimm et al. [2]. Our model and supporting analyses were conducted in R [3], the agent-based framework was implemented with the package *NetLogoR (0.3.7)* [4].

1. Overview

1.1 Purpose

The purpose of our model is to test whether disperser characteristics, environmental conditions, and disperser movement rules can explain seed dispersal for one the largest aggregations of the rare shrub, *Lindera subcoriacea* Wofford (bog spicebush). The model is driven by the interaction between avian frugivores and the environment.

1.2 Entities, state variables, and scale

1.2.1 Entities

The model includes the following entities: LISU (aggregated *L. subcoriacea*), individual Birds, and the Landscape.

LISU represent all of the *L. subcoriacea* individuals that were located within one 30 x 30 m Landscape cell when abstracting the real Fort Liberty (previously known as Fort Bragg) landscape into the model Landscape. Within the model Landscape, the coordinates for LISU are located at the cell center.

Birds represent the dispersers in this model. Birds represent five generalist bird species: *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 frugivorous/seasonally frugivorous bird species were observed on or near *L. subcoriacea* during mid-August (i.e. post-breeding), which coincides with peak fruit ripening of *L. subcoriacea* at Fort Liberty. These dispersers were included because they spanned a range of body masses (~11–88 g; [5]) and exhibited varying landscape occupancy patterns (*unpublished data*). For *L. subcoriacea*, which is dispersed by generalists, understanding the dispersal characteristics of a complement of potential dispersers should provide a good summary of dispersal [e.g., 6]. The bird species in our study are assumed to have a comparable preference for *L. subcoriacea* fruits, due to their rarity and scarcity [7,8] and the high quality fruit of *Lindera* spp. [9,10].

Landscape represents the virtual world upon which we are modelling *L. subcoriacea* seed dispersal. The Landscape is comprised of a lattice of approximately 665,000 30 x 30 m cells. Each cell contains information on location and environmental characteristics. The location of Landscape cells is used to determine distance (e.g., flight, dispersal, between locations).

1.2.2 State variables

Entities, parameters, and state variables of the model are listed in Tables A1-A3.

1.2.3 Scale

The Landscape lattice consists of approximately 665 thousand cells that each represent an area of 30 x 30 m in reality, matching the spatial extent of Fort Liberty at this resolution. The state of each cell is characterized by its location, occupancy likelihood (per disperser species), and fruit availability of non-*Lindera* species [11]. We use this resolution because it matches the resolution of the remotely-sensed and derivative data used in the parameterization of the model. Moreover, the resolution is appropriate for post-breeding birds because they are not defending territories and fledglings would be dispersing. Thus, birds would likely utilize larger areas of the landscape as compared to usage when defending breeding territories. The Landscape is bounded; therefore, Birds cannot travel across an edge to reach to reach cells on the opposite edge.

The overall time step of the model is one day. Within that day, bird activity (foraging, perching, and moving; known as events) occurs for a constant 240 minutes per day and is accounted for by the minute. We used 4 hours in our models as the daily activity time based on anticipated and observed patterns of avian activity at our study site where activity is expected to peak at sunrise and decline within ~4 hours [12,13]. The model represents activity during the peak fruiting time, late July to early August, of *L. subcoriacea* on Fort Liberty [8]. The model runs for seven days representing the mean duration of ripe *L. subcoriacea* fruit dispersal/removal [8].

1.3 Process overview and scheduling

1.3.1 Processes

Our model covers a period representing the peak dispersal/removal of ripe fruit on *L. subcoriacea* [8]. The critical processes of the model, which are repeated throughout each day while Birds have active time remaining, are the consumption *L. subcoriacea* fruit and subsequent dispersal of seeds. (1) Birds are active for 240 minutes per day. (2) Birds select their next location to move to based on the attractiveness of that next location; attractiveness is estimated as a function of the distance (m) to other locations and their quantity of available fruit. Distance is estimated in one of two ways in our experiments. (3) Birds eat a quantity of fruit based on fruit availability and their fullness. (4) Birds have a seed retention time (SRT) for eaten fruit, after the SRT elapses they disperse seeds. (5) For each fruit/seed, records are maintained of the starting (*startLoc)* and dispersal (*dispersedLoc*) location, dispersal occurs and is recorded when a seed is consumed and deposited at location that is not the *startLoc*. A replicate completes when seven days have elapsed, or all LISU fruit have been consumed. There are experiments for both landscape permeability and straight path movement (determines distance and route between locations). The model is executed with one Bird species at a time. Experiments for each Bird species and movement type were executed using the same physiological parameters for all Birds (those of *Turdus migratorius,* see Section 3.3.5).

1.3.2 Schedule

The model begins at Day = 1, Time Spent = 0, Event = 0. The Landscape is initialized with LISU at starting fruit values (maximum value of *nFruit*). Individual Birds (*n* = 5) of a given species are pseudo-randomly assigned to a LISU (state variable: *currentLoc*), weighted by occupancy.

1) After initialization, the model begins with the birdNewEvent submodel, which updates the Bird state variables *Event*, *perchTime*, *spentTime*, *fruit2eat*, *seedTime,* and the LISU state variables *nFruit*, *startLoc*, and *dispersedLoc*.
2) Next the Birds execute the perchDispersal submodel, this updates the state variables *nSeed* and the LISU variable *dispersedLoc* as needed.
3) Then the timesUpDispersal submodel is executed, this updates the state variables *nSeed* and the LISU *dispersedLoc* as needed.

4) The following submodel will select the next location for a given Bird:
    a. If the Bird is currently located in a LISU cell, one of the following submodels will be executed based on the draw of a random number from a uniform distribution. If the random number exceeds the *propNonLISU* parameter:
        i. nextLISU

    else:

        ii. nextLISU_nonLISU
    b. If the Bird is currently located in a non-LISU cell, one of the following submodels will be executed based on the draw of a random number from a uniform distribution. If the random number exceeds *propNonLISU* parameter:
        i. nextNon_Non

    else:

        ii. nextNonLISU_LISU
5) Next the submodel flightSeedDropAndWhere is executed and moves the Bird to the next location (identified in Schedule Step 4) and updates the Bird state variables *currentLoc* and *spentTime*. If a seed is dispersed during flight the Bird state variable *nSeed* and the LISU state variable *dispersedLoc* are updated.
6) Then the backgroundLoss submodel is executed, this updates the LISU state variables *nFruit* and *dispersedLoc*.

2. Design Concepts

2.1 Basic principles

L. subcoriacea is a rare plant that produces, on average, few fruits (each with a single seed) and occurs in dense shrubby habitats [7,14]. The former precludes estimation of dispersal from seed rain, and the latter precludes direct or automated (i.e., camera traps) observations of dispersers/dispersal. As such, our model is used to represent *L. subcoriacea* dispersal via the movement of avian dispersers as modulated through their interactions with the environment. Birds select destinations based on attraction, the product of the distance to and fruit availability of a potential destination. The foraging [e.g., 15–17] and movement [e.g., 18–20] of the Birds as represented in the model draws upon other published works. Yet, there are few reports of models that include both animal movement and environmental heterogeneity to describe seed dispersal. The model also utilizes extensive ecological work at our study site, by the authors and others, to parametrize the model [7,11,14,21,22].

2.2 Emergence

The principal outcomes of our model are *L. subcoriacea* dispersal patterns that result from Bird species foraging and movement decisions.

2.3 Adaptation

A Bird selects the next, unoccupied location (LISU or non-LISU Landscape cell) to move to based on the process described below (see submodels that begin with "next" in Section 3.3 Submodels).

2.4 Objective

The objective measure used by Birds to select their next location is based upon distance and fruit availability. These components are combined to estimate the attractiveness of other locations within the Landscape.

2.5 Sensing

Birds make decisions regarding the selection of their next location based on distance from their current location and fruit availability of the potential next location. Birds are assumed to have perfect sensing regarding distances and fruit availability across the Landscape.

2.6 Interaction

Individual Birds do not interact directly. However, as LISU *nFruit* is depleted, the distances Birds travel between locations will increase.

2.7 Stochasticity

Stochasticity is used in the model in a few ways. First, during model initialization, the location of Birds is determined pseudo-randomly, weighted by bird species occupancy likelihoods. The state variables *perchTime*, *seedTime*, *fruit2eat*, and the selection of next locations and background fruit loss are probabilistic. The functions that drive these are described below.

2.8 Observation

The principal outputs of the model are seed dispersal distances (calculated from *startLoc* and *dispersedLoc*), dispersal type (i.e., perched, flight), count of dispersed seeds, and habitat suitability of the dispersal locations. The outputs were aggregated by bird species across experiments (30 replicates per experiment). Experiments involved executing models for different movement methods, straight line or landscape permeability, and Bird physiological parameter sets (distinct, *T. migratorius*).

3. Details

3.1 Initialization

At initialization, each LISU starts with their maximum amount of *nFruit*. Each non-LISU cell in the Landscape maintains a static fruit availability value based on habitat type and month for the real Fort Liberty landscape [11]. Birds are pseudo-randomly placed, weighted by species-specific occupancy likelihood, on a LISU cell. Birds begin with *Event*, *nSeed,* and *spentTime* equal to zero. Each model run (replicate) is executed with one Bird species (n = 5). Experiments are conducted with one movement type (n = 2) and one set Bird parameters (n = 2; distinct or the same) for a total four experiments per Bird species.

3.2 Input data

Input data consists of the parameters listed in Table A1. Those parameters that require additional background are described here.

Occupancy: A separate effort (*unpublished data*) created spatially-explicit occupancy maps for each bird species, where each 30 × 30 m map cell was assigned an occupancy probability value (0–1). Briefly, these probabilities were derived from key environmental conditions, including mean canopy cover, understory heterogeneity, normalized difference vegetation index, and time since last burn. We used these probabilities for our permeability calculations; cells with high occupancy probabilities have greater permeability than cells with low occupancy probabilities. We calculated the landscape permeability for the Moore neighborhood (3x3) of each cell using the *gdistance::transition* function which utilizes Dijkstra's algorithm [23] to produce a permeability matrix [24]. The permeability matrix was used to determine distances between locations (see Section 3.3.3 below).

Landscape fruit: Landscape fruit availability varied by vegetation type and here we use estimates for upland hardwood, bottomland hardwood, and upland pine vegetation types on Fort Liberty as reported by Lashley et al. [11]. We estimated the August fruit availability for each Landscape cell as the mean of the Moore neighborhood, to approximate neighborhood effects on frugivore attraction.

3.3 Submodels

3.3.1 Pre-initialization

The full modelling Landscape consists of approximately 665 thousand cells. Computing the distance and/or finding the most permeable path between each pair of cells is not computationally feasible. As such, for each bird species, we pseudo-randomly selected 100 non-LISU locations to make computation tenable. For the pseudo-random draw, we used the product of occupancy probability, landscape fruit availability, and distance from a LISU cell (distance decay), 'environmental heterogeneity', as a weight. We normalized (0–1) the values of the fruit and distance inputs before multiplication.

We calculated the distance between locations, the route between two cell centroids, using two approaches for disperser movement: (1) landscape permeability [25], or (2) straight path. For the permeability approach, we estimate distance between locations based on a path that is identified for each bird species using a permeability surface that is the same spatial extent and resolution as the landscape.

3.3.2 Initialization

<u>initLindera</u>

This submodel initializes LISU cells for the model. The Landscape location of LISU reflects the location based on previously reported spatial coordinates of 88 mature female *L. subcoriacea* individuals [7,14]. These real *L. subcoriacea* coordinates were then used to place LISU on the modeling Landscape. If multiple *L. subcoriacea* would be co-located within the same cell, they were aggregated and represented as one LISU. The starting fruit availability (i.e., the maximum *nFruit* value) for each LISU cell was the maximum annual number of fruits reported for the *L. subcoriacea* in that cell, if individuals were aggregated for LISU, the sum of those maximum values was used. LISU fruit availability was estimated from nine previously reported annual fruit counting surveys conducted from 2011–2019 [7,14].

<u>initBird</u>

This submodel initializes Birds for the model. All state variables start at zero, except for *currentLoc* which is the identifier of a given Bird's current location.

3.3.3 Events

<u>birdNewEvent</u>

This submodel is first executed at the beginning of the model, immediately after initialization and sets up the beginning of each *Event* in the model. The Bird state variables *Event*, *perchTime*, *spentTime*, *fruit2eat*, *SRT, nSeed,* and the LISU state variable *nFruit* may be updated here. The submodel continues to be executed for the duration of the experiment.

The <u>birdNewEvent</u> submodel calls and executes sub-submodels; their descriptions follow. The sub-submodel <u>*perch*</u> determines how long a bird will remain at the *currentLISU* and updates *perchTime* and *spentTime* state variables. *perchTime* is the time (minutes) between arrival and departure at a given location. The *perchTime* value is drawn from a gamma distribution using the shape and scale parameters listed in Table A1. The shape and scale parameters were derived from previous multi-species seed dispersal modelling efforts [15,26,27]. The sub-submodel <u>*seedRentention*</u> determines how long (minutes) fruits/seeds are retained by a bird before dispersal and updates the *seedTime* state variable. The *seedTime* values were also drawn from a gamma distribution. The shape and scale of the Gamma distribution for the SRT are estimated as the allometrically-derived mean SRT (body mass based) and a standard deviation equal to 50% of the mean [26,28]. The gamma distribution has been used in estimates of perching time and SRT in other seed dispersal models with avian dispersers [e.g., 15,26].

When a Bird is located at a LISU cell, the *fruitAte* sub-submodel determines the LISU fruit consumption quantity for a given Event. The amount of fruit to be consumed is estimated with a hyperbolic function [see 26] bounded by a Bird species' fruit capacity (Table A3). The fruit to be consumed (C_F) is described in Eq. A1:

$$C_F = min\begin{cases} \dfrac{\alpha \times n_F}{\beta + n_F} \\ (1 - G_F) \times \ G_C \end{cases} \qquad (Eq. A1)$$

Where α is the maximum fruit consumption amount (Table A3) and β [15,2; 26,29] is the half saturation value in the hyperbolic functional response, n_F is the number of fruit at the current location, G_F is the proportion of the Bird's gut that is full, and G_C is the gut capacity of the Bird species. If a bird has gut capacity, the number of fruits to consume is identified from the estimated functional response (Eq. A1) or *nFruit*, whichever is smallest.

perchDispersal

This submodel determines if any seeds are to be dispersed at a Bird's current location as a result of the *seedTime* elapsing before *perchTime* does. This submodel updates the state variables *nSeed* and *dispersedLoc* as needed.

timesUpDispersal

This submodel determines if a Bird's *spentTime* will exceed the 240 minutes of daily activity while at the current location (based on the *perchTime* for that Event). If so, the Bird will disperse any remaining seeds at their current location. This submodel updates the state variables *nSeed* and *dispersedLoc* as needed. Birds remain at that location until the next Day starts.

nextLISU, nextLISU_nonLISU, nextNonLISU_LISU, and nextNon_Non

L. subcoriacea has no specialist avian frugivores, and for modeling simplicity, the probability of moving to a *L. subcoriacea* location is generically set at 25% and at 75% for a non-*Lindera* location. The submodels discussed next, described the selection of a given LISU or non-LISU. These proportions are informed by (1) L. subcoriacea is high quality resource and their fruits should be preferred/selected over lower quality fruits and (2) the birds are not omniscient and also seek to complement their consumption of *L. subcoriacea* fruits.

Each of these submodels identifies the location a Bird will move to next based on the attractiveness of the other unoccupied cells. The overall attractiveness of any given landscape cell is estimated as the normalized product of two attraction components: distance and fruit. A Bird can move from LISU to LISU, LISU to non-LISU, non-LISU to LISU, and non-LISU to non-LISU. Movement to a LISU or non-LISU locations is determined by pseudo-random draw from a uniform distribution. If the value of the draw was less than the *propNonLISU* parameter value, the next location would be non-LISU, otherwise LISU.

The distances used as input values for the distance component of attraction were estimated using a landscape permeability or straight-line approach. We used the permeability matrix (see section 3.2 Input data) to identify and select the shortest path—most permeable—between potential next locations with the *gdistance::shortestPath* function. The length (m) of this route is recorded as the distance moved by a Bird. For the straight path approach, we calculated Euclidean distances between the current location and each potential next location. However, for both movement approaches, we record seed dispersal distance as the Euclidean distance between the centroids of the starting LISU (*startLoc*) and the cell dispersed to (*dispersedLoc*).

To estimate fruit availability, we use LISU fruits (*nFruit*) and total landscape fruit availability values (see Section 3.2 Input data). These fruit availabilities are used to estimate the fruit availability component of attraction. Fruit availability values are normalized to a value of 0–1.

After determining fruit availability and distance, we estimated the attraction for each component separately, before combining into a total attractiveness estimate (Figure S1C). The procedure for these estimations differs for movement to a LISU or a non-LISU cell; rules for these estimations are described in Section 3.3.5.

The next location for a Bird is selected via a pseudo-random draw weighted by the total attraction value (i.e., the product of fruit and distance attraction). Both LISU and non-LISU cells can only host one Bird at a time. If all remaining, unoccupied cells have attraction values that are equal to zero, Birds are assigned an unoccupied cell as their next location via a pseudo-random draw. The following submodel moveFlightDispersal moves the Birds to the identified locations.

moveFlightDispersal

This submodel moves Birds to the next location and determines if any Birds will disperse seeds while in flight. Using the next location as identified above, this submodel first determines how long (minutes) it will take the bird to fly there. Flight routes (every cell along the route) and their distances were pre-identified for each location pairing (LISU [*n* = 75 total cells], non-LISU [*n* = 100 total cells per Bird species]) for each Bird species for computational efficiency. For permeability-based experiments, distance was calculated as a path through the centroid of each landscape cell within the previously identified, most-permeable path. For straight path experiments, Bird movement is the straight path that connects cell centroids. Bird species move at different, but constant speeds for modeling simplicity (Table A3). Flight speeds [30] for each Bird species were estimated with mass-based allometry with mass as reported in Dunning, Jr. [5].

After determining the flight time, the state variable *spentTime* is updated to include the time spent flying to the next location. If the *seedTime* elapses for any *nSeed* during the flight, the dispersal location is determined by the sub-submodel *flightDispersal*. This sub-submodel pseudo-randomly selects a cell along the flight path to disperse the seeds. Seeds deposited during flight are dispersed to the centroid of the receiving cell. Finally, the state variable *currentLoc* is updated to reflect the location for the Bird after flight and *nSeed, startLoc*, and *dispersedLoc* are updated as needed.

3.3.4 Other activity

backgroundLoss

This submodel probabilistically determines a percentage (0–3%) of LISU *nFruit*, via a pseudo-random draw, to remove due to non-dispersal related factors such as pre-dispersal seed predation and fruit abscission each day [8]. The state variable *nFruit* is updated as needed after the execution of this submodel.

3.3.5 Additional movement method and bird parameter details

Movement method

For movement to a LISU cell (submodels nextLISU, nextNonLISU_LISU), we first estimated the attraction value for LISU fruit availability (*nFruit*) with a hyperbolic tangent function (Eq. A2).

$$A_F = tanh\left(\alpha_F \times {n_F}^{\beta_F}\right) \qquad (Eq. A2)$$

The attraction value for LISU fruit availability, A_F, for a given LISU is based on total fruit availability (n_F) and α_F and β_F are coefficients that determine the shape of function [15,see 26].This value is normalized to a value of 0–1 before proceeding. Next, we summed the normalized attraction value for LISU fruit availability and the normalized landscape fruit availability, this is the attraction value for fruit when a Bird moves to LISU. For movement to a non-LISU location, only the normalized landscape fruit availability was used (see submodels nextLISU_nonLISU, nextNon_Non). We calculated the attraction for distance with an exponential distance decay function, the inverse of the squared distance, [31,32] and then normalized the value (0–1). Total attraction was the normalized product of attraction value for fruit availability and distance.

Distinct or *T. migratorius* physiological parameters

For experiments using the same Bird parameters across species, we opted to use those for *T. migratorius*. It was selected as it was moderately sized among the five study species. We adopted this approach instead of averaging values among the species because we could not assume that a frugivorous bird of that size/mass (~55 g) was ecologically viable given constraints imposed by scale dependent resource availability [33,34].

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Tables

Table A1 Model parameter descriptions.

Entity	Parameter	Description	Source
LISU	No. of LISU	Number of LISU cells (n = 75)	
	Location	Location of LISU cells within the Landscape	1,2
	fruitLoss	Background fruit loss per day (0-3%)	3
Bird	Species	Bird species (See Table A3)	4
	fruit capacity	Bird species' gut capacity for *L. subcoriacea* fruit (See Table A3)	5
	flight speed	Allometrically-derived flight speed (m/s) (See Table A3)	6
	Mass	Mean bird species body mass (g) (See Table A3)	7
	Mean SRT	For *seedTime*. Mean SRT time per Bird species (minutes); this was allometrically derived and used to determine the scale parameter (β) for the Gamma distribution. (See Table A3)	8, 9
	SD SRT	For *seedTime*. Standard deviation of the mean SRT time per Bird species (minutes); this was allometrically derived and used to determine the shape (α) parameter for the Gamma distribution. (See Table A3)	8, 9
	$\alpha_{perchTime}$	Gamma distribution shape parameter for *perchTime* (4 minutes)	8
	$\beta_{perchTime}$	Gamma distribution scale parameter for *perchTime* (1.25 minutes)	8
Landscape	No. of cells	Number of cells within the Landscape (See Table A3)	
	Location	Location of Non-LISU cells within the Landscape	
	Occupancy likelihood	Occupancy likelihood values per landscape cell for each of the 5 disperser species (0-1; normalized)	4
	Neighborhood fruit availability	non-LISU Fruit availability (0-1; normalized)	10
	L. subcoriacea suitability	Binary suitability of location for L. subcoriacea	11

Sources for parameter values 1,2 = [7,14]; 3 = [8]; 4 = authors unpublished data; 5 = [28]; 6 = [30]; 7 = [5]; 8, 9 = [26,28], 10 = [11]; 11 = [21]

Table A2 Model state variables.

Entity	Variable	Description
LISU	*startLoc*	Landscape location where fruit is consumed (n=75)
	dispersedLoc	Landscape location where seed is dispersed
	nFruit	Number of fruits remaining for a given LISU (min. 0, mean 130.5 ± 33.5 (SE), max. 1500)
Bird	*Event*	A counter for Bird activity within the model, including initial placement. When a bird arrives at their next location, an event is tallied (value varies; mean 363.8 ± 1.3 (SE)).
	fruit2eat	Number of fruits to be eaten during current event by a given Bird (value varies; min. 0, max. see Table A3 [Maximum fruit]).
	nSeed	Current number of seeds in the gut of a given Bird (max. values for each species reported in Table A3)
	spentTime	Time spent foraging, flying, and perching. Restarts each Day. (max. value = 240 minutes).
	seedTime	Seed residence time (SRT). The residence time of fruit within a bird before seed dispersal. All seeds from the same Event are dispersed at the same time (value varies; see Table A3).
	currentLoc	The current Landscape location of a Bird
	perchTime	How long a Bird will remain at the current location (value varies; mean 5.0 ± 0.01 minutes)
Landscape / Other	*propNonLISU*	On average, the proportion of Events where a Bird will move to a non-LISU location (0.75)

Table A3 (Reproduction of Table 1 from the main manuscript)**.** 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.)
C. cristata	88.0	10	15	35.8 (17.92)	695.6
M. erythrocephalus	69.5	8	12	28.51 (14.27)	674.5
S. sialis	27.5	4	6	11.96 (5.99)	597.9
T. migratorius	78.5	9	14	32.05 (16.04)	685.3
V. griseus	11.4	3	4	5.62 (2.81)	533.3

Flight speed [30] and SRT [28] were determined with body mass [5] based allometry.