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RESEARCH ARTICLE

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The spatial complexity of seed movement: Animal-generated seed dispersal patterns in fragmented landscapes revealed by animal movement models

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Abstract

1. Large animals provide crucial seed dispersal services, yet face continued threats and are susceptible to changes in landscape composition and configuration. Thus, there is a growing imperative to improve understanding of animal-generated seed dispersal using models that incorporate spatial complexity in a realistic, yet tractable, way.
2. We developed a spatially explicit agent-based seed dispersal model, with disperser movements informed by biotelemetry data, to evaluate how landscape composition and configuration affect seed dispersal patterns. We illustrated this approach for the world's second largest ratite, the emu (*Dromaius novaehollandiae*), a highly mobile generalist frugivore considered an important long-distance disperser for many plant species across Australia.
3. When animal movement is unrestricted, model parameters related to seed gut passage largely determine seed dispersal kernels. However, as habitat loss and fragmentation increase, the extent of long-distance dispersal events is reduced and seed shadows became progressively more aggregated. This effect is due to the emu not being able to move between disconnected parts of the landscape, with small changes in habitat structure causing decreased long-distance dispersal.
4. We simulated seed dispersal patterns generated by three commonly used generic models of animal movement – unbiased and biased correlated random walks and Lévy walks – to evaluate how different representations of movement affect estimations of animal movements and emergent seed dispersal patterns. Simulated movements informed by the emu biotelemetry data resulted in longer median seed dispersal distances than do the three generic models.
5. *Synthesis.* Changes in landscape composition and configuration can dramatically alter patterns of zoochorous seed dispersal as they influence animal movement. However, when models are used to simulate the patterns of seed dispersal, decisions about how animal movement is represented also affect estimates of seed dispersal.

KEYWORDS
dispersal kernel, emu, frugivore, long-distance dispersal, movement ecology, point pattern

1 | INTRODUCTION

Dispersal is the primary movement process during the plant life cycle, leading to the establishment of next-generation individuals both near to and far away from their parents (Nathan & Muller-Landau, 2000). Long-distance dispersal, in which seeds are transported great distances from the parent plant in single infrequent events, substantially affects ecosystem dynamics, particularly with regard to plant invasions and range expansions under climate change (Nathan, 2006; Trakhtenbrot, Nathan, Perry, & Richardson, 2005). However, their rarity makes the frequency and extent of such events difficult to quantify (Nathan, Perry, Cronin, Strand, & Cain, 2003; Robledo-Arnuncio, Klein, Muller-Landau, & Santamaría, 2014), even if recent statistical advances provide promising avenues for their estimation (García & Borda-de-Água, 2017). Seed dispersal is inherently spatial, and its fundamental descriptor is the dispersal distance from the source (mother) plant to the establishment site. The dispersal kernel, a statistical description of the distribution of dispersal distances, quantitatively summarizes seed dispersal and portrays the probability of a seed dispersal event ending at a certain distance relative to the source point (see box 15.1 in Nathan, Klein, Robledo-Arnuncio, & Revilla, 2012 for clarifications of terminology and formulations). The most general mechanistic model of seed dispersal requires quantifying: (a) seed uptake by the vector, (b) the displacement velocity of the vector while transporting seeds and (c) the seed passage time (gut retention time) during this transportation (Nathan, Schurr, et al., 2008). For zoochorous seed dispersal, components of animal space use such as territory and/or home range size are also important (Côrtes & Uriarte, 2013). However, these factors (co)vary across space and time in ways that are not predictable simply as a function of distance from the source plant. As a result, a simple mechanistic dispersal kernel approach derived from a single spatial context cannot adequately represent the complexity and variability of seed dispersal (Kremer et al., 2012; Nathan et al., 2012). Seeds dispersed by frugivores tend to travel short distances, but with relatively high variance and clumping compared to wind-generated kernels (Clark, Poulsen, Bolker, Connor, & Parker, 2005). However, the seed dispersal patterns generated by frugivores emerge from animal movement and behaviour controlled by internal and external factors that vary across multiple spatial scales, which are not adequately described by simple dispersal kernels (Schupp, Milleron, & Russo, 2002). This spatial complexity arises from frugivore–plant, frugivore–environment and frugivore–frugivore interactions, such as obstacles to movement and sites of differing attractiveness affecting movement speed and direction and, ultimately, the location of seed deposition sites (Schupp et al., 2002).

The spatial complexity of seed dispersal patterns has motivated the development of new methods of data analysis to characterize the patterns of seed dispersal (Lavabre, Stouffer, Sanz, & Bascompte, 2014; Nathan et al., 2012; Robledo-Arnuncio et al., 2014). Habitat loss and fragmentation directly impact animal movement (Tucker et al., 2018), with significant negative flow-on effects for seed dispersal, including a reduction in seed dispersal distances (Jones, Duke-Sylvester, Leberg, & Johnson, 2017) and altered seed rain composition (McConkey et al., 2012). Habitat fragmentation can result in animals being unable to move between disconnected patches of habitat, with these difficulties increasing with the size of the organism (Bovo et al., 2018; McKinney, 1997). Large frugivores are often key actors in plant–seed interaction networks (Pigot et al., 2016), and can disperse many seeds in a single event, making their role difficult to replace (Jordano, Garcia, Godoy, & Garcia-Castano, 2007; Ripple et al., 2015).

Predicting how frugivore response to changing landscape structure (composition and configuration) might alter seed dispersal patterns requires tools that capture the feedbacks between frugivore movement, resource availability and landscape structure (Côrtes & Uriarte, 2013; Pegman, Perry, & Clout, 2017). Schupp, Jordano, and Gómez (2010) highlight the need to develop spatially explicit methods to understand the patterns of seed dispersal in heterogeneous landscapes. For example, Morales and Carlo (2006) demonstrate that the scale (e.g. mean) and shape (e.g. 'tailedness') of seed dispersal kernels are influenced by plant spatial pattern and frugivore density. Carlo and Morales (2008) show that spatial structure in plant populations can impact seed dispersal by generating and amplifying local variations in seed removal rates, with seed dispersal distances reduced in spatially aggregated stands. Studies linking animal behaviour with landscape heterogeneity to predict the emergent patterns of seed dispersal generally suggest that landscape heterogeneity reduces dispersal distances and increases seed deposition aggregation as frugivores are held in a suitable habitat patch sufficiently long to deposit locally sourced material (Levey, Tewksbury, & Bolker, 2008; Pegman et al., 2017; Russo, Portnoy, & Augspurger, 2006). Several studies have used GPS tracking to simulate spatially explicit seed shadows generated by fruit bats (Lenz et al., 2011; Oleksy, Giuggioli, McKetterick, Racey, & Jones, 2017; Tsoar, Shohami, & Nathan, 2010), but did not thoroughly investigate the underlying mechanisms. More recently, Bialozyt, Flinkerbusch, Niggemann, and Heymann (2014) illustrated how incorporating standard GPS and behavioural data into spatially explicit agent-based models can improve understanding of how seed shadows emerge from frugivore (primate) activity.

Here, we present an agent-based model to elucidate the effects of landscape spatial heterogeneity on patterns of seed dispersal for seeds dispersed by the emu (*Dromaius novaehollandiae*). Emus

are the world's second largest ratite (up to 60 kg mass) and are the primary dispersal agent and long-distance dispersal vector for many plant species in the Australian landscape (Calviño-Cancela, Dunn, Etten, & Lamont, 2006; Davies, 1978; Dunstan, Florentine, Calviño-Cancela, Westbrooke, & Palmer, 2013). The emu breeding season is from late autumn to spring (the wet season), mature males tend the eggs and their mobility may be reduced during these periods. Emus may deposit many large seeds (e.g. members of the Ericaceae and Podocarpaceae) in a single event, with Nield (2014) describing 15 *Leucopogon nutans* (Ericaceae) seedlings emerging from a single scat. Furthermore, their long gut passage time (>100 days in some instances; Davies, 1978) and extended movements (from tens to hundreds of kilometres over time-scales of weeks to months; Davies, 2002) make emu a good candidate for examining the impact of spatially explicit processes on seed dispersal.

The relatively recent and rapid habit loss and fragmentation that has occurred across the Australian landscape, with some areas losing more than 90% of native vegetation cover in the last 120 years (Saunders, Hobbs, & Margules, 1991), provides an excellent context for investigating changing landscape structure and frugivore behaviour on seed dispersal. We represent habitat loss by including impassable habitat in the landscape and habitat fragmentation by altering the size (which equates to habitat vs. non-habitat edges) of the impassable habitat patches (Figure S3). This approach allows us to manipulate independently these two components of landscape structure. We illustrate the impact of the spatial structure of the landscape on dispersal kernels and seed shadows produced by dispersers whose movement is represented by different widely used phenomenological models: a correlated random walk (diffusive), a biased correlated random walk (advective-diffusive) and a Lévy walk (super-diffusive) (Codling, Plank, & Benhamou, 2008). Finally, we compare these three phenomenological models with a fourth model derived from biotelemetry information for the emu. Using our model, we address the following:

1. How do changes in the probability distribution and parameterization used for gut passage time affect the seed dispersal kernel that emerges from the biotelemetry-informed emu movement model in landscapes without habitat loss or fragmentation?
2. How do the extent (composition) and spatial pattern (configuration) of habitat loss in the landscape affect the seed dispersal kernel emerging from the emu movement model?
3. Do changes in landscape structure (composition and configuration) affect seed dispersal kernels for generic random walk models in the same way as they do the emu movement model?

The first two questions are concerned with the primary controls on emergent patterns of seed dispersal in spatially homogeneous and heterogeneous landscapes, and the third with how decisions about representing movement in agent-based models affect the inferences made from them about seed dispersal processes.

2 | MATERIALS AND METHODS

2.1 | Emu GPS data collection

We used data collected using GPS biotelemetry to develop the emu movement model; the description here summarizes the information in Nield, Enright, and Ladd (2015). Emus were released into the Avon Valley National Park (31.63°S, 116.19°E) c. 50 km north-east of Perth, Western Australia. The Avon Valley lies at the northern end of the Darling Scarp on the transition between the northern extent of jarrah forest (*Eucalyptus marginata*) and the drier wandoo forest (*E. wandoo*). The Avon Valley has a Mediterranean-type climate, receiving a mean annual rainfall of 816 mm, largely confined to the winter months (June–August; Lower Chittering meteorological station, 31.61°S, 116.11°E; Bureau of Meteorology, BOM, 2014).

We characterized emu activity by tracking the movements of individual birds using GPS (described in detail by Nield et al., 2015). It was not feasible to capture wild birds in jarrah forest for GPS tracking owing to their elusive behaviours, speed and resistance to anaesthetics (Dr. T. Oldfield, personal communication, August 17, 2011). Young birds (pre-reproductive) were sourced from the Clackline Free Range Emu Farm near Toodyay, Western Australia. Captive-reared ratites use habitat in the same manner as their wild-born counterparts (Bellis, Martella, & Navarro, 2004). GPS tracking devices were custom-made by Telemetry Solutions, following a design used on another large ratite, the Southern Cassowary (*Casuarius casuarius*; Campbell et al., 2012). The total weight of the GPS tracking unit and attachment cuff was 310 g, <1% of the weight of the birds used in the study. Males on average weigh 31.5 kg and females 36.9 kg (Davies, 2002). During March 2013, five birds were selected from the young (1-year-old) cohort at the Clackline Free Range Emu Farm, tagged and released into the Avon Valley National Park area in southwestern Australia. Five birds was the most individuals that could be handled logistically (cost and effort considerations) and in relation to animal ethics approval (risk of animal death or other adverse impacts). Individuals were not sexed at the time of GPS attachment to minimize the time taken to physically restrain and tag the birds. The GPS download schedule varied from short intervals (data collected every 15 min) to long intervals (data collected every hour) as a trade-off between resolution of movement information and battery conservation. GPS data were collected for 18–48 days, from the end of March to May 2013, yielding a total of 2,130 data points (Nield et al., 2015). One GPS device detached from the emu after 18 days; hence, the range of periods covered by the movement data. Nield et al., 2015 observed individual emus moving up to 8 km from the point of release during a 1-week period. Because these movement data were collected in a fragmented landscape, they may underestimate movement distances in more uniform landscapes.

2.2 | Emu trajectory analysis

We used the ADEHABITATLT package (Calenge, 2006) in R version 2.15.2 (R-Development-Core-Team, 2018) to examine the parameters of the trajectories for each of the tagged birds. The emu

relocation step length and turning angle data were analysed at hourly intervals. We used an autocorrelation function to examine potential correlations between step length and turning angles. A permutation approach (following Dray, Royer-Carenzi, & Calenge, 2010) was used to examine autocorrelation in step lengths, up to a lag of 6 hr. We used a similar permutation procedure to examine autocorrelation in turning angles, with the chord distance (i.e. net displacement rather than total distance travelled) between successive relocations examined. The chord distances are expected to be low when successive turning angles are similar (Calenge, 2006; Dray et al., 2010). For both step length and turning angles, correlograms were generated from the permutations to check for any potential significant correlations. Potential autocorrelations in missing values were examined with a runs test using 999 replications (Calenge, 2006). A log-normal distribution was fitted to the hourly interval step length emu data using the FITDISTRPLUS package in R (Delignette-Muller & Dutang, 2015). The distribution of step length data was selected based on the Akaike information criterion values comparing other distributions as well (log-normal, gamma, Poisson and exponential).

2.3 | Simulation model description

The description here is an abbreviated version of the full model description according to the Overview, Design concepts, Details protocol (Grimm et al., 2010), which can be found in Appendix S1. The agent-based model was implemented in the NetLogo modelling environment version 6.04 (Wilensky, 1999), with simulations hosted in R version 3.4.4 (R-Development-Core-Team, 2018) using the RNETLOGO package v 1.0–4 (Thiele, Kurth, & Grimm, 2012).

Simulations were run on a toroidally wrapped lattice of 200 × 200 cells, with each cell representing an area of 50 × 50 m (total extent: 10.0 × 10.0 km); the size of the grid did not affect model outcomes (Figure S5). Although the grid is toroidally wrapped, we track the location of the emu and seed deposition using non-wrapped coordinates (i.e. if the agent moves from the right to the left side of the grid, then the grid *x* co-ordinate changes from 200 to 1, but we keep track that the agent is at *x* co-ordinate 201 in 'true' Cartesian space; Figure S1). Each grid cell is classified as containing plants with seeds that the simulated frugivore can consume, is empty, or impassable. The proportion of the grid consisting of each cell type is defined during the model initialization process (Table 1) and according to baseline parameters (Table 2). Cells containing plants followed a random spatial pattern. Where there was habitat loss (i.e. impassable habitat in the landscape), its spatial structure was represented by its amount ('habitat loss') and spatial configuration ('fragmentation').

The model's temporal extent is a single fruiting season for a generic plant species at a temporal grain of 1 hr for 1,000 hr, during which time a single agent traverses the model landscape according to simple decision rules (Figure S2). This temporal extent means that plant phenology and associated emu movements are not represented, although we acknowledge their potential role in seed

TABLE 1 Processes, scheduling, pseudocode and parameters of the simulation model

Process	Decision description	Parameters
Model initialization		
Sprout plants	Ask *n-plant-grid-cells* of total world grid cells to become a plant grid cell	*n-plant-grid cells* ($\lambda_{\text{grid cells}}$)
Create landscape structure	Seed the grid with one initial impassable grid cell.	
	Sequentially fill the landscape by selecting grid cells and making them impassable.	
	Generate a random uniform deviate $U(0,1)$ and if it is less than *attract-suitable* then one randomly selected *passable* patch that is immediately adjacent to an impassable patch is tagged impassable	*attract-suitable*, $P_{(\text{impassable})}$
	Continue this process until the desired proportion of impassable habitat cells, $P_{(\text{impassable})}$, is met	
Create dispersal agents	Generate *n-agents*, all on grid cells that are passable	*n-agents*
	Set gut retention time (GRT) (hr) and distribution	GRT (hr)
	Set movement model. See submodel section for further information on each of the models.	
Model run		
Move dispersal agents	Follow rules as described in Supporting Information, with agent moving along turning angle ϕ and along step length (S_L) as defined by the movement model and avoiding barriers as appropriate	*detection-dist*, β_0, S_L, ϕ, real *x*, real *y*
	Calculate real *x*- and *y*-coordinates of the dispersal agent from the point of origin (i.e. true distance moved accounting for toroidal wrap)	
Consume seed	If agent is on a plant habitat cell, consume Poisson($0.5 \times \lambda_{\text{seeds}}$)	
	Record the coordinates of the plant habitat cell that seeds are consumed from	
Deposit seeds	Deposit scats containing *n-seeds-consumed* according to distribution of mean gut retention time (hr).	Mean and var GRT, GRT distribution

TABLE 2 Model parameters for each animal movement model for the initial (baseline) model; numbers in square brackets represent the ranges over which uncertainty analyses were conducted

Parameters	Correlated random walk (CRW)	Biased CRW	Lévy walk (LW)	Emu (EMM)
General				
Simulation length (hr)/*n* steps in model	1,000	1,000	1,000	1,000
n-agents	1	1	1	1
Habitat cells				
n-plant-grid cells	25%	25%	25%	25%
Dispersal agents				
Step length (S_L)	3	3	Cauchy (0,1)[a]	3.36[b]
Turning angle φ	*SD* 180[c]	*SD* 180	Uniform	Uniform
Bias	–	0.25	–	–
Gut retention time (hr)[d]	5	5 [2–10]	5	5
Detection-dist	10 [5–15]	10	10	10
β_0	0.01 [0.005–0.0015]	0.01	0.01	0.01
p_{lazy}	0.0 [0.0–0.1]	0.0	0.0	0.0

Abbreviation: EMM, emu movement model.
[a]S_L (in habitat cells) for the LW is drawn from a random Cauchy distribution with location and scale parameters of 0 and 1 respectively.
[b]S_L (in habitat cells of 50 m) for the emu model is drawn from a log-normal distribution with mean 4.76 and *SD* 1.46 (based on model fit to the hourly emu step length data).
[c]CRW has a standard deviation of the turning angle of 180 degrees.
[d]Gut retention time is drawn from either a random Exponential distribution with mean 1/rate (5 hr) or a random Gamma distribution with mean 5 hr and variance 0.4 hr (means and variances from Herd & Dawson, 1984).

dispersal processes over broader spatial and temporal extents. During a given time-step, there is a chance (p_{lazy}) that the agent does not leave the grid cell. Otherwise, during each time-step, the agent moves according to step length and turning angle parameters (Table 2).

At each movement step, a new target location (grid cell) is selected and the agent moves in a straight line towards it. The movement model (i.e. distance travelled and turning angle in each time-step) was parameterized using the emu biotelemetry data (the 'emu movement model'; Figure 1). The movement of agents is not affected by fruit abundance (i.e. they do not directly track resources). Where impassable habitat is present in the landscape, the probability of an agent detecting and reacting to a patch of impassable habitat (p_a) is:

$$p_a = \begin{cases} 0.0, & d \geq d_{max} \\ 1.0, & d \leq 1.0 \\ a \cdot \exp^{(-\beta_0 \times d)}, & \text{otherwise} \end{cases}, \quad (1)$$

where β_0 = the steepness of the distance response to impassable habitat (default of 0.01), d_{max} is the maximum distance at which an agent can detect impassable habitat and d = distance to nearest impassable habitat.

Based on a test against a random uniform deviate, if impassable habitat is detected the agent stops (the time-step ends) and selects a new target patch; p_a = 1.0 if the agent is immediately adjacent to a grid cell containing impassable habitat. We conducted a sensitivity analysis of the effects of β_0 and d_{max} on the emergent seed dispersal kernel (Figures S8–S10). If after moving the disperser agent is located in a plant patch, it feeds on seeds in that patch, which are then excreted after a retention time drawn from either an Exponential or Gamma probability distribution for each feeding bout, with M = 5 hr and (for the Gamma) variance = 0.4 hr (see Supporting Information: Appendix S1). We assume that: (a) after consumption seeds will not be defecated until at least the next time-step (depending on the movement model used, this may mean that the dispersal agent is in the same grid cell) and (b) frugivory is not intense enough to remove all fruit from a grid cell.

2.4 | Movement models

Besides the emu movement model, we evaluated three well-established random walk models (Figure 1; Benhamou, 2014; O'Sullivan & Perry, 2013) – a correlated random walk (diffusive), biased correlated random walk (advecto-diffusive) and Lévy walk (super-diffusive). In a correlated random walk, individuals move through the landscape with a fixed step length and with turning angles sequentially correlated (in this case by drawing headings from a Gaussian

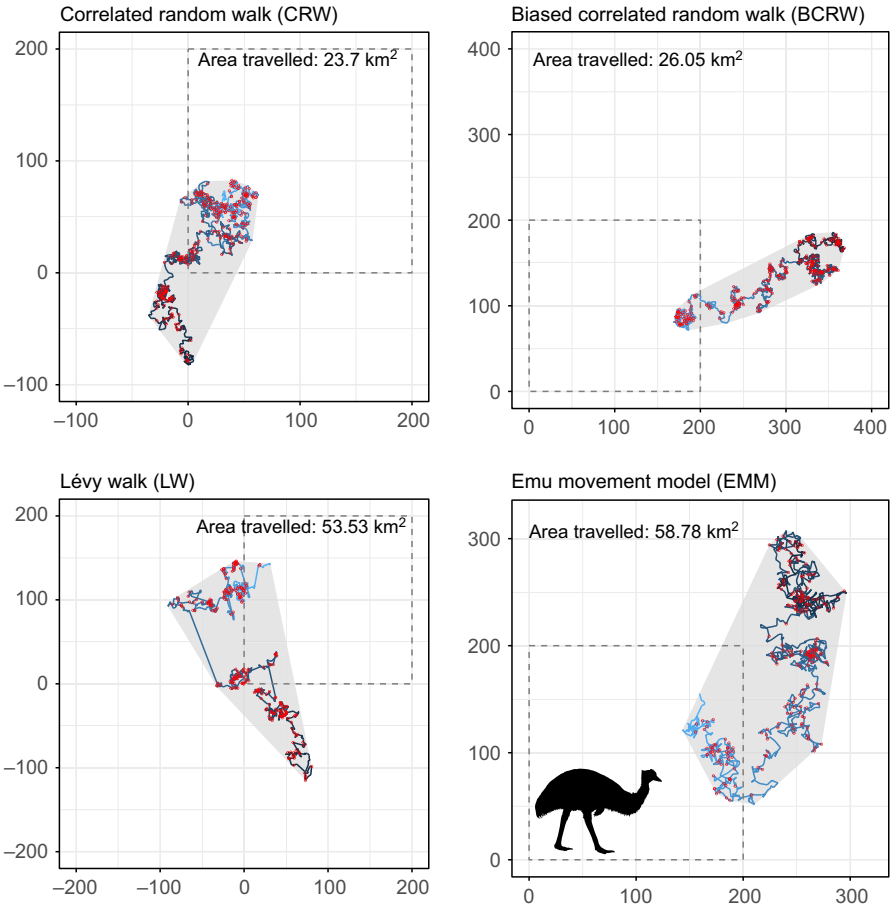

FIGURE 1 Example trajectories for the four types of movement models that we evaluated. The dashed grey line represents the simulated area; if an agent moves beyond the arena, although they will re-appear on the 'other side' of the grid under toroidal wrapping (Figure S1), we track their true spatial location. The walks are coloured from start (light) to finish (dark), red dots are seed depositions and the grey shaded area the convex hull containing the sites visited by the agent. Note the axes vary in their scaling across the four plots. Emu silhouette: Darren Naish (http://www.phylopic.org)

distribution centred on the current heading with the standard deviation controlling the strength of the autocorrelation). In a biased correlated random walk, the step length is fixed but the turning angle is a weighted average of a new random heading (as per the correlated random walk) and a fixed directional bias (as the weighting towards the bias increases movement is more strongly oriented in that direction). In the Lévy walk, turning angles are randomly selected but step length at each time interval is drawn from a Cauchy distribution with location = 0.0 and scale = 1.0; sample movement paths across the model environment can be seen in Figure 1.

2.5 | Model analysis

We used the median and 99th percentile of seed dispersal distance as measures of typical and long-distance dispersal (Nathan et al., 2003). We described the seed dispersal kernel with the *a* (scale) and *b* (shape) parameters of the log-secant distribution, which was identified by Bullock et al. (2017) as among the best empirical descriptors of seed dispersal kernels (see also Nathan et al., 2012). We computed the area over which the agent deposited seeds (the convex hull formed by the bounding box of locations visited) and the median nearest neighbour (NN) distance between seed (scat) depositions using the R package spatstat v 1.56–0 (Baddeley & Turner, 2005).

In evaluating the sensitivity of the model to changes in its parameterization, we focussed our analyses on the effects on the seed dispersal kernel of: (a) changes in the mean gut passage time and the probability distribution used for the gut passage time and (b) habitat loss and fragmentation in the landscape. Finally, for the emu movement model, we conducted a multidimensional uncertainty analysis using a Latin hypercube (Stein, 1987) across 2×10^4 combinations of nine parameters in landscapes with and without habitat loss. We then built 1×10^3 boosted regression trees (BRTs; see Elith, Leathwick, & Hastie, 2008) for subsamples of $n = 1 \times 10^3$ from these 2×10^4 parameter combinations and estimated the mean and variability in the importance of each model parameter; we also derived partial dependence curves (effect of individual parameters on predicted values while holding all others constant) for each predictor. We trained BRTs to predict median and 99th percentile seed dispersal distances, the *a* and *b* parameters of the log-secant distribution, the NN deposition distance and the area the agent moved through during the 1,000 hr simulation. The BRTs were implemented in the R library GBM3 v 2.2 (Hickey et al., 2016) and the Latin hypercube using the R library LHS v 0.16 (Carnell, 2018).

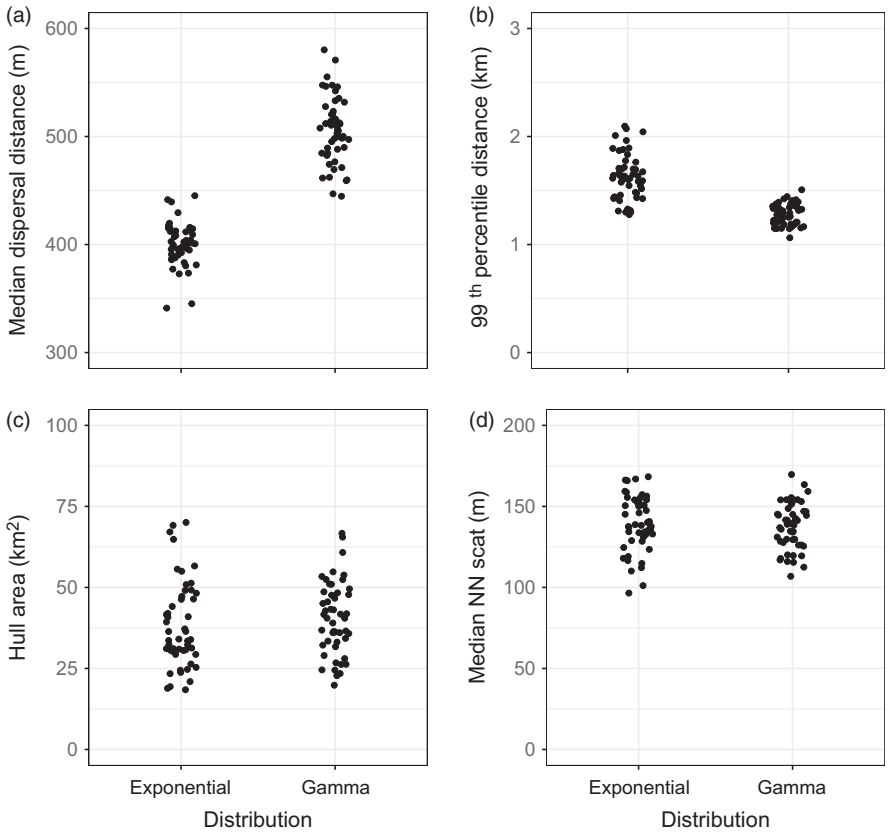

FIGURE 2 Median and 99th percentile of seed dispersal distance (a and b, respectively), hull area and median nearest neighbour distance between scats (c and d, respectively) for the emu movement model, in a homogeneous landscape. Using a Gamma distribution to describe gut retention time produces longer median seed dispersal distances than the Exponential

3 | RESULTS

3.1 | Emu trajectory analysis

The median and maximum step length in the hourly interval biotelemetry data were 150 and 2,172 m, respectively, and the turning angles for the hourly-interval data revealed some persistence around zero radians (Figure S4). There were few significant autocorrelations in turning angle and step length (up to a lag of 6 hr) and there was no significant autocorrelation in the missing values. We used this information to parameterize the emu movement model.

3.2 | Baseline emu movement model dynamics and effects of gut retention time on dispersal kernels generated by the emu

In a landscape with no habitat loss under baseline conditions and a Gamma gut retention time distribution (Table 2), the median and 99th percentile (a measure of long-distance dispersal) dispersal distances for the emu movement model were 505–575 m (50–99th percentile) and 1,266–1,475 m respectively (Figure 2). The maximum seed dispersal distance across all realizations exceeded 2,500 m. The median NN distance between scat depositions was 139–158 m.

Both mean gut retention time and the probability distribution used to describe gut retention time affected the distance over which seeds are dispersed (Figure 2). Median seed dispersal distances increased with mean gut retention time and for the same mean gut retention time were higher under a Gamma than an Exponential distribution, but the 99th percentile dispersal distances were higher for the Exponential. These parameters affected neither the area over which seeds were deposited nor the median distance between NN depositions (Figure S13).

3.3 | BRT analysis of emu seed dispersal in an unfragmented landscape

Resampled BRT analysis showed that the median and 99th percentile dispersal distance and the *a* and *b* parameters of the log-secant distribution are controlled by the mean gut passage time and the probability distribution used for the gut passage time. The median NN scat distance is controlled by the probability that an agent leaves a cell during a given time-step (p_{lazy}) and the gut retention time distribution. BRTs for the hull area did not have strong predictive performance, but identified p_{lazy} as important (Figures S14 and S15).

3.4 | Effects of habitat loss and fragmentation on seed dispersal kernels emerging from the emu movement model

Habitat loss strongly influenced agent movement and hence seed dispersal; even a small amount of habitat loss reduced seed dispersal

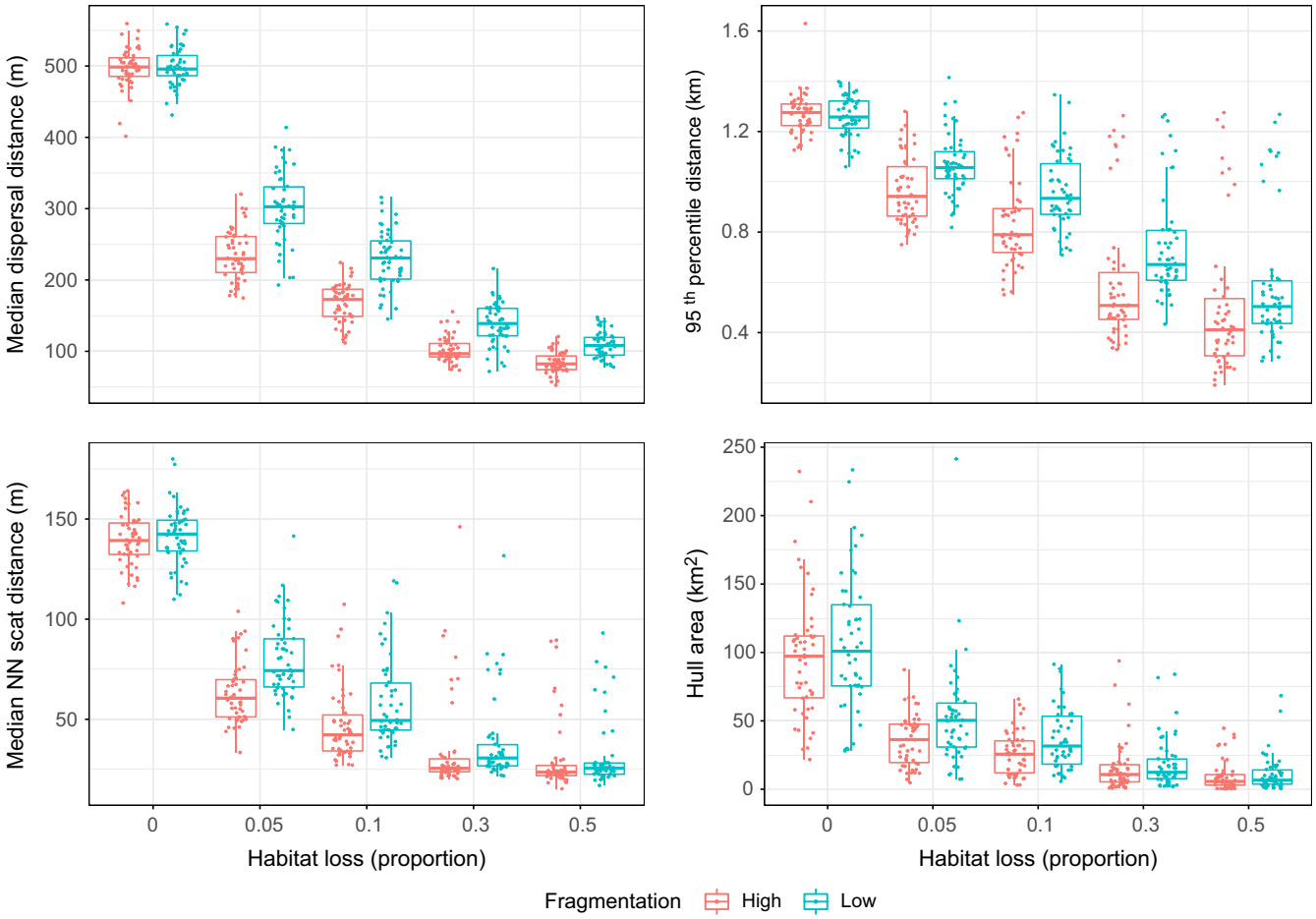

FIGURE 3 Effects of habitat loss and fragmentation on seed dispersal kernels under the emu movement model, with low and high fragmentation levels (attract-impassable = 0.9 [low fragmentation] and 0.5 [high fragmentation] respectively)

distances, distance between seed depositions and the area over which seeds were deposited (Figure 3). For the same amount of habitat loss, where fragmentation was constrained to just a few large areas the effect on the dispersal kernel was much less than where the landscape consisted of many, small patches of impassable habitat (Figure 3). The scale (*a*) and shape (*b*) parameters of the log-secant emu seed dispersal kernels declined with landscape fragmentation, reflecting a decrease in the potential for, and extent of, long-distance dispersal (Figure 4).

3.5 | BRT analysis of emu movement under habitat loss and fragmentation

In landscapes with habitat loss and fragmentation, these are the dominant controls of agent movement and seed deposition. The only state variable for which a combination of habitat loss and habitat fragmentation were not the most important predictors (habitat loss median relative importance: 61.1%) was the *b* parameter of the log-secant distribution, which was controlled by the gut passage time distribution used, and then the amount of habitat loss. In short, in unfragmented landscapes, model parameters related to gut passage time were the most important determinants of the dispersal kernel, but under habitat loss and fragmentation, landscape structure was most important (Figures S20 and S21).

3.6 | Effects of gut retention time and habitat loss and fragmentation on seed dispersal kernels for generic random walk movement models

In landscapes without habitat loss, for the three generic movement models (correlated random walk, biased correlated random walk and Lévy walk), median seed dispersal distances were higher for the Gamma than the Exponential distribution, but the 99th percentile distance was lower (Figure 5). As habitat loss and fragmentation increased, median and 99th percentile dispersal distances decreased for all the generic movement models (Figures S16 and S17). The 99th percentile dispersal distance in the Lévy walk declined more than in the correlated random walk under habitat loss, especially as fragmentation increased. Compared to the emu movement model, the Lévy walk produced dispersal kernels with shorter median dispersal distances (log-secant parameter *a*) but longer tailed distributions (log-secant parameter *b*; Figure S12). The decrease in the mean NN distance between scats and the area seeds was deposited

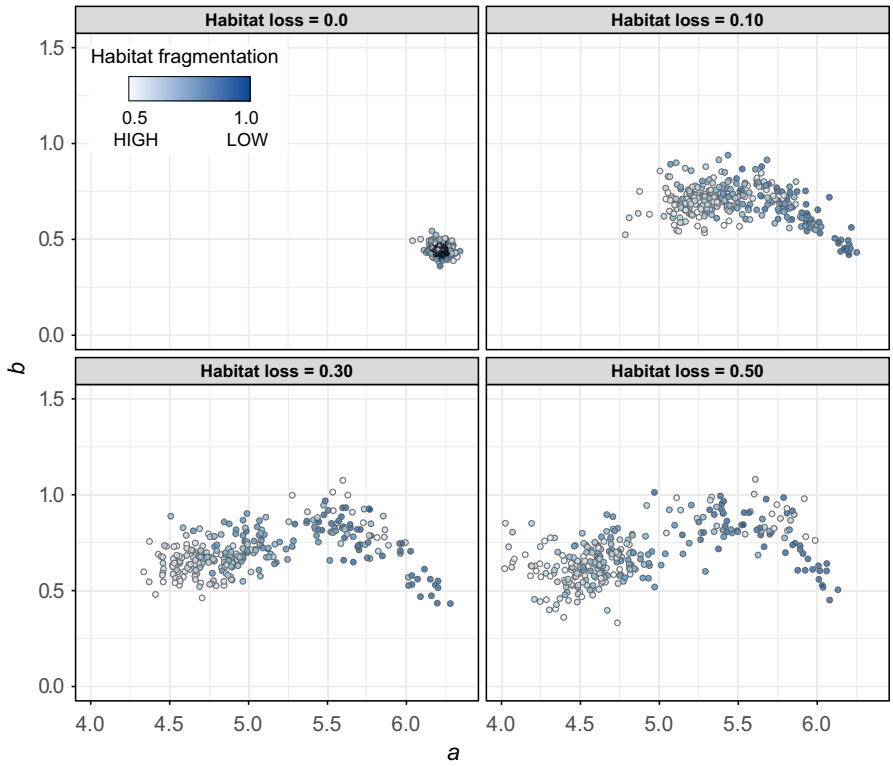

FIGURE 4 Effects of increasing habitat loss and fragmentation on estimates of *a* and *b* for the log-secant distribution describing the seed dispersal kernel under the emu movement model. As fragmentation increases the effects of habitat loss become more pronounced

over as habitat loss and fragmentation increased was most pronounced in the emu movement model (Figures S16 and S17).

The seed dispersal kernel's shape (*a*) and scale (*b*) parameters reduced with habitat loss, and more so as landscape fragmentation increased (Figures 6 and S16–S19). For the two correlated random walks, the strongest effect of habitat loss and fragmentation was on *a* (scale), whereas for the Lévy walk, it affected *a* and *b*. The effect of the spatial configuration of habitat loss increased with the amount of habitat loss.

4 | DISCUSSION

Our analyses confirm that the spatial patterns of seed dispersal emerging from animal movement are influenced by landscape structure (composition and configuration) and biological traits (animal movement and seed retention); other studies have found the same complex suite of interactions influence seed dispersal (Pegman et al., 2017; Uriarte et al., 2011). However, unlike some other generic simulation models (e.g. Jones et al., 2017), we found for the emu movement model that habitat loss and fragmentation consistently reduced median and 99th percentile seed dispersal distances. The outcomes of our model-based experiments clearly highlight the importance of decisions about how animal movement is represented in simulations of seed dispersal dynamics.

4.1 | Effects of the extent and spatial pattern of habitat loss and fragmentation on the seed dispersal kernels and seed rain shadows emerging from animal movement

As a critical determinant of the ability of animals to move between habitat patches (Atkins, Perry, & Dennis, 2019), landscape structure has a considerable impact on patterns of seed dispersal, both in itself and by influencing animal movement (Damschen et al., 2014; Lenz et al., 2011; Levey, Bolker, Tewksbury, Sargent, & Haddad, 2005; Levey et al., 2008). In an analysis of 57 species, Tucker et al. (2018) report that movement is reduced by an average of one-third in landscapes where human activity is high. In each of the four movement models we evaluated, increased habitat loss and landscape fragmentation interacted to decrease key seed dispersal parameters. This reduction in seed dispersal is a result of agents adhering to habitat edges (and their vicinity) so that in fragmented landscapes, movement between disconnected parts of the landscape is impeded (similar to the 'entrapment' dynamic described by Jones et al., 2017).

The landscape changes that we simulated represent a worst-case scenario, where habitat loss results in entirely impermeable habitat edges between areas of passable landscape. Frugivore mobility is a key determinant of the rate of seed dispersal between fragments. Critically, as habitat becomes increasingly disconnected, the ratio of edges to continuous/natural habitat increases, with a significant effect on frugivore behaviour (Restrepo, Gomez, & Heredia, 1999). Beyer et al. (2016) demonstrated that anthropogenic linear features can substantially impede animal movement. However, the response of frugivores to habitat edges is likely to be species specific and context dependent. While Levey et al. (2005) show how local edge observations can inform broader, landscape models of habitat use and seed dispersal, there is still much work to be done in examining frugivores' edge responses. Our analyses highlight how critical understanding frugivore response to changes in habitat structure is for reasonable seed dispersal kernel estimation (see also Côrtes & Uriarte, 2013). For example, if we increase

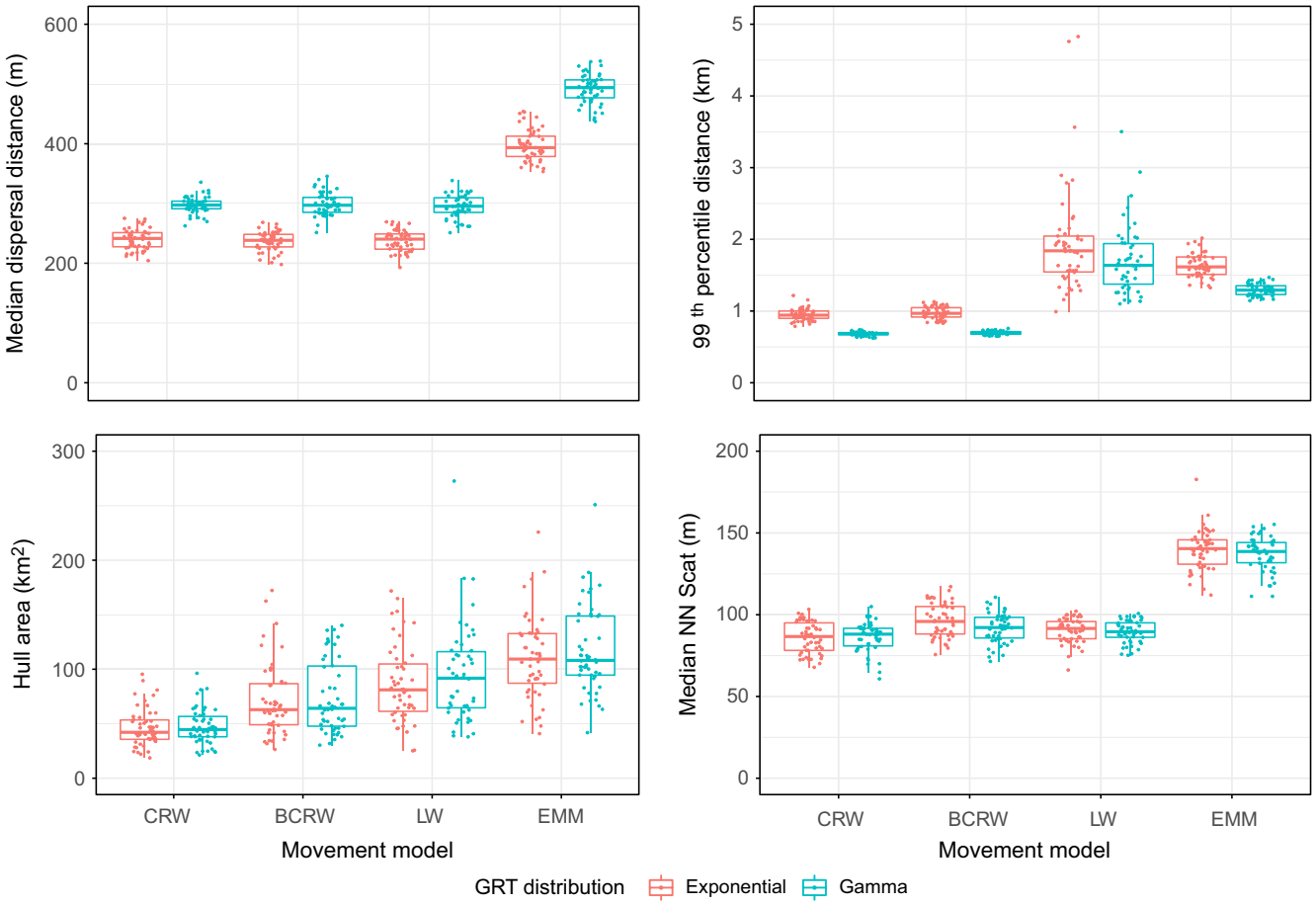

FIGURE 5 Seed dispersal kernel parameters for the four movement models, evaluated in a homogeneous landscape. Using a Gamma distribution for GRT increases median seed dispersal distances relative to the Exponential. Abbreviations: BCRW, biased correlated random walk; CRW, correlated random walk; EMM, emu movement model; GRT, gut retention time; LW, Lévy walk

the capacity for an organism to escape impassable habitat edges, then the median and long-distance seed dispersal estimates increase and the mean NN distances between seed deposition events drop commensurately. These results suggest that the provision of linking corridors to facilitate animal movement could help to maintain ecosystem services such as seed dispersal, and models such as that developed here could inform optimal provisioning of such habitat features.

4.2 | Potential effects of habitat loss and fragmentation on seed dispersal by emu

The pioneering banding and recapture of emus by Davies, Beck, and Kruiskamp (1971) revealed a remarkable capacity for these birds to travel long distances over relatively short periods, and has resulted in focus on the emu as a long-distance dispersal vector (Calviño-Cancela, He, & Lamont, 2008; Calviño-Cancela et al., 2006; Dunstan et al., 2013; McGrath & Bass, 1999). Our median and 99th percentile dispersal distance estimates of 505 and 1,266 m highlight the important contribution that this ratite plays in seed dispersal and plant dynamics. These values are even more remarkable considering they are, in part, derived from a rather conservative gut retention time (5 hr; Herd & Dawson, 1984). With some material reported to be retained in the gut for many weeks (Willson, 1989), and with the seeds of many Australian species possessing hard endocarps, likely resistant to prolonged retention, emus are likely responsible for extremely long-distance dispersal of seeds. The dispersal distances we report are similar to those of Westcott, Setter, Bradford, McKeown, and Setter (2007) for the southern Cassowary (*C. casuarius*), a large ratite found in tropical northern Australia, who estimated median and maximum dispersal distances of 387 and 5,212 m, respectively, for cassowary-dispersed seed of the invasive, tropical rainforest plant *Annona glabra* (Annonaceae). Our simulations demonstrated that the response of the emu to habitat edges substantially reduced median and 99th percentile dispersal distances. Overall, the response of the emu movement model to changes in habitat structure was similar to the Lévy walk, with commensurate decreases in median and long-distance dispersal estimates from unfragmented landscapes to those containing increasing amounts of impassable habitat. It is perhaps unsurprising that the Lévy and emu movement models responded similar to increasing habitat fragmentation as both possess heavy-tailed step length distributions (a power law for the Lévy walk and a log-normal distribution for the emu movement model).

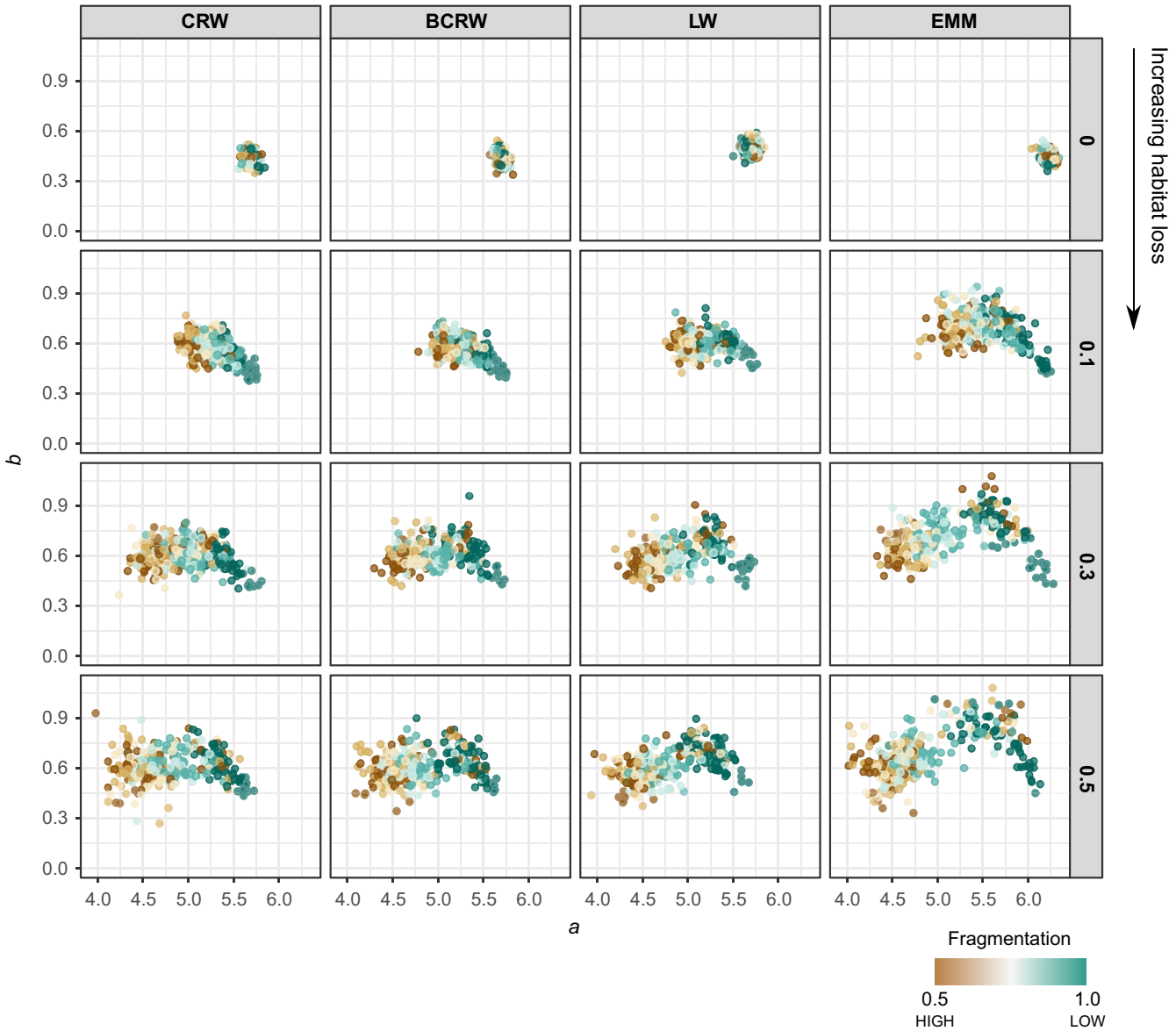

FIGURE 6 Effects of increasing habitat loss (grid rows) and fragmentation (colours) on estimates of *a* and *b* for the log-secant distribution describing the seed dispersal kernel for each of the four movement models. As fragmentation increases the effects of habitat loss become more pronounced. Abbreviations: BCRW, biased correlated random walk; CRW, correlated random walk; EMM, emu movement model; LW, Lévy walk

The complex movement decisions undertaken by frugivores, as encapsulated in the movement ecology framework (Nathan, Getz, et al., 2008), pose challenges for the adequate representation of frugivore behaviour and associated ecological functions in simulation models. Most agent-based approaches to modelling seed dispersal by frugivores use either: (a) a single model of animal movement in a single or limited landscape context or (b) behavioural information to construct dispersal models from animal movement. In the latter case, a typical approach is to classify discrete behaviours (i.e. sleeping/foraging/travelling), with the resulting movement pattern emerging as a hybrid of random and correlated random walks (Bialozyt et al., 2014; Zhang, Dennis, Landers, Bell, & Perry, 2017). The composite movement approach is supported by fine-grained observations of captive frugivores (specifically primates), with movement patterns shifting from Brownian to Lévy walks depending on behaviour; this conceptualization reflects the state–space approach to analysing movement data (Sueur, Briard, & Petit, 2011). It is, however, uncertain how these observations apply at the landscape level and our results highlight the caution required in selecting between generic models of movement to describe frugivore behaviour. In the ecosystems we consider, other (now extinct) megafauna (e.g. the giant flightless birds in *Genyornis*) may once have been important seed dispersers (Murray & Rich, 2004). Pires, Guimarães, Galetti, and Jordano (2018) reconstructed seed dispersal by South American megafauna drawing on random walk models; allometric random walk theory (Hirt et al., 2018) also offers a potential route to reconstructing dispersal for extinct or

data-depauperate species. However, our analyses suggest that using simulation approaches to reconstruct the seed dispersal of extinct animals requires careful consideration of appropriate movement models.

The inferences we make from our simulations arise from our representation of movement dynamics, a key component of which is the disperser's response to habitat edges. The sensitivity of our model to the representation of how agents perceive and respond to the habitat edge highlights the need for robust data describing these behaviours (Fortin et al., 2013; Nams, 2014). The GPS biotelemetry data used to develop our emu movement model are at a spatial grain that precludes detailed analysis of edge response and so we used a phenomenological, but biologically informed, representation of this effect. Understanding the general and specific responses of seed dispersers to habitat edges requires further research (Beyer et al., 2016; Jakes, Jones, Paige, Seidler, & Huijser, 2018). Our model does not represent the spatial memory of frugivores (Fagan et al., 2013), which mediates foraging strategies and detection, and potentially reaction to habitat edges. Frugivore spatial memory is likely a key component in better understanding emergent patterns of seed dispersal, but is extremely challenging to quantify (Bracis & Mueller, 2017; John, Soldati, Burman, Wilkinson, & Pike, 2016).

4.3 | Model capabilities and limitations

A limitation of our agent-based representation of seed dispersal is that it estimates dispersal parameters in a static environment. While typical patterns of animal movement are emergent properties of the landscape, the structure of the landscape is itself an emergent property of animal movement. Although over the temporal extents we considered the landscape is effectively static, future work should identify landscape-dispersal feedback mechanisms. In the context of emu dispersal, for example, emus defecate seeds in dense aggregations that may undergo density-dependent thinning, which can reduce the per capita probability of a seed to survive and mature to reproduction (Spiegel & Nathan, 2010, 2012). Over longer durations, these types of dynamics will affect long-term patterns of plant recruitment and survival.

The effects of shifts in frugivore activity and density on seed dispersal and demography of long-lived plant species may be difficult to observe or predict (Nield, Enright, Ladd, & Perry, 2019). Our model simulations were limited to a single fruiting season for a generic plant species, so we did not consider the long-term resource (seed) depletion that may occur during extended periods of localized foraging in extremely fragmented landscapes or where desirable resources are extremely localized (Smith & McWilliams, 2014). Over long periods of time, local fruit production may decrease in small habitat remnants (Cunningham, 2000), thus ultimately decreasing fruit availability and the potential for long-distance seed dispersal. However, for masting species representing a single fruiting episode may be adequate as the intense fruit production will attract frugivores and lead to extensive dispersal as they become attuned to the masting species and seek locations of fruiting plants. An example is *Podocarpus drounyianus* that produces seed after fire and is dispersed by emus (Chalwell & Ladd, 2005).

5 | CONCLUSIONS

Large frugivores play essential ecological roles in many ecosystems. If plant species dependent on frugivores for seed dispersal are to shift their ranges in response to environmental change, it is necessary to understand how habitat loss and fragmentation affect animal movement. With habitat loss and fragmentation continuing globally, simulation models provide an opportunity to explore the feedbacks between the landscape, frugivore behaviour and seed dispersal outcomes. Future modelling efforts should focus on exploring how these persistent landscape changes alter keystone disperser species behaviour, seed dispersal dynamics and, in turn, future landscape construction.

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AUTHORS' CONTRIBUTIONS

A.P.N., P.G.L., R.N. and N.J.E. designed the field component of the study and conducted the fieldwork. A.P.N. and G.L.W.P. designed and implemented the agent-based model, analysed the results and jointly led manuscript writing. All authors contributed substantially to revisions of the manuscript.

DATA AVAILABILITY STATEMENT

Source code for the NetLogo model is available at: https://auckland.figshare.com/s/0edcb8f0e32a5d456ed3

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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