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RESEARCH ARTICLE

A framework for linking dispersal biology to connectivity across landscapes

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Abstract
Context Dispersal typically consists of three components—departure, transience and settlement—each of which can be influenced by the landscape. A fundamental aspect of dispersal is the dispersal kernel, which describes how the likelihood of settlement varies as a function of the distance from the departure location. Dispersal concepts are often closely connected to the interpretation of landscape connectivity, yet models of landscape connectivity often do not generate dispersal kernels nor explicitly capture the three components of dispersal.
Objectives We apply Markov chain theory for the generation of random-walk dispersal kernels that are based on the three components of dispersal to better link dispersal processes to landscape connectivity.
Methods We extend the spatial absorbing Markov chain (SAMC) framework, which is aimed at addressing a broad range of problems in landscape connectivity, to explicitly model dispersal kernels that acknowledge each component of the dispersal process and how the landscape can alter each of these components. We provide an example with the Florida black bear (*Ursus americanus floridanus*), a species of conservation and management concern, where we contrast expected connectivity between key subpopulations when models do and do not consider random-walk dispersal kernels.
Results Our extensions show how the SAMC can generate different types of random-walk kernels that include information on how the landscape alters departure, transience and settlement processes. Importantly, this framework can also readily incorporate mortality into predictions and be applied to make time-explicit predictions across landscapes. Connectivity for the Florida black bear is predicted to be much lower when acknowledging dispersal kernels and suggests that the settlement process may be more influential to connectivity predictions than landscape resistance.
Conclusion These results provide a foundation for applying the SAMC to dispersal kernels. Not only do these extensions provide a formal linkage of

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connectivity to concepts in dispersal biology, but also help to bring together concepts from common connectivity models (e.g., circuit theory and least-cost resistant kernels) to facilitate predicting connectivity across landscapes.

Keywords Dispersal kernel · Functional connectivity · Landscape connectivity · Markov chain · Movement

Introduction

Dispersal underpins several theoretical frameworks in ecology and evolution (Slatkin 1993; Hanski 1999) and lies at the heart of the rapidly growing sub-discipline of movement ecology (Nathan et al. 2008). Understanding dispersal is central to conservation and management plans, which often emphasize connecting habitat remnants to facilitate the movement of species through landscapes increasingly altered by human activities (Heller and Zavaleta 2009; Albert et al. 2017). As a consequence, dispersal concepts are often closely linked to interpreting landscape connectivity (Vasudev et al. 2015; Diniz et al. 2020).

Landscape connectivity arises from movement across landscapes (Taylor et al. 1993), and dispersal is a key movement with broad implications due to its impacts on the fitness of organisms (Bonte et al. 2012; Baguette et al. 2013). We define dispersal as the movement from one location to another wherein this movement can result in reproduction and thus gene flow (Clobert et al. 2012). This definition accommodates both natal and breeding dispersal (Greenwood and Harvey 1982) and that 'effective dispersal' may or may not occur (Pfluger and Balkenhol 2014; Vasudev and Fletcher 2016; Robertson et al. 2018). Dispersal is often decomposed into three components or stages: departure (emigration), transience (transfer), and settlement (immigration) (Fig. 1a; Clobert et al. 2012). It is generally quantified in terms of changes in sites or locations, such that summaries of these changes (e.g., dispersal distances) have been essential in interpreting the causes of dispersal and its consequences for populations and communities (Bowler and Benton 2005).

Dispersal kernels are fundamental descriptors in dispersal biology and movement ecology. A dispersal kernel is a probability density function (or probability mass function when distance units are discrete / binned) describing the probability that an individual disperses to any position relative to the start location (e.g., natal site) (Nathan et al. 2012). Dispersal kernels show nearly universal patterns of distance decay: expectations of dispersal decline with distance from the departure location, the extent to which can be modified based on variation in habitat availability and other factors, such as mortality risk (Fig. 1b–d; Koenig et al. 1996; Van Houtan et al. 2007; Bocedi et al. 2014). Despite this ubiquitous

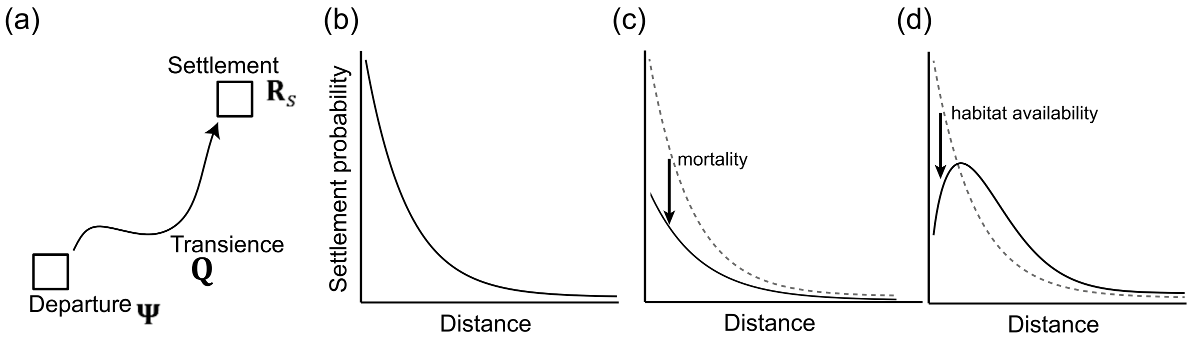

Fig. 1 The random-walk dispersal kernel as envisioned with the spatial absorbing Markov chain (SAMC). **a** The departure, transience, and settlement stages of dispersal and associated parameters of the SAMC. In this context, dispersal is described with the SAMC as: $\mathbf{\Psi}^T(\mathbf{I}-\mathbf{Q})^{-1}\widetilde{\mathbf{R}}_s$ (see Eqs. 3, 4 of main text). **b** An example dispersal kernel generated from the SAMC, which approximates the negative exponential kernel when settlement probabilities are constant per time step. **c** Mortality can alter expectations for dispersal kernels (dashed line represents expectation with no mortality). **d** Variation in habitat availability can also alter expectations for dispersal kernels. Shown is a scenario with low habitat availability near departure location (e.g., departure occurring from an isolated patch) but high availability at farther distances (dashed line represents expectation in contiguous habitat)

pattern, incorporating dispersal kernels directly into models for mapping landscape connectivity remains limited or ad hoc. One exception is the development of least-cost resistant kernels, which have been used to address this limitation (Compton et al. 2007). This approach combines concepts of least-cost paths with home-range estimation using kernel estimators (Worton 1989) to capture the problem of distance decay in expectations of movement based on cumulative least costs (Compton et al. 2007). This approach has proven useful (e.g., Cushman and Landguth 2012; Cushman et al. 2018), yet more broadly least-cost modeling has been criticized based on some of its underlying assumptions, such as individual knowledge of optimal routes to a distant destination (Sawyer et al. 2011). Furthermore, this approach does not explicitly incorporate each of the three dispersal stages into the model formulation.

A recently introduced framework advanced random-walk theory with absorbing Markov chains, termed the spatial absorbing Markov chain (SAMC), to better capture different processes influencing movement and connectivity (Fletcher et al. 2019). The SAMC is an analytical framework like least-cost analysis (Etherington 2016), randomized shortest paths (Saerens et al. 2009) and circuit theory (McRae et al. 2008), all of which assume that variation in landscape features influence the movement process. Overall, the SAMC is most similar to circuit theory: Fletcher et al. (2022) show how circuit theory is a special, simplified case of the SAMC. Yet the SAMC moves beyond circuit theory and other analytical frameworks by providing short- and long-term predictions and a means to account for time-specific movement, directional movement, species distribution and mortality.

Here we extend the SAMC framework to the problem of dispersal kernels, illustrating how this framework can be used to create random-walk dispersal kernels for landscape connectivity assessments that readily capture all three components of the dispersal process. We then illustrate how random-walk dispersal kernels can incorporate time-explicit predictions, different types of movement summaries and can decompose dispersal success from that of failure. We illustrate the use of this model by contrasting predicted connectivity between key subpopulations of the Florida black bear (*Ursus americanus floridanus*), a species of conservation and management concern, when ignoring dispersal kernels versus acknowledging them. Finally, we discuss the relationship of random-walk dispersal kernels to least-cost resistant kernels. Not only do these extensions provide a formal linkage of landscape connectivity to dispersal biology, but they also help to link common connectivity models in a unified way to facilitate predicting connectivity across landscapes.

Methods

The spatial absorbing Markov chain

The SAMC models connectivity based on extensions of discrete-time absorbing Markov chain theory. This framework assumes that landscapes are discrete representations of the environment, represented as raster maps or in a network context where populations or patches are nodes (or vertices) on a spatial graph (Acevedo et al. 2015; Sefair et al. 2017; Fletcher et al. 2019).

We introduce this model in the context of dispersal and illustrate how its parameters relate to dispersal kernels. For each time step during which an organism disperses across a complex landscape, it can either survive and stay at the same location (i.e., site fidelity), survive and move to a nearby site, or terminate movement (e.g., from settlement or death). The SAMC framework honors this idea by considering 'transient' states that capture fidelity and movement, and an 'absorbing' state that captures the termination of movement, which could reflect a variety of issues, such as natural mortality (Fletcher et al. 2019), coalescence in population genetics (Fletcher et al. 2022) or human-wildlife conflict (Vasudev et al. 2023). Here we focus on the scenario where the absorbing state reflects settlement, the third component of the dispersal process (Fig. 1a).

The SAMC framework captures transient and absorption states through the construction of a probability matrix, $\mathbf{P}$ (throughout we use bold capital letters to denote matrices, bold lower-case letters to denote vectors, and non-bold letters to denote scalars). For a landscape divided into C cells or patches, $\mathbf{P}$ can be written as:

$$\begin{pmatrix} \mathbf{Q} & \mathbf{R} \\ 0 & 1 \end{pmatrix} \tag{1}$$

where $\mathbf{Q}$ is a sparse, $C \times C$ transition matrix reflecting transitions between transient states, $\mathbf{R}$ is a $C \times r$

matrix containing transition probabilities from the transient states to r absorbing states, and 0 is a $1 \times C$ vector of zeros. $\mathbf{Q}$ is sparse because we assume that transitions between transient states can only occur locally between consecutive time steps, based on a 4- or 8-neighbor rule (this assumption can be relaxed but increases computational burden). The elements p_{ij} of $\mathbf{P}$ describe the probability of transitioning from state i to j in one time step. A variety of connectivity-related metrics can be quantified using $\mathbf{P}$. Here we extend this framework to interpret dispersal kernels.

Extending the SAMC to dispersal kernels

This model can be extended to include multiple absorbing states, which can be helpful for capturing dispersal kernels. Here we show how two different absorbing states can be considered: one reflecting mortality and a second reflecting absorption due to settlement by a disperser. Our new $\mathbf{P}$ matrix can be described as:

$$\begin{pmatrix} \mathbf{Q} & \mathbf{R}_m & \mathbf{R}_s \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \tag{2}$$

where $\mathbf{R}_m$ and $\mathbf{R}_s$ are $C \times C$ diagonal matrices with diagonal elements equal to absorption probabilities reflecting mortality and settlement, respectively, and off-diagonal elements equal to zero. For each row, $\sum_j p_{ij} = 1$. Consequently, this extension allows the decomposition of different types of absorption on dispersal across landscapes.

With this matrix, we can map the long-term (asymptotic) probability of settlement at location j if starting in location i as the (i, j)th element of $\mathbf{B}_s$,

$$\mathbf{B}_s = \mathbf{F}\mathbf{R}_s \tag{3}$$

where $\mathbf{F} = (\mathbf{I} - \mathbf{Q})^{-1}$ (aka the 'fundamental matrix'), and $\mathbf{I}$ is an identity matrix. Dispersal kernels then naturally emerge from mapping $\mathbf{B}_s$ as a function of distance from a departure location, which can be calculated as:

$$\boldsymbol{\Psi}^{\boldsymbol{T}}\mathbf{B}_s \tag{4}$$

where $\boldsymbol{\Psi}$ is a vector of length C, equal to 1 for the starting (or departing) location i and 0 otherwise, and $\boldsymbol{T}$ is the transpose of this vector. The mapping of the ith row of $\mathbf{B}_s$ represents the dispersal kernel if individuals start at location i. When $\mathbf{R}_m = 0$, Eq. 4 generates a probability mass function (probabilities that sum to 1) that encapsulates all stages of the dispersal process. This model will generate dispersal kernels that approximate an exponential distribution when $\mathbf{R}_s$ is constant (See Supporting Information S1, Fig. S1 for more details), consistent with the idea that exponential kernels arise from random movement when there is a constant probability of settling per unit of time (Paradis et al. 2002; Bullock et al. 2017). Exponential kernels are a common formulation for dispersal in metapopulation ecology (Hanski 1999), yet other types of kernels (e.g., fat-tailed) could also be approximated by altering $\mathbf{R}_s$ as a function of the departure location (e.g., smaller values of $\mathbf{R}_s$ near source locations will result in more fat-tailed distributions).

The above model is an asymptotic expectation for dispersal. This framework can also be applied in such a way that it is time-explicit to accommodate temporal or dynamic connectivity (Zeigler and Fagan 2014; Zeller et al. 2020). We can map the probability of settlement at location j within t or fewer time steps if starting in location i as the (i, j)th element of $\mathbf{B}_{s,t}$,

$$\mathbf{B}_{s,t} = (\mathbf{I} - \mathbf{Q})^{-1}\left(\mathbf{I} - \mathbf{Q}^t\right)\mathbf{R}_s \tag{5}$$

A time-explicit dispersal kernel can then be quantified as $\boldsymbol{\Psi}^{\boldsymbol{T}}\mathbf{B}_{s,t}$.

Taken together, this random-walk formulation of dispersal kernels for landscape connectivity provides a flexible means for accommodating distance decay in movement that is common in plants and animals and it directly captures all three components of the dispersal process (i.e., departure, transience and settlement). In this way, departure ($\boldsymbol{\Psi}$) reflects the distribution of initial locations, which will typically be considered a model input based on a variety of data (e.g., species distribution or occupancy models, locations of populations in protected area, etc.). Transience ($\mathbf{Q}$) reflects how the landscape alters movement behavior or trajectories via resistance, which can also be parameterized using a variety of techniques (e.g., Zeller et al. 2012). Finally, settlement ($\mathbf{R}_s$) describes the likelihood of settling in at each location in the landscape per unit time. See Supporting Information on details regarding guidance on parameterizing $\mathbf{R}_s$.

Applications of random-walk kernels

The random-walk kernel can be applied in at least four general ways, each of which can be based on long-term expectations or time-explicit expectations. We provide a simple example of these alternatives in Figs. 2 and 3, where we generate habitat and landscape resistance using a neutral landscape model and apply it to the problem of dispersal kernels. See the Supporting Information for details on the construction of this model and its application to dispersal kernels.

Random-walk dispersal kernels

When $\mathbf{Q} = 1$, $\mathbf{R}_s$ is constant in suitable habitat across the landscape, and $\mathbf{R}_m = 0$, the model will reflect a simple random-walk dispersal process,

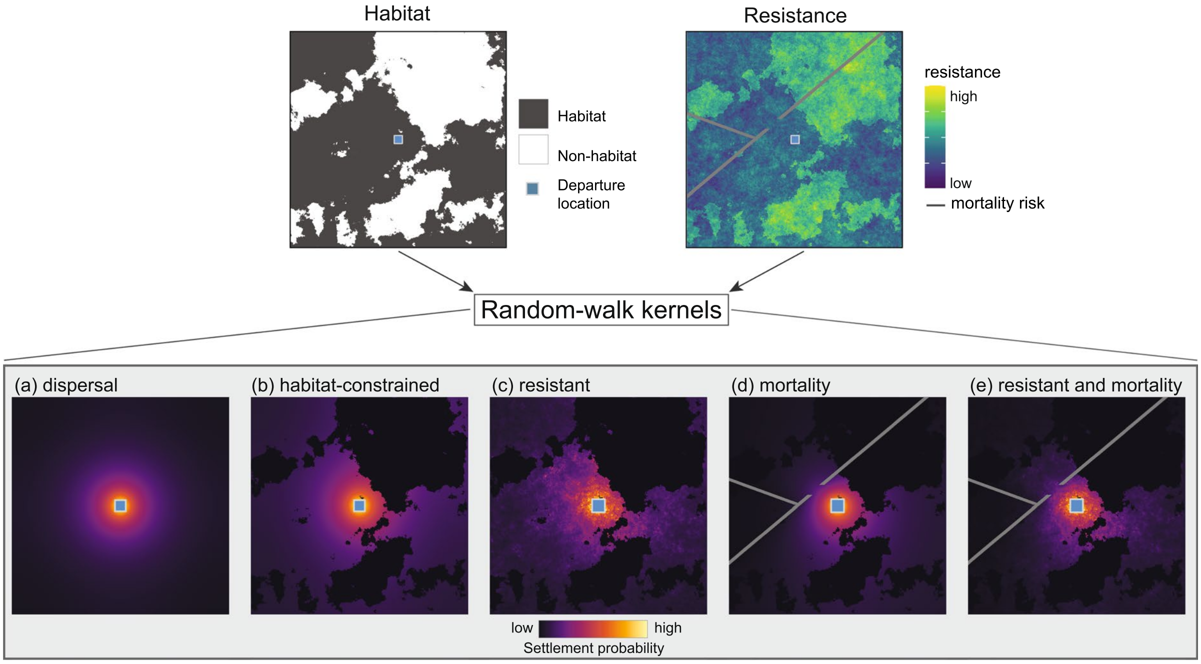

Fig. 2 The flexibility of random-walk movement kernels for landscape connectivity assessments. Habitat, resistance, mortality and the departure location for dispersal are potential model inputs for random-walk dispersal kernels. With this information, the spatial absorbing Markov chain can generate several types of random-walk dispersal kernels that vary in how the landscape may affect settlement. **a** Simple dispersal kernels in contiguous space are un-affected by landscape resistance. **b** Habitat-constrained dispersal kernels are those where settlement can only occur in habitat. **c** Resistant kernels are those where the landscape alters movement trajectories via resistance. **d** Mortality kernels are those where the landscape alters kernels based on dispersal failure via mortality. Finally, **e** resistant and mortality kernels arise when the landscape affects both movement via resistance and mortality

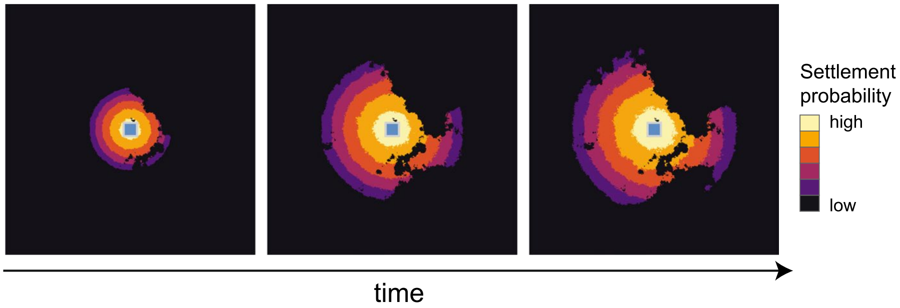

Fig. 3 Time-explicit random-walk kernels. Shown is the example of a random-walk resistant kernel in Fig. 2c, but as time progresses. Probability scale binned on a log scale for visualization

wherein settlement declines with distance, but landscape resistance does not alter movement pathways (Fig. 2a). This approach reveals the expectations for dispersal in the absence of landscape permeability effects altering outcomes and can be constrained by assuming settlement only occurs within habitat ('habitat-constrained dispersal kernels'; Fig. 2b).

Random-walk resistant kernels

When $\mathbf{Q}$ is not constant, $\mathbf{R}_s$ is constant in suitable habitat across the landscape and $\mathbf{R}_m = 0$, the model will reflect a random-walk dispersal process, wherein movement directionality is affected by landscape resistance $\mathbf{Q}$ (Fig. 2c). This model assumes that mortality does not occur and instead focuses on spatial variation in the settlement process due to landscape resistance.

Random-walk mortality kernels

When $\mathbf{Q} = 1$, $\mathbf{R}_s$ is constant in suitable habitat across the landscape and $\mathbf{R}_m \neq 0$, this model will reflect a random-walk dispersal process, wherein movement directionality is affected solely from the landscape altering survival during movement (Fig. 2d). In this context, $1 - \sum \boldsymbol{\Psi}^T \mathbf{B}_s$ is the overall expectation for dispersal failure across the entire landscape, such that $\boldsymbol{\Psi}^T \mathbf{B}_s$ does not sum to 1 (it is no longer a probability mass function). This formulation generates a dispersal survival function of relevance to metapopulation ecology (Schnell et al. 2013; Brodie et al. 2016). In addition to mapping settlement, mortality can be mapped as $\boldsymbol{\Psi}^T \mathbf{B}_m$, where $\mathbf{B}_m = \mathbf{F}\widetilde{\mathbf{R}}_m$, thereby providing expectations for where mortality occurs across the landscape.

Random-walk resistant and mortality kernels

When $\mathbf{Q}$ is not constant, $\mathbf{R}_s$ is constant in suitable habitat across the landscape, and $\mathbf{R}_m \neq 0$, this model will reflect a random-walk dispersal process, wherein movement directionality is affected by landscape resistance $\mathbf{Q}$ and the landscape also affects dispersal success by altering survival during movement (Fig. 2e).

These different types of kernels can be compared to better understand how landscape effects on movement and mortality alter predicted settlement across the landscape. Furthermore, although the focus above is on creating maps of the dispersal kernel (i.e., spatial variation in settlement), we note that the SAMC provides a means to quantify and map a variety of connectivity-related metrics (Fletcher et al. 2019, 2022). For example, with the above dispersal constraints, other metrics could be mapped that reflect different aspects of the movement and dispersal process, such as the time spent in locations, the probability of reaching locations, or the time needed to reach settlement locations (see Fletcher et al. 2019, 2022 for more details).

Model calibration and tuning

Fitting the random-walk kernel requires setting absorption values $\mathbf{R}_s$ for pixels in a landscape at locations of potential settlement. Absorption values are probabilities bound to the 0–1 interval. In this context, larger values of $\mathbf{R}_s$ will lead to shorter expected dispersal distances. $\mathbf{R}_s$ can be calibrated based on the mean expected dispersal distances of the species being considered (Marx et al. 2020). In the Supporting Information, we provide guidance on using the `samc` package in R (Marx et al. 2020) for modeling random-walk kernels (Supporting Information S2), and information on calibrating and tuning potential starting values for $\mathbf{R}_s$ based on the grain of a landscape and mean expected dispersal distances (Supporting Information S3). This guidance illustrates that there is a fundamental relationship between mean expected dispersal distances and absorption values in the SAMC for random-walk dispersal kernels, which is linear on a log–log scale (Fig. S3). See Fletcher et al. (2019, 2022), Vasudev et al. (2023) and Marx et al. (2020) for discussions on calibrating $\mathbf{R}_m$.

An illustration with black bears

We provide an example with connectivity mapping for the Florida black bear. Florida black bears are of conservation and management concern and connectivity has been of considerable interest (Maehr et al. 2003; Larkin et al. 2004; Dixon et al. 2006; Fletcher et al. 2013). In particular, one subpopulation located within the Greater Chassahowitzka Ecosystem (GCE) at the Weekiwachee Preserve is small and relatively isolated from other subpopulations, such that there has been concern about its viability given its isolation. Previously, connectivity models were applied to determine potential corridors that may connect the GCE subpopulation to six other subpopulations within a ‘dispersal zone’ of 140 km from this location (Big Bend, Goethe State Forest, Ocala National Forest, Withlaoccohee River Basin, Green Swamp and lower Hillsborough River basin; see Fig. 4), which was based on the maximum known dispersal distance by black bears in Florida (Larkin et al. 2004). Within this zone, least-cost paths were identified that connect these subpopulations. This approach was useful for conservation planning and acknowledged the maximum potential distance for dispersal. However, the temporal nature of movement imposes natural constraints on dispersal distance, which cannot be naturally incorporated into least-cost paths modelling of connectivity. Here we revisit this problem by modeling random-walk dispersal kernels to more fully capture the dispersal process.

We illustrating mapping a single dispersal kernel and subsequently extend this to interpreting synoptic connectivity for the entire landscape by modeling both dispersal kernels for all six subpopulations in the dispersal zone for Weekiwachee Preserve as well as a metric of net movement rates that is analogous to current density mapping using circuit theory (Fletcher et al. 2022; Vasudev et al. 2023). For the single dispersal kernel, we illustrate mapping a simple (Fig. 2a), habitat-constrained (Fig. 2b), and resistant kernel (Fig. 2c). We do not focus on incorporating mortality here.

The first step of applying random-walk kernels is the creation of a resistance map or related information to parameterize **Q**. There are currently a wide variety of ways in which resistance and can be determined for connectivity models and ideally such estimates should typically come from information on dispersal paths (Zeller et al. 2016, 2012). Evaluating resistance estimation here is beyond the scope of our application but we note that many of the issues of applying resistance to circuit theory and least-cost analysis are similar to the SAMC. To compare with prior results, we used the resistance classification described in Larkin et al. (2004), updated to the most recent and reliable land-cover map for Florida (the Florida Cooperative Land Cover Map, v.3.5), reclassified to a resolution of 200 m (2.2 M pixels). This resistance classification was based on collating results from several studies on black bear biology. Larkin et al. (2004) classified landscape resistance as: 1, core habitat (e.g., upland coniferous forest); 10, marginal bear habitat (e.g., shrub and brushland), 50, high human disturbance (e.g., low density residential areas), 100 as surmountable barriers (e.g., roads), and NA as insurmountable (Table S2). We re-classified insurmountable as a resistance value of 1000, as calculations from the SAMC require that areas with 0 absorption (e.g., zero settlement probability) are not isolated from other areas in the landscape.

The second step of applying random-walk kernels is to create an absorption map, which captures the probability of settlement at each location on a landscape. For simple dispersal kernels (Fig. 2a), this map is would be a constant value across the map extent that reflects a settlement probability per time step, the value of which can be calibrated to generate an expected dispersal distance based on the grain size (resolution) of the map. In the Supporting Information Section S3, we show that the log of expected (mean) number of pixels dispersed $\overline{d}_p$ is accurately predicted by the log of absorption values r_s ($R^2 = 0.997$), such that with the mean dispersal distance of a species (in units of pixels), we can identify an approximate absorption value as:

$$r_s = \exp(-1.247 - 1.788 \times \log\left(\overline{d}_p\right)) \tag{6}$$

We use Eq. 6 as a starting point for the absorption map to reflect settlement probabilities $\mathbf{R}_s$. Note landscape boundaries and irregular landscape extents may alter realized dispersal distances modeled by the SAMC. In addition, if settlement only occurs in habitat that is patchy across the landscape (habitat-constrained kernels; Fig. 2b), the realized dispersal distances from the SAMC will vary. Consequently, Eq. 6 should be used as a starting point for modeling. We profiled across values at 10% increments above or below this starting value (depending on the initial estimate of dispersal distance from Eq. 6) for each scenario considered, selecting the absorption value that most closely matched known mean dispersal distances in black bears (11.8 km; Maehr 1996).

The third step of applying random-walk kernels is to consider departure locations, which can be described as individual points or as a raster map. We illustrate how this can be done for a situation where the departure location is an entire protected area rather than a single point location. To do so, we set

$\mathbf{\Psi}$ to reflect the outer boundary of the departure protected area by setting the pixels along this boundary to sum to 1 and the interior of the protected area to NA. This reflects the idea that an individual could randomly start from any location along the boundary of the study area and disperses out of the protected area (dispersal within the protected area is not considered); such parameterization will lead to a probability mass function that describes the dispersal kernel for the polygon.

With the resistance, absorption, and departure location maps, we calculated random-walk kernels using the `mortality()` function in the `samc` package (Marx et al. 2020). To illustrate single dispersal kernels, we map simple, habitat-constrained, and resistant kernels (Fig. 2a–c) based on dispersal from the Withlacoochee State Forest, a centrally located protected area in the study area. For habitat-constrained and resistant kernels, we only allowed settlement to occur in suitable habitats. We then illustrate how random-walk resistant kernels can be similarly applied to all subpopulations to map dispersal expectations across the region. Finally, we contrast mapping net visitation rates, or expected net movement probabilities through locations (e.g., pixels) (Fletcher et al. 2022), across the region with and without expectations from dispersal kernels. In a simple scenario where absorption can only occur at a destination location, net visitation rates are identical to mapping current density from circuit theory (Fletcher et al. 2022). However, with absorption parameterized to reflect dispersal kernels, net visitation rates will now account for expectations of movement declining with distances from departure locations, essentially analogous to 'kernel-informed' current density. To do so, we calculated net visitation rates between all pairs of subpopulations, using the centroid of each area (Fig. 4a) as the departure and destination locations.

Results

Single dispersal kernels

We first tuned absorption values for each kernel to approximately match known mean dispersal distances of Florida black bears (11.8 km) based on bears departing from Withlaoccohee River Basin, a centrally located subpopulation (Fig. 4a). The starting value for absorption taken from Eq. 6 ($r_s = 0.0002$) generated an expected dispersal distance of 9.7 km for the simple kernel, 17.3 km for the habitat-constrained kernel, and 4.7 km for the resistant kernel. In this case, patchy habitat for settlement (Fig. 1d) led to expectations of dispersers moving farther distances when resistance was assumed constant, yet incorporating resistance led to much shorter predicted dispersal distances due to potential landscape barriers. As reported dispersal distances implicitly incorporate variation in habitat and resistance, we then profiled across values to identify appropriate absorption values for each scenario that generate ~ 11.8 km expected dispersal distances in this landscape (Fig. S5).

Based on these tuned models, expected dispersal across the landscape varied (Fig. 4b–d), with much of the spatial variability being driven by habitat availability for settlement rather than resistance. When comparing the resulting expected kernels as a function of distance, resistant kernels led to higher expectations for settlement close to the departure location, and both habitat-constrained and resistant kernels led to more irregular predictions for settlement as a function of distance (Fig. 5).

Landscape connectivity

Using the resistant kernel parameters estimated above, we mapped settlement probabilities for dispersal from all subpopulations surrounding Weekiwachee Preserve to determine expectations for potential settlement into Weekiwachee Preserve when incorporating dispersal kernels. Overall, predicted settlement probabilities into Weekiwachee Preserve were low (Fig. 6a). Pairwise analysis based on the centroids of each subpopulation suggested that the highest settlement probability came from Withlacoochee State Forest and secondarily Green Swamp Forest, and the lowest from Ocala National Forest. Contrasting net visitation rates (analogous to current density) that did not incorporate dispersal kernels (Fig. 6b) to a model that incorporated dispersal kernels (Fig. 6c) highlighted that expected movement in the vicinity of Weekiwachee Preserve is predicted to be much lower when accounting for dispersal kernels.

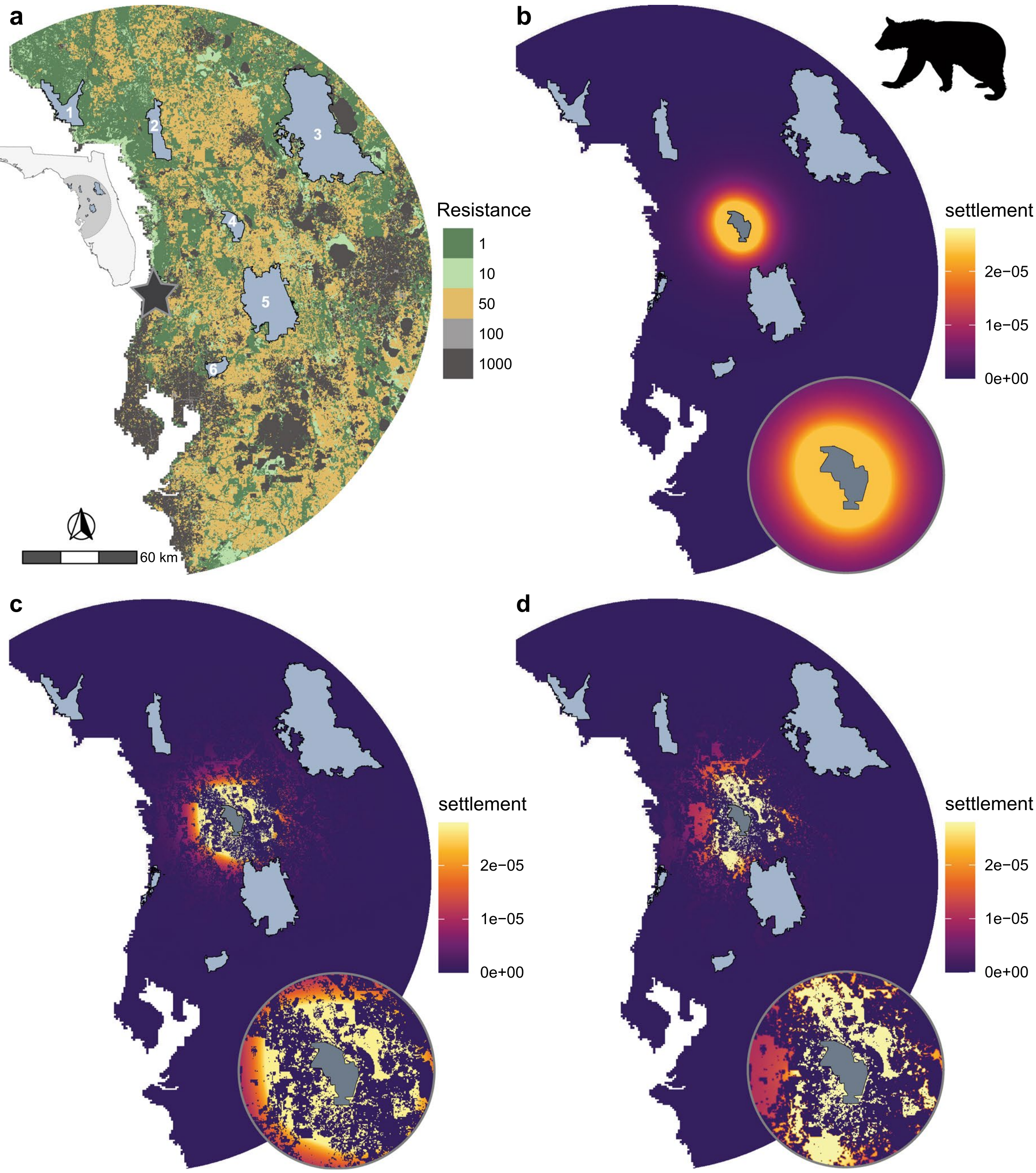

Fig. 4 Random-walk dispersal kernels and the Florida black bear. **a** Resistance map for a region in central Florida where six subpopulations of black bears occur. Inset shows the location in Florida, which encompasses a 140 km dispersal zone from the Weekiwachee Preserve (star). Subpopulations considered include: 1 = Suwannee River National Wildlife Refuge; 2 = Goethe State Forest; 3 = Ocala National Forest; 4 = Withlacoochee River Basin; 5 = Green Swamp; 6 = Lower Hillsborough River Basin. **b** A simple random-walk dispersal kernel, **c** a habitat-constrained random-walk kernel and **d** a random-walk resistant kernel. We illustrate each kernel based on a centralized subpopulation at Withlaoccohee River Basin. Insets show a 25 km radius centered on Withlaoccohee River Basin

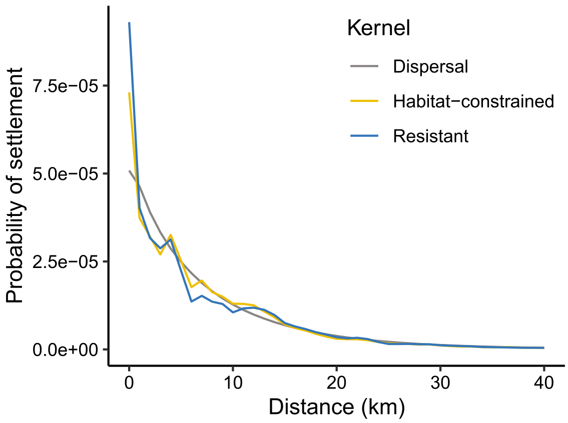

Fig. 5 Settlement probabilities as a function of distance based on random-walk dispersal kernels for the Florida black bear. Expected probabilities as a function of distance are based on Fig. 4b–d. Each kernel is based on a centralized subpopulation at Withlaoccohee River Basin

Discussion

We provide a framework for incorporating dispersal kernels into landscape connectivity modeling. This framework explicitly acknowledges each component of the dispersal process—departure, transience and settlement (Fig. 1)—and provides a flexible means to incorporate several aspects of movement and dispersal processes. We illustrate the use of this approach to interpret connectivity between protected areas for the Florida black bear, finding that incorporating dispersal kernels greatly reduced expectations of connectivity across the region in comparison to prior analysis using least-cost paths. The underlying movement model of our framework is built from random-walk theory with Markov chains and can capture several aspects of dispersal biology, which may provide more realistic predictions of dispersal than current algorithms that use the isolation-by-resistance paradigm.

A niche for the random-walk kernel in connectivity modeling

The random-walk kernel provided here shares some similarities with the least-cost resistant kernels (LCRK; Table 1) (Compton et al. 2007). The similarities and differences can be understood by comparing the steps used in LCRK. The LCRK generally requires three steps. First, the cumulative least cost from a departure (or starting) location to each pixel within a specified maximum number of cost units. Second, this cumulative cost is then rescaled

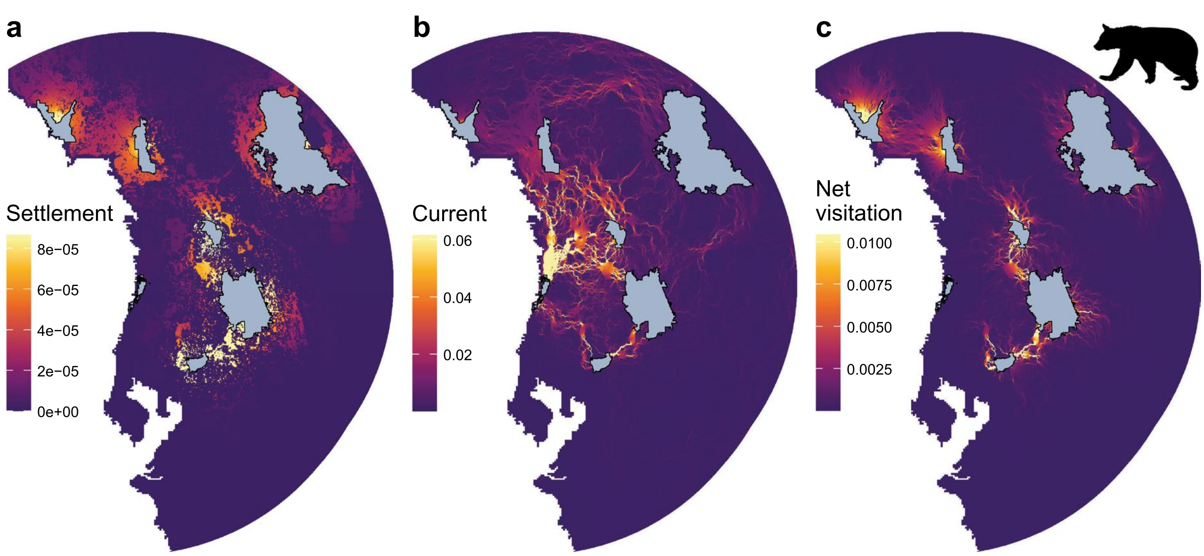

Fig. 6 From random-walk dispersal kernels to landscape connectivity for the Florida black bear. **a** Random-walk resistant kernels for each subpopulation in the landscape that have the potential to immigrate into Weekewachee Preserve. **b** Net visitation rates for flow from subpopulations into Weekewachee Preserve in the absence of considering dispersal kernels. This scenario is identical to current density mapping using circuit theory. **c** Net visitation rates for flow from subpopulations into Weekewachee Preserve when accounting for dispersal kernels (based on the resistant kernel shown in **a**)

Table 1 Contrasting assumptions and applications of random-walk kernels to least-cost resistant kernels

Characteristic/assumption	Resistant kernel	Random-walk kernel
Least-cost movement process	Yes	No
Random-walk movement process	No	Yes
Landscape resistance considered	Yes	Yes
Distinguishes movement versus settlement	No	Yes
Probability mass function	Possible	Yes
Tuning parameters	Maximum number of cost units	Absorption
Scaling to synoptic connectivity	Iterative	Simultaneous
Decomposition of mortality	No	Yes
Time-explicit predictions possible	No	Yes
Multiple movement metrics	No	Yes

to reflect a measure of (relative) probability of use. This rescaling can be simply the inverse of the cumulative cost (Cushman and Landguth 2012), or it can more formally be re-scaled based on kernel functions (Compton et al. 2007). Third, this process is then repeated for all potential starting locations on the landscape to provide a synoptic perspective on connectivity for the entire landscape.

In contrast to the LCRK, the random-walk kernel uses absorption to directly quantify the probability of settlement, rather than rescaling a measure of cumulative cost. Cumulative cost may better reflect expectations for use or movement to pixels rather than the settlement process. We note that in the context of the SAMC, related metrics referred to as the 'spatially explicit dispersal' and 'visitation' metrics (Fletcher et al. 2019) would provide more similar information on movement (rather than settlement) and can be used once settlement probabilities are calibrated (e.g., Fig. 6c). The random-walk kernel does not require rescaling and instead directly estimates a probability mass function describing the dispersal kernel. The random-walk kernel also does not require an iterative process for connectivity mapping across the entire landscape; instead, calculations for the entire landscape use the same kind of information as for calculations from a single location and can be done simultaneously (see Eq. 4). These differences, along with the assumption of a random-walk process and the ability to extend modeling to account for mortality and be time-explicit (Fig. 3), suggest that the random-walk kernel may provide a useful alternative to the LCRK in several situations, such as modeling plant dispersal, animal dispersal when 'least cost' assumptions are not warranted, modeling redistribution over specified periods of time, or addressing mortality risks (e.g., Hughes et al. 2023; Veals et al. 2023).

Random-walk processes with the SAMC are directly related to concepts from circuit theory and they share similarities with continuous time and continuous space random-walk models (Holmes et al. 1994; Ovaskainen et al. 2008; Brennan et al. 2018). In fact, circuit theory is a special case of the SAMC: if the SAMC is parameterized such that the only absorption state is the destination location, the SAMC will provide identical results to circuit theory calculations of commute time and current density (Fletcher et al. 2022). Here, random-walk dispersal kernels illustrate one way in which the SAMC can extend circuit-theoretic concepts by providing a means to generate dispersal kernels through the decomposition of absorption states as well as time-explicit analyses. Consequently, users familiar with circuit theory and interested in applying circuit-theoretic concepts while acknowledging dispersal processes can apply the SAMC to deliver insights. While both the SAMC and circuit theory are based on biased local random walks, because the SAMC can incorporate directionality it is also possible to extend the SAMC to also accommodate correlated random walks (Codling et al. 2008; Fletcher et al. 2019), which are commonly observed in animal dispersal (Kareiva and Shigesada 1983). We built the SAMC using a discrete time and discrete space formulation, which can be more tractable than continuous models and can be readily applied to raster maps. However, continuous space and time models can be beneficial in some situations, particularly when there is interest to vary the grain of models (Brennan et al. 2018).

Connectivity for the Florida black bear

Our application to connectivity for the Florida black bear illustrates how directly incorporating dispersal kernels into connectivity assessments can alter conclusions about connectivity across landscapes. A previous assessment incorporated dispersal constraints by simply working within a 'dispersal zone' based on the maximum known dispersal distance for this species (Larkin et al. 2004). This type of masking of relevant landscape extents or only considering protected areas within a maximum dispersal distance is common in landscape connectivity mapping. While such approaches are a useful first step to acknowledge dispersal limitations, our results suggest that that they may over-estimate expectations for connectivity across landscapes (see also Fletcher et al. 2011).

Our modeling also provides a means of determining the likelihood of settlement into key areas from other protected areas. We found that while expected dispersal into Weekiwachee Preserve was low, it was much more likely to occur from Withlacoochee State Forest than from other areas: given that dispersal occurs, there is a 66% chance dispersal will occur from Withlacoochee State Forest, a 20% chance from Green Swamp and a less than 1% chance it will occur from Ocala National Forest. Information like this can help prioritize where dispersal may be most likely to occur and subsequently how linkages between these areas can be prioritized to facilitate connectivity. We note that we did not include information on population size in each of these subpopulations, but including such information when available into predictions is straightforward with the SAMC (Vasudev et al. 2023).

Extensions

We focused on situations where settlement probabilities were constant across potential habitat in the landscape. However, these probabilities could also be based on variation in habitat quality, such that they capture the potential for habitat selection to alter where individuals immigrate and settle across the landscape. Settlement probabilities could be parameterized based on habitat suitability models or related information (Guisan et al. 2017). Resistance optimization techniques (e.g., Peterman 2018; Peterman and Pope 2021) could be extended to optimize resistance surfaces with the SAMC, both for interpreting land-cover resistance and also for settlement probabilities. We also note that the SAMC can incorporate information on fidelity (Fletcher et al. 2022), which may alter the speed and distance of expected dispersal. Finally, by altering settlement probabilities as a function of distance from departure location, random-walk kernels could potentially better capture other dispersal kernel shapes, such as 'fat-tailed' kernels that are common in some taxa (Fandos et al. 2023).

Conclusion

The spatial absorbing Markov chain framework provides an explicit scaffolding for the analysis of dispersal kernels for connectivity modeling. This framework extends circuit-theoretic concepts, which have seen widespread use to interpret connectivity across landscapes in ecology, evolution, and conservation (Fletcher et al. 2016; Dickson et al. 2019). Our results and associated code (See Supporting Information) provide guidance for applying spatial absorbing Markov chains to the problem of dispersal across landscapes. Future landscape connectivity studies considering the use of least-cost resistant kernels can potentially relax some assumptions of that approach using the SAMC and can extend applications to address dispersal mortality and time-explicit predictions for interpreting connectivity across complex landscapes.

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Author contributions RJF conceived the ideas and designed methodology. RJF and MI formatted and analyzed data. RJF led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability Data for bear example are provided at Figshare (https://figshare.com/; DOI: https://doi.org/10.6084/m9.figshare.22776218).

Code availability We provide the R code used to generate examples in Figures 2-3 using the `samc` package in the Supporting Information. Code for the black bear example is deposited at Figshare (https://figshare.com/:DOI: https://doi.org/10.6084/m9.figshare.22776218).

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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