

METHOD

Towards a unified framework for connectivity that disentangles movement and mortality in space and time

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Abstract

Predicting connectivity, or how landscapes alter movement, is essential for understanding the scope for species persistence with environmental change. Although it is well known that movement is risky, connectivity modelling often conflates behavioural responses to the matrix through which animals disperse with mortality risk. We derive new connectivity models using random walk theory, based on the concept of spatial absorbing Markov chains. These models decompose the role of matrix on movement behaviour and mortality risk, can incorporate species distribution to predict the amount of flow, and provide both short- and long-term analytical solutions for multiple connectivity metrics. We validate the framework using data on movement of an insect herbivore in 15 experimental landscapes. Our results demonstrate that disentangling the roles of movement behaviour and mortality risk is fundamental to accurately interpreting landscape connectivity, and that spatial absorbing Markov chains provide a generalisable and powerful framework with which to do so.

Keywords

Circuit theory, dispersal, fragmentation, habitat loss, least cost, Markov chain, matrix effects, random walk, networks.

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INTRODUCTION

Dispersal underpins several theoretical frameworks in ecology and evolution (Slatkin 1993; Hanski 1999) and lies at the heart of the emerging sub-discipline of movement ecology (Nathan *et al.* 2008). Understanding dispersal is central to conservation and management plans (Harrison & Bruna 1999), which often emphasise connecting habitat remnants to facilitate the movement of species through landscapes increasingly altered by human activities (Heller & Zavaleta 2009; Albert *et al.* 2017).

Dispersal is inherently risky. Organisms that attempt to disperse through the matrix surrounding fragments risk mortality due to predation, human-induced causes, resource deprivation, or environmental conditions exceeding their physiological limits (Bonte *et al.* 2012). Some matrix environments are more challenging than others for movement – what has been termed ‘matrix resistance’ (Ricketts 2001) – leading to slower travel or changes in movement paths. Understanding matrix resistance can be critical for predicting and mapping landscape connectivity (Beier *et al.* 2011), or the degree to which the landscape alters movements among resources (Taylor *et al.* 1993).

Currently, most frameworks for mapping connectivity rely on a spatially explicit perspective of matrix resistance. These approaches have seen widespread use in conservation biology and landscape genetics as a means to identify corridors,

evaluate restoration potential, and understand limits to gene flow (Spear *et al.* 2010; Dickson *et al.* 2019). Key areas of potential connectivity are typically mapped and evaluated through the use of least-cost approaches and/or circuit theory (McRae *et al.* 2008; Pinto & Keitt 2009; Etherington 2016). Least-cost approaches identify potential routes of connectivity based on minimum resistance to movement between locations, whereas circuit theory can account for path redundancies and non-optimal movement. While these applications have proven very useful (Dickson *et al.* 2019), they typically do not explicitly consider mortality risk when assessing ‘resistance’. As a result, the interpretation of matrix resistance often conflates effects of variation in movement behaviour with that of mortality (Zeller *et al.* 2012). Because the demographic effects of mortality when moving through the matrix could ultimately be greater than those resulting from changes in movement routes, failing to distinguish between these two issues could lead to implementing incorrect or even counterproductive conservation actions (Fig. 1; Vasudev *et al.* 2015). Although some experiments have made strides in understanding these different effects (e.g. Nowakowski *et al.* 2015), a unified framework for modelling connectivity that honors the problem of both movement behaviour and mortality risk has proven elusive.

Here, we derive a new framework to predict movement and connectivity across landscapes that incorporates the concept of matrix resistance while decomposing the role of the

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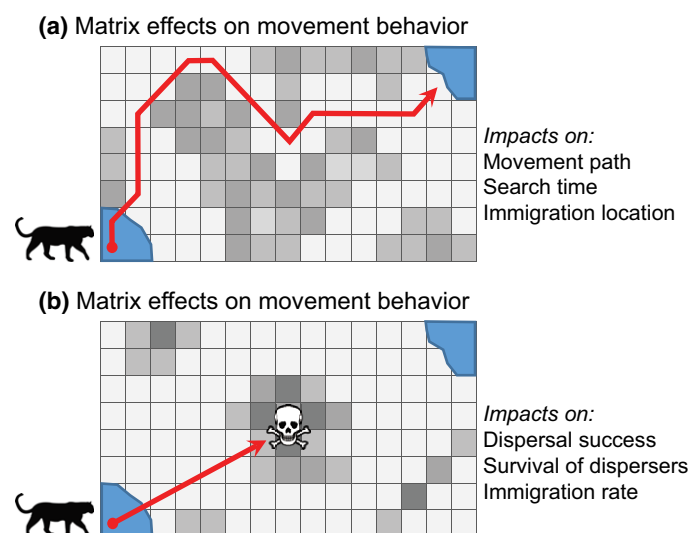


Figure 1 How the landscape can impact movement and connectivity. (a) Matrix resistance (darker grey indicates higher resistance) can alter movement behaviour and trajectories across landscapes. Matrix resistance to movement is commonly assumed in connectivity mapping, with least-cost paths being one of the most common approaches to mapping corridors and connectivity (Fletcher *et al.* 2016). Red shows the least-cost path between two protected areas (in blue). (b) The matrix can also alter mortality risk, impacting survival and dispersal success (darker gray indicates higher mortality). The role of the matrix on mortality risk is currently poorly acknowledged in connectivity predictions and mapping despite its clear importance for dispersal success across landscapes.

matrix on movement behaviour and mortality. This framework extends random walk theory with absorbing Markov chains, which explicitly acknowledge the potential for ‘absorption’, such as mortality (Ross 2010). Our spatial absorbing Markov chain (SAMC) framework allows for probabilistic accounting of both movement behaviour and mortality risk of dispersers across landscapes. Furthermore, it improves on commonly used least-cost analysis and circuit theory in several other ways. This framework can: (1) provide both short- and long-term predictions of connectivity; (2) incorporate population distribution and abundance into predictions of connectivity; and (3) quantify demographic parameters related to connectivity. We begin by introducing the SAMC framework and illustrating how this framework can make predictions of movement across complex landscapes. We apply and evaluate this framework with a spatially structured population undergoing experimental habitat destruction to ask: (1) does the inclusion of mortality risk improve predictions for dispersal across fragmented landscapes; and (2) can the SAMC improve predictions relative to commonly used least-cost and circuit theory approaches? We end by discussing potential extensions and applications of the SAMC for connectivity science.

METHODS

The spatial absorbing Markov chain for complex landscapes

We start by considering successful movement across landscapes as a stochastic process driven by both movement

behaviour and mortality risk, each of which can be influenced by spatial heterogeneity in the landscape. In connectivity mapping, landscapes are generally considered as discrete representations of the environment via the use of raster maps; our framework assumes this discretisation. We also treat time as a discrete variable, which matches the typical discretisation of movement data.

Formally, we consider a stochastic process X with a finite number of states; $X_t = i$ means that the process is in state i at time t (e.g. an individual is in one of a set of discrete cells). We assume that transitions are Markovian, meaning that the probability of visiting state i at time step $t+1$ depends only on the state at t . For a landscape divided into C cells (Fig. 2), we define a sparse, $C \times C$ transition matrix, denoted $\mathbf{Q}$ (we generally use the term ‘matrix’ to denote the interstitial region among patches. When referring to the mathematical term, ‘matrix’ will be preceded by adjectives such as ‘transition’). Element (i, j) of $\mathbf{Q}$, q_{ij} , is the probability of an individual transitioning from cell i to j in one time step, which is often formalised based on ‘cost’ or ‘friction’ maps that reflect matrix resistance to movement. Matrix $\mathbf{Q}$ reflects the permeability of the landscape to movement and is sparse because we assume that transitions occur locally over short time steps (e.g. via a 4- or 8-neighbour rule). This matrix can be obtained using the inverse of mean cost values between two cells, c_i and c_j , of a cost map (Fig. 2a; McRae *et al.* 2008), such that:

$$q_{ij} \propto \frac{1}{(c_i + c_j)/2}. \quad (1)$$

Such transition matrices lie at the heart of most current connectivity modelling (e.g. McRae *et al.* 2008). Absorbing Markov chains add one or more ‘absorbing’ states to $\mathbf{Q}$, which in this case represents mortality (Ross 2010).

To explicitly incorporate mortality risk for dispersers, we define a $(C+1) \times (C+1)$ transition probability matrix, $\mathbf{P}$, that contains both transition probabilities between transient states (i.e. landscape cells) and an absorbing state representing death (Fig. 2b). Matrix $\mathbf{P}$ can be written as:

$$\begin{pmatrix} \mathbf{Q} & \mathbf{R} \\ 0 & 1 \end{pmatrix}, \quad (2)$$

where $\mathbf{R}$ is a $C \times 1$ vector containing transition probabilities from the transient states to the absorbing state, and 0 is a $1 \times C$ vector of zeros. Element (i, j) of $\mathbf{P}$, p_{ij} , is the probability of transitioning from state i to j in one time step, such that $p_{i,C+1}$ (i.e. the i -th element of $\mathbf{R}$) is the probability of death in one time step for an individual located in cell i and $p_{C+1,C+1} = 1$, since a dead individual remains dead. For each row, $\sum_{j=1}^{C+1} p_{ij} = 1$, because being in any location i at time t , the total probability at time $t+1$ of being in an adjacent cell – including cell i – or being dead must be 1. The likelihood of movements across the landscape is captured by the elements of $\mathbf{P}$, leading to a biased random walk model based on spatial heterogeneity that can include asymmetric flows across landscapes (e.g. Acevedo *et al.* 2015a), a notable limitation of circuit theory (McRae *et al.* 2008). By acknowledging the potential for fidelity to any cell (e.g. $p_{ii} > 0$), it can also

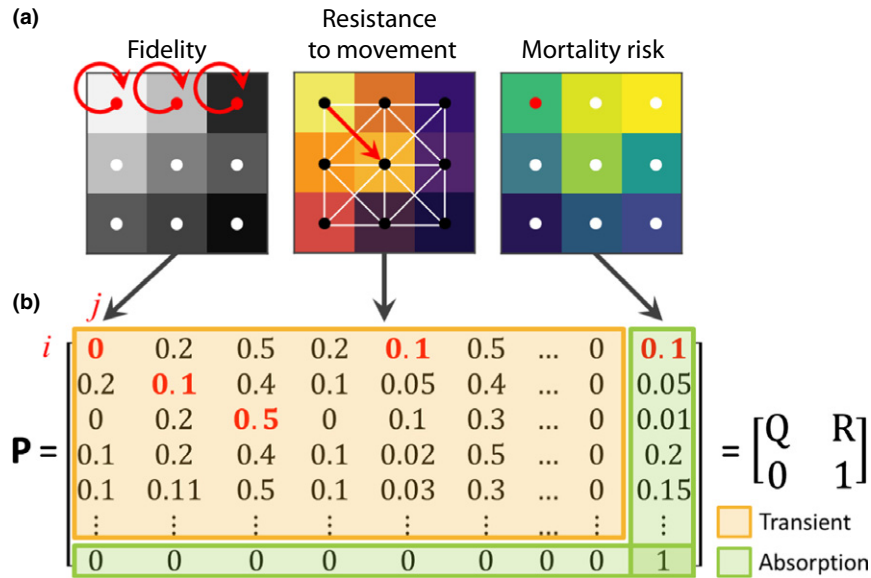


Figure 2 Absorbing Markov chains, the matrix, and connectivity. (a) Across landscapes, raster maps can depict three key aspects for potential movement and connectivity: fidelity to locations, resistance to movement, and mortality risk. For resistance to movement, network theory is often used to convert raster maps into sparse networks, where cells (pixels) are linked to neighbours based on ‘resistance’ of the matrix to movement (shown is an 8-neighbour rule). (b) Absorbing Markov chain theory takes each of these components to create a transition matrix, $\mathbf{P}$, which explicitly accounts for both movement (transient transitions among landscape cells, $\mathbf{Q}$, shown in orange) and mortality (absorption, $\mathbf{R}$, shown in green) by adding absorbing column and row vectors to the $\mathbf{Q}$ matrix. Note that in this example, $\mathbf{P}$ is a 9×9 matrix but only a portion is shown.

account for variation in movement velocity through landscapes (Hanks *et al.* 2011).

Parameterising $\mathbf{P}$ requires a minimum of two maps as input: one of permeability (e.g. the inverse of resistance or cost) to movement, and a second of mortality risk (Fig. 2). When fidelity is of interest, a map of potential site fidelity could be used to parameterise the diagonal of $\mathbf{Q}$ (Fig. 2); we do not focus on fidelity here and set $\text{diag}(\mathbf{Q}) = 0$ to emphasise dispersal behaviour. To assure that $\sum_{j=1}^{C+1} p_{ij} = 1$, a normalisation constant may be needed. A natural way to normalise $\mathbf{P}$ is to adjust q_{ij} as:

$$q_{ij} = \frac{(1-R_j)q_{ij}}{\sum_{j=1}^C q_{ij}}. \quad (3)$$

This normalisation ensures that spatial variation in mortality risk matches input maps on mortality risk and that row sums equal one (i.e. $\sum_{j=1}^{C+1} p_{ij} = 1$ for all i).

Short-term connectivity

This framework readily generates two broad classes of short-term predictions of connectivity (Table 1). First, time-specific predictions are possible, which can be helpful for interpreting problems of range expansion and spread of species across complex landscapes (e.g. Hudgins *et al.* 2017). Second, cumulative predictions across given time periods can be made, such as asking whether a location might be colonised over the next 10 years.

Predictions for specific time steps can be accomplished using Chapman–Kolmogorov equations (Ross 2010). For instance,

the probability of being in state j after t steps if starting at state i is the (i, j) -th element of $\mathbf{Q}^t$. In this way, temporally explicit predictions of movement and connectivity can be made for a time series.

Cumulative predictions over time can include the probability of ever visiting location j if an individual starts at location i , $j \neq i$, within t or fewer steps. Such predictions can be obtained by transforming location j into an absorbing state, as follows: (1) remove the j -th row and column of $\mathbf{P}$, which results in modified transition matrices $\mathbf{Q}_j$ and $\mathbf{R}_j$; (2) create a new absorbing state whose incoming probabilities are given by p_{ij} , for each location $i \neq j$, which we store in vector $\tilde{\mathbf{q}}_j$ (i.e. $\tilde{\mathbf{q}}_j$ is the j -th column of $\mathbf{Q}$ without p_{jj}); and (3) add a new row reflecting that location j is now an absorbing state. After these modifications, the new $(C+1) \times (C+1)$ transition matrix is given by:

$$\begin{pmatrix} \mathbf{Q}_j & \mathbf{R}_j & \tilde{\mathbf{q}}_j \\ \mathbf{0} & \mathbf{1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{1} \end{pmatrix}. \quad (4)$$

These modifications allow for counting the transitions that include visiting location j within the interval $[1, t]$. As a result, the probability of ever visiting location j , if starting at location $i \neq j$, within t or fewer steps is the element corresponding to location i in the $(C-1) \times 1$ vector:

$$\tilde{\mathbf{D}}_{jt} = \left(\sum_{n=0}^{t-1} \mathbf{Q}_j^n \right) \tilde{\mathbf{q}}_j = (\mathbf{I} - \mathbf{Q}_j)^{-1} (\mathbf{I} - \mathbf{Q}_j^t) \tilde{\mathbf{q}}_j, \quad (5)$$

where $\mathbf{I}$ is the identity matrix.

Similarly, the spatiotemporal information provided by $\mathbf{P}^t$ allows for calculating mortality risk over time. The probability

of experiencing mortality at location j within t or fewer steps if starting in location i is the (i, j) -th element of the matrix:

$$\tilde{\mathbf{B}}_t = \left(\sum_{n=0}^{t-1} \mathbf{Q}^n \right) \tilde{\mathbf{R}} = (\mathbf{I} - \mathbf{Q})^{-1} (\mathbf{I} - \mathbf{Q}^t) \tilde{\mathbf{R}}, \quad (6)$$

where $\tilde{\mathbf{R}}$ is a $C \times C$ matrix with diagonal elements equal to the mortality probabilities ($\tilde{R}_{jj} = R_j$ for all j) and off-diagonal elements equal to 0.

Local population distributions and abundance can be important parameters for predicting and mapping functional connectivity, because each provides information on the potential pool of emigrants. Species distributions can be formally incorporated when information on presence or abundance of organisms across the landscape is available at the initiation of the study (i.e. $t = 0$). If Ψ is a $C \times 1$ vector whose i -th element, ψ_i , describes the probability that an individual is located at cell i at time $t = 0$, then the i -th element of vector:

$$\mathbf{M}_t = \Psi^T \mathbf{Q}^t, \quad (7)$$

describes the unconditional probability of finding an individual in location i after t steps. In this case T is the transpose operator and $\mathbf{M}_t$ is a $1 \times C$ vector. If Ψ describes the population occupancy (i.e. a probability density function) at time $t = 0$, then M_{it} describes the expected probability of an individual at location i after t steps. Spatial patterns of population abundance, N , can also be included as $(N\Psi)^T \mathbf{Q}^t$, which describes the expected number of individuals in location i after t steps. Similarly, $\tilde{\Psi}_j^T \tilde{\mathbf{D}}_t$ describes the unconditional probability of ever visiting location j within t or fewer steps, where $\tilde{\Psi}_j$ is vector Ψ without the j -th component. The j -th element of vector $\Psi^T \tilde{\mathbf{B}}_t$ is the

unconditional probability of experiencing mortality at location j within t or fewer steps.

Long-term connectivity and demographic rates

A primary benefit of this framework is that time-specific predictions can be scaled to provide asymptotic predictions for long-term connectivity ($t \rightarrow \infty$; Table 1). Summing $\mathbf{Q}^t$ over all t gives the “fundamental matrix”, $\mathbf{F}$, which can be written as:

$$\mathbf{F} = (\mathbf{I} - \mathbf{Q})^{-1}. \quad (8)$$

Matrix $\mathbf{F}$ has several important properties and provides a means for numerous extensions (Kemeny & Snell 1976). First, element f_{ij} of $\mathbf{F}$ is the expected number of times an individual that starts in i uses j before it dies; the sum of row i is the expected number of time steps that an individual initially at i spends in the landscape before death. Therefore, $\mathbf{F}$ provides a time-focused description of long-term visitation rates and survival across complex landscapes.

We extend time-specific predictions of $\tilde{\mathbf{D}}$ to long-term predictions of movement and dispersal. The probability that location j is visited starting from location i is the (i, j) -th element of matrix:

$$\mathbf{D} = (\mathbf{F} - \mathbf{I}) \text{diag}(\mathbf{F})^{-1}, \quad (9)$$

where $\text{diag}(\mathbf{F})$ is a matrix with diagonal elements from $\mathbf{F}$ and zeros otherwise (Kemeny & Snell 1976). This calculation excludes the initial visit to the starting location. As a result, the (j, j) -th element of $\mathbf{D}$ represents the probability of revisiting location j when starting at j . The unconditional

Table 1 A summary of metrics derived from spatial absorbing Markov chains and their interpretation

Parameter	Equation	Interpretation/definition
Short-term dynamics		
Movement between locations after t steps	$\mathbf{Q}^t$	Element (i, j) is the probability of being at location j after t steps if starting at location i
Disperser distribution at time t	$\mathbf{M}_t = \Psi^T \mathbf{Q}^t$	Element i is the unconditional probability of finding an individual (or expected number of individuals) in location i after t steps
Cumulative mortality rate at time t	$\tilde{\mathbf{B}}_t = \left(\sum_{n=0}^{t-1} \mathbf{Q}^n \right) \tilde{\mathbf{R}}$	Element (i, j) is the probability of experiencing mortality at location j within t or fewer steps if starting in location i .
Cumulative immigration rate at time t	$\tilde{\mathbf{D}}_{jt} = \left(\sum_{n=0}^{t-1} \tilde{\mathbf{Q}}^n \right) \tilde{\mathbf{q}}_j$	Element k is the probability of ever visiting location j , if starting at location $i \neq j$, within t or fewer steps. Note that $\tilde{\mathbf{Q}}$ is obtained by deleting the j -th row and column of $\mathbf{P}$, thus i is the location associated with the k -th row of $\tilde{\mathbf{Q}}$
Cumulative disperser distribution at time t	$\tilde{\Psi}_j^T \tilde{\mathbf{D}}_{jt}$	The unconditional probability of ever visiting (or the expected number of individuals that visited) location j within t or fewer steps; $\tilde{\Psi}_j$ is vector Ψ without the j -th component
Cumulative mortality distribution at time t	$\Psi^T \tilde{\mathbf{B}}_t$	The unconditional probability of experiencing mortality at location j within t or fewer steps
Long-term dynamics		
Visitation rate	$\mathbf{F} = (\mathbf{I} - \mathbf{Q})^{-1}$	Element (i, j) is the expected number of times an individual that starts in i uses j before it dies; the sum of row i is the expected number of time steps that an individual initially at i spends in the landscape before death
Spatially explicit dispersal	$\mathbf{D} = (\mathbf{F} - \mathbf{I}) \text{diag}(\mathbf{F})^{-1}$	Element (i, j) is the probability that location j is visited when starting from location i .
Spatially explicit mortality	$\mathbf{B} = \mathbf{F} \tilde{\mathbf{R}}$	Element (i, j) is the probability of suffering mortality in location j if starting in location i .
Life expectancy of dispersers	$\mathbf{z} = (\mathbf{I} - \mathbf{Q})^{-1} \mathbf{1} = \mathbf{F} \cdot \mathbf{1}$	Element i is the expected amount of time that individuals survive when starting at location i .
Dispersal distribution	$\Psi^T \mathbf{D}$	Element j is the unconditional probability distribution of ever visiting state j , taking into account the probability of each initial state
Mortality distribution	$\Psi^T \mathbf{B}$	Element j is the unconditional probability of suffering mortality in location j , taking into account the probability of each initial state
Overall life expectancy	$\Psi^T \mathbf{z}$	Expected time that any individual stays in the landscape before death, taking into account the probability of each initial state

probability distribution of ever visiting state j , taking into account the probability of each initial state, is given by the j -th element of $\Psi^T \mathbf{D}$. $\mathbf{D}$ provides a long-term approximation of the probability of movement between locations, and $\mathbf{D}_{ij}$ can be interpreted as dispersal probability from i to j if we set j to have a high probability of fidelity or consider it a different type of absorbing state (i.e. individuals ‘absorb’ because they settle to reproduce). Consistent with the short-term analysis, $\lim_{t \rightarrow \infty} \tilde{\mathbf{D}}_{ji}$ corresponds to the non-diagonal elements in the j -th column of $\mathbf{D}$.

The fundamental matrix also provides other demographic metrics, both at location j and across the entire landscape. For instance, the probability of suffering mortality in location j if starting in location i is the (i, j) -th element of $\mathbf{B}$, where:

$$\mathbf{B} = \mathbf{F}\tilde{\mathbf{R}}. \quad (10)$$

Such quantification may be useful when interpreting impacts of potential barriers, such as roads, to connectivity across landscapes (Galpern *et al.* 2012; McRae *et al.* 2012). The i -th element of $\Psi^T \mathbf{B}$ represents the unconditional probability of suffering mortality in location i . Consistent with the short-term analysis, $\lim_{t \rightarrow \infty} \tilde{\mathbf{B}}_i = \mathbf{B}$.

The life expectancy of individuals starting at different locations can be derived from the fundamental matrix as a demographic metric to describe the blended effects of movement and survival across landscapes (Acevedo *et al.* 2015b; Sefair *et al.* 2017). The life expectancy if starting from location i is defined as the i -th element of vector:

$$\mathbf{z} = (\mathbf{I} - \mathbf{Q})^{-1} \mathbf{1} = \mathbf{F} \cdot \mathbf{1} \quad (11)$$

where $\mathbf{1}$ is a $C \times 1$ vector of ones. Species initial distribution or abundance can also be incorporated (Table 1).

Application: contrasting corridors that differ in movement resistance and mortality risk

We illustrate some of the properties of this framework using a simple example of individuals dispersing from a start location through two possible corridors that connect to a destination location. In this scenario, one corridor has higher ‘resistance’ than the other, wherein ‘resistance’ may reflect resistance to movement alone, mortality risk, or both (Fig. 3a). When focusing on resistance to movement alone, we set mortality risk as a constant low rate (mortality risk = 0.0002 for all cells); when focusing on mortality risk, we set resistance to movement as a constant rate (resistance = 1 for all cells). For both resistance to movement and resistance based on mortality risk, we then increase resistance and mortality risk 10-fold. Mortality risk was set at a low value to assure dispersers could potentially survive moving across the entire landscape. Comparing resistance to movement, mortality risk, or both permits understanding how predictions for connectivity can change when ‘resistance’ arises from these distinct mechanisms.

With these resistance and mortality maps (Fig. 3a), we calculate $\mathbf{D}$ and $\mathbf{B}$ (eq. 9, 10) to map movement and mortality, respectively. We also illustrate how predictions change for $\mathbf{D}$ when we vary the density of dispersing individuals leaving the two locations (ranging from 0 to 10 dispersers). Finally, we

map time-specific mortality probabilities $\tilde{\mathbf{B}}_t$ to illustrate how this framework can be used to interpret short-term dynamics. When applying the SAMC to time-specific predictions, we note that the framework assumes only local movement in a single time step, such that relevant time periods for modelling may be dependent, in part, on the grain and extent of the landscape. Given the random walk nature of the model, time periods considered should be much greater than the number of cells in the longest dimension of a map. We plot a cumulative mortality risk map for dispersers over time, $\tilde{\mathbf{B}}_t$, where t is scaled to $1-500 \times$ the number of cells in the longest dimension of the corridor being considered.

Application: model evaluation under experimental habitat destruction

We illustrate the SAMC with a model system for which experiments can isolate the role of the matrix on movement and mortality and where we can evaluate predictions of connectivity with observed movements across landscapes. We conducted experiments at the Ordway-Swisher Biological Station in north-central FL, USA. The cactus bug, *Chelinidea vittiger* (Hemiptera: Coreidae), is a pest insect that depends upon its host, prickly pear cacti (*Opuntia* spp.), across its life-cycle. *Opuntia humifusa* is patchily distributed in the study area; we defined patches based on movement behaviours of *C. vittiger* (Fletcher *et al.* 2018). Adults are winged but rarely fly; rather, adult cactus bugs typically walk between cactus patches through a hostile matrix. The relatively local movements of adults can be measured using mark-recapture techniques (Fletcher *et al.* 2011).

We evaluated the utility of the SAMC to predict observed movements of cactus bugs across $15 \times 50 \times 50$ m landscapes. These landscapes were part of a larger experiment on the roles of habitat loss and fragmentation on population dynamics (Fletcher *et al.* 2018). We briefly describe relevant aspects of this experiment for parameterising the SAMC (see Supporting Information and Fletcher *et al.* 2018 for more). In May–June 2014, we first removed all in situ *C. vittiger* and released 100 individuals (50 males, 50 females) in each landscape. In February 2015, we randomly applied habitat loss treatments to cactus patches (12–94% patch loss; Fig. S1) to 12 landscapes, leaving three landscapes as controls. We focused on removing entire patches rather than altering sizes of patches given that reducing patch size may reduce quality of the remaining cactus patch. From March 2015 to April 2016, we surveyed all remaining patches in each landscape every 2 weeks, marking all *C. vittiger* adults observed with a unique 3-letter code on their pronotum. We quantified observed movements between patches using mark–resight data. During fall 2015, we measured vegetation height at points on square grids with 2-m spacing ($n = 676$ points/landscape) and created maps of the matrix using ordinary kriging (Fig. 4a).

To parametrise the SAMC, we used information from prior experiments in both Florida and Colorado suggesting the height of the matrix vegetation influences cactus bug movements (Schooley & Wiens 2004; Fletcher *et al.* 2014; Acevedo & Fletcher 2017); greater matrix vegetation height linearly increases resistance to movement (Fig. 4b). Here, we use the inverse of matrix height to parameterise $\mathbf{Q}$ (eq. 1, 3) and assumed no fidelity

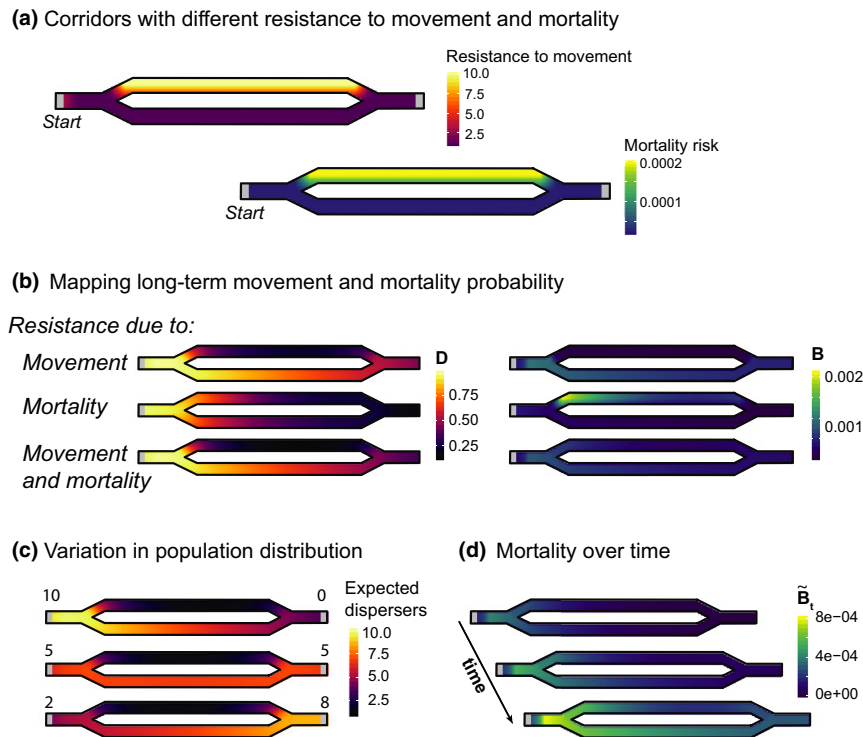


Figure 3 Spatial absorbing Markov chains illustrate the roles of resistance to movement and mortality on predicted movement and connectivity across two potential corridors. (a) We consider a simplified scenario of movement from a start location (grey, left) along two potential corridors that connect to a destination location (grey, right), where either resistance to movement or mortality risk (or both) can impact connectivity. In this situation, we varied resistance and mortality risk 10 fold across the landscape. (b) Differences in the impacts of mortality risk and resistance to movement are predicted based on spatial absorbing Markov chains, both in terms of expected visitation probabilities, **D**, and where mortality is expected to occur, **B**. (c) Incorporating population distribution alters predictions of **D**. Shown are the number of individuals expected to enter each cell for three scenarios in which 10 dispersers start either on one end of the corridor or on both ends, as indicated by the numbers at the ends. (d) The spatial absorbing Markov chain can also be applied to interpret short-term (or time-specific) aspects of connectivity. Shown are predictions for mortality probabilities over time, **B_t**. For (c, d), both resistance to movement and mortality risk shown in (a) are included.

in the matrix so as to focus on movement (i.e. $\text{diag}(\mathbf{Q}) = 0$). To parametrise mortality risk, **R**, we used a tethering experiment to quantify daily rates of mortality by placing tethered individuals across a stratified gradient of matrix vegetation height ($n = 46$); we used a complementary log–log survival model to test for the influence of matrix height on daily mortality probabilities (Fig. 4b). When linking mortality risk to movement behaviour, **R** may need to be rescaled to account for variation in the time scale for data on resistance to movement and mortality risk because these two processes are assumed to operate on the same time scale in the SAMC. To address this issue, we profiled across variation in absolute mortality risk estimated from the tethering experiment by altering the intercept of the complementary log–log model, selecting the value that best fit the movement data based on model likelihoods (Fig. S2).

We used generalised linear mixed models, with a logit link function and assuming a binomial error distribution, where the response variable was the presence/absence of observed movement between patch i and j , the explanatory variable was D_{ij} (eqn 9), and landscape was a random effect to account for non-independence within landscapes. We contrasted **D** to the Euclidean distance between patches, least-cost distance based on least-cost analysis, and commute distance based on circuit theory (Marrotte & Bowman 2017). For the latter two effective distances, we calculated two alternative metrics; one used

matrix height as a measure of resistance to movement only (Fletcher *et al.* 2014), whereas the second combined information on both resistance to movement and results from the mortality experiment (eqn S1). Finally, we calculated life expectancy of potential dispersers from cactus patches, $\Psi^T \mathbf{z}$. We relate this metric to variation in estimated population sizes, taken from Fletcher *et al.* (2018), to interpret the role of disperser survival in driving population size across landscapes. See Supporting Information for more details.

RESULTS

Corridors that differ in movement resistance and mortality risk

The corridor example illustrates that asymptotic predictions for movement, **D** (and $\Psi^T \mathbf{D}$), across the landscape vary considerably (Fig. 3b). Not only does this framework predict that movement is expected to decline with distance due to the demographic costs of mortality, it illustrates how the role of the landscape on movement resistance versus mortality risk fundamentally differ: if resistance is driven by movement alone, individuals are expected to avoid areas of high resistance, but dispersal success remains high. Across these three scenarios (Fig. 3b), the probability of an individual reaching the destination location is 0.46 when resistance is based on

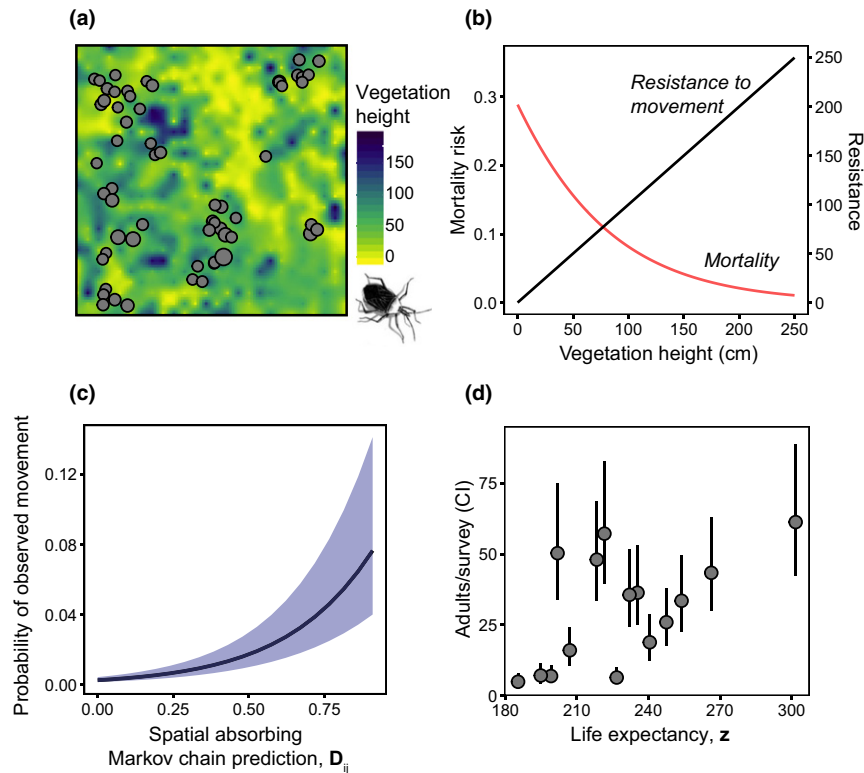


Figure 4 Spatial absorbing Markov chains predict movement across patchy landscapes in the cactus bug. (a) An example landscape, where patches are denoted as grey dots and the matrix is shown as a kriged map of vegetation height (cm) taken from in situ measurements. (b) Functional relationships for resistance of movement and mortality risk to variation in the matrix (vegetation height), taken from experiments. (c) Predictions for movements and (d) estimated population size across 15 landscapes, as a function of absorbing Markov chain parameters (movement, $\Psi^T \mathbf{D}$, and life expectancy, $\Psi^T \mathbf{z}$).

movement alone, 0.15 when based on mortality alone, and 0.37 when based on both. This framework also identifies key locations where mortality risk is expected to be high (**B**; Fig. 3b). Finally, the framework can account for variation in initial disperser distribution (Fig. 3c). Time-specific predictions for mortality $\hat{\mathbf{B}}_t$ illustrate that over the short-term, most mortality risk is near the starting patch, but over time there is a spreading of risk across the landscape, especially in the low-movement-cost corridor, even though mortality risk there is lower (Fig. 3d).

Model evaluation under experimental habitat destruction

Overall, we observed 653 movements of *C. vittiger* across 15 landscapes. Based on the tethering experiment, mortality risk decreased with increasing vegetation height in the matrix (z -value = -2.09 , $\beta = -0.01 \pm 0.006$ SE; $P = 0.036$; Fig. 4b), where resistance to movement is higher. When using model selection to compare the ability of the SAMC, circuit theory, least cost distances, and simple Euclidean distances to predict observed movement across landscapes, support for the **D** metric from the SAMC model was overwhelming (AICc model weight = 1.0; next best model, $\Delta\text{AICc} = 51.4$; Table S1). The relationship between D_{ij} and observed movements was positive (z -value = 12.93 , $\beta = 0.30 \pm 0.02$ SE; $P < 0.0001$; Fig. 4c). There was also a strong correlation between estimated life expectancy of dispersers, z , and estimated population sizes across landscapes ($r = 0.37$, $P < 0.0001$; Fig. 4d). We used the

SAMC to map $\Psi^T \mathbf{D}$ and $\Psi^T \mathbf{B}$ across landscapes (Fig. 5); these maps identify key areas of connectivity and mortality risk for dispersers across landscapes and highlight that predicted areas for high movement and mortality risk need not be the same.

DISCUSSION

Decomposition of movement and mortality for understanding connectivity

A major advance in our understanding of connectivity has been made through focusing on landscape resistance for movement of organisms (Zeller *et al.* 2012). Nonetheless, resistance can emerge for two fundamentally different reasons: (1) organisms may be less likely to move through a location (e.g. Elliot *et al.* 2014); or (2) organisms may suffer mortality at a location (e.g. Nowakowski *et al.* 2015).

Our example highlights the value of isolating these effects. The SAMC explained observed dispersal of *C. vittiger* across landscapes undergoing habitat loss and fragmentation better than other commonly used frameworks. The primary difference between the SAMC and these other frameworks in this application, particularly circuit theory (McRae *et al.* 2008), is in how mortality risk is incorporated when predicting disperser success. Applications of circuit theory and least-cost approaches typically either do not incorporate mortality risk or consider it as just another aspect of resistance, implicitly assuming that such risk alters movement routes rather than

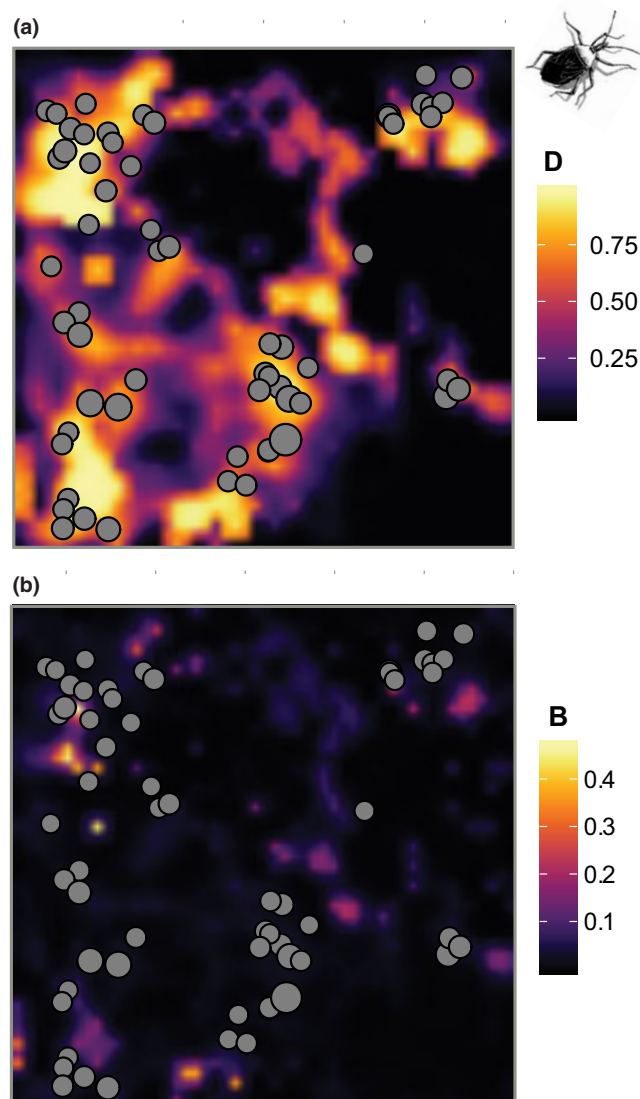


Figure 5 Mapping connectivity via the spatial absorbing Markov chain. (a) Predicted movements across the landscape from individuals starting in patches (denoted in grey). (b) Predicted mortality risk, given the initial distribution of dispersers and landscape variation in risk.

dispersal failure. By directly incorporating mortality, the SAMC provides information on life expectancy of dispersers, which was correlated with variation in population sizes across treatments (Fig. 4d). This result emphasizes the importance of connectivity for population dynamics in landscapes undergoing habitat loss and fragmentation (Fletcher *et al.* 2018).

Our framework embraces the complementary role that movement behaviour and mortality have in their contribution to connectivity. The role of movement behaviour relative to mortality risk can be adaptive, wherein organisms avoid areas of high mortality risk, or maladaptive, wherein organisms prefer moving through areas of high mortality risk, what has been termed ‘dispersal traps’ (Vasudev *et al.* 2015), a type of evolutionary trap (Schlaepfer *et al.* 2002). Our results suggest a potential dispersal trap because of the conflicting effect of the matrix on mortality and movement behaviour, where

relatively open matrix environments are preferred for movement yet individuals suffer a higher risk of mortality there. Our framework permits asking how the relationship between movement behaviour and mortality risk can impact disperser survival and landscape connectivity.

The niche for spatial absorbing Markov chains in connectivity science

We have provided a general and expandable framework for connectivity modelling. Among alternative approaches, the SAMC is most closely related to the use of circuit theory. As with SAMC, circuit theory can be derived from a discrete-time Markov chain process. Doyle & Snell (1984), Chandra *et al.* (1997), and Klein & Randic (1993) show that current, voltage, and resistance in electrical circuits have specific interpretations as Markov random walks. Mortality can be potentially be incorporated to some degree via a ground (McRae *et al.* 2008) and different amounts of current could be modelled to indirectly reflect variation in population abundance, though in practice these issues are rarely applied in connectivity modelling. Yet circuit theory assumes that resistance to current flow is symmetric between locations and focuses on long-term indices (McRae *et al.* 2008), whereas the SAMC provides both transient and long-term analysis, explicitly incorporates population distribution, and allows the probabilistic mapping of movement and mortality processes (e.g. Fig. 5). Circuit theory may be considered a special case of SAMC, illustrating that SAMC can be viewed as a building towards a unified framework for connectivity modelling.

Some of the generalisation that SAMC provides can also be captured with individual-based modelling. For example, individual-based modelling approaches often model movement behaviours in temporally explicit ways and can incorporate mortality risk per time step (e.g. Rangeshifter; Bocedi *et al.* 2014), similar to the SAMC. Yet our framework provides analytical solutions grounded in probability theory that does not require individual-based simulations, and consequently may require less knowledge of movement behaviour and could often be more tractable for implementation.

With the generality comes greater complexity and computational issues. In its simplest form, the SAMC requires two maps: a resistance map relevant to movement and a mortality risk map. Least-cost and circuit theory approaches only require a single map of ‘resistance’ for modelling. One challenge is the appropriate estimation of the absorbing Markov chain matrix, $\mathbf{P}$; the SAMC does not solve challenges of estimating resistance, although it may facilitate linking empirical data to connectivity modelling (See Supporting Information for guidance). A second challenge is the fact that the SAMC is currently more computationally demanding than least-cost and circuit theory modelling. Different metrics vary in computational efficiency: we have applied all metrics described here on landscapes with $> 100\,000$ cells and some metrics (e.g. $\Psi^T \mathbf{B}$) to landscapes with $> 2\text{M}$ cells (See Supporting Information). We are actively developing an R package *samc* to improve computational efficiency and application of the SAMC (Marx *et al.* *unpublished*). With ongoing programming developments, we expect that SAMC will be capable for

applications at scales comparable to that of circuit theory (Leonard *et al.* 2017).

Extensions and applications

The SAMC could be extended and applied in several fruitful ways. First, this framework is currently based on biased random walks, as in circuit theory, but this assumption could be relaxed. For instance, correlated random walks could be incorporated by adjusting the SAMC to be based on edge–edge connections rather than node–node connections (Prasad & Borges 2006). While feasible, such a formulation would increase computation time due to an increase in the size of **P**. Alternatively, directed movement could be incorporated by including a cost map on directional flow when parameterising **Q**.

Second, the SAMC provides a means to map mortality risk and human–wildlife conflict for dispersers across landscapes. The SAMC framework could be extended to incorporate different mortality sources by including multiple absorbing states, such as mortality from hunting (Hill *et al.* 2019). It may be useful in planning for underpasses and over-passes that aim to increase the survival of dispersers (Ascensao *et al.* 2013). By accounting for mortality risk, issues of energetic reserves on movement success can also be readily incorporated (Zollner & Lima 2005).

Third, because the SAMC explicitly accounts for variation in population abundance and distribution, this modelling framework could be applied to account for individual variation within and among populations. For instance, the SAMC could be applied to males and females that may vary in movement behaviour and survival rate (Elliot *et al.* 2014) or to account for natal experience on connectivity (Fletcher *et al.* 2015). In a related way, state-dependent extensions of the SAMC may allow for accounting for variation in the internal states of dispersers.

Fourth, the SAMC treats dispersers as independently moving entities. Yet movement and dispersal can be altered by conspecifics (Delgado *et al.* 2014), and dispersers can experience density dependence as they move (Matthysen 2005). Extensions of SAMCs that account for such dynamics would be valuable.

Finally, we expect that this framework could also be applied to interpret genetic connectivity, a topic of widespread interest in landscape genetics (Manel *et al.* 2003). Resistance maps are often used in understanding genetic connectivity (Spear *et al.* 2010), which is driven by a combination of movement and successful reproduction (Pfluger & Balkenhol 2014; Robertson *et al.* 2018). In this way, absorption could be interpreted as the potential for movement to fail to result in successful reproduction.

Conclusions

Connectivity reflects both behavioural and demographic processes, which can have drastically different effects on populations. Although it has long been emphasised that dispersal has major costs (Hamilton & May 1977), the demographic costs of dispersal in connectivity modelling has been less appreciated. Our framework provides a means to address this problem that is well grounded in probability theory. We expect

our framework will provide new insight into connectivity in demographically variable, spatially complex landscapes.

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AUTHORSHIP

RJF and MAA conceived the study; RJF, JAS, CW and AJM derived connectivity models and related code; RJF, TS and CP collected data on case study and applied models; RJF and JAS wrote first draft of the manuscript, and all authors provided substantial effort in ideas and revision of the manuscript.

DATA AVAILABILITY STATEMENT

The data supporting the results are archived in an appropriate public repository (Figshare; <https://doi.org/10.6084/m9.figshare.8248826>).

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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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