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

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Predicting and mapping connectivity is essential for understanding the scope for species persistence in the face of environmental change. Yet connectivity modeling is challenging because it requires understanding how organisms successfully move across complex landscapes. Although it is well known that movement is risky, connectivity modeling often conflates behavioral responses to the matrix through which animals disperse with mortality risk. Here we derive new connectivity models using random walk theory, based on the concept of spatial absorbing Markov chains (SAMC). These models decompose the role of matrix on movement behavior 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 in inter-patch movement from a specialist insect herbivore in 15 experimental landscapes. Our framework explains insect movements across the fragmented landscapes better than other frameworks commonly used to map connectivity, including circuit theory and the use of least-cost paths. Our results demonstrate that disentangling the roles of movement behavior and mortality risk is fundamental to accurately interpreting landscape connectivity, and that spatial absorbing Markov chains provide a generalizable and powerful framework with which to do so.

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

The ability to accurately describe 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 and Bruna 1999), which often emphasize connecting habitat remnants via corridors and otherwise facilitating the movement of species through landscapes increasingly altered by human activities (Heller and Zavaleta 2009, Lawler et al. 2013).

Dispersal is inherently risky. Organisms that attempt to disperse through the matrix habitats 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 (Spear et al. 2010, 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 landscape genetics and conservation biology as a means to identify corridors, evaluate restoration potential, and understand limits to gene flow (Cushman et al. 2006, McRae et al. 2012, 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 (Adriaensen et al. 2003, McRae et al. 2008, 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 methods have proven very useful (Dickson et al. 2019), they do not explicitly consider mortality risk when assessing ‘resistance’. As a result, the interpretation of matrix resistance conflates effects of variation in movement behavior with that of mortality (Zeller et al. 2012). Because the demographic effects of mortality when moving through the matrix could ultimately be much greater than those resulting from changes in movement routes, failing to distinguish between these two could lead to implementing incorrect or even counterproductive conservation action (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 modeling connectivity that honors the problem of both movement behavior 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 matrix on movement behavior and mortality. This framework builds upon random walk theory with absorbing Markov chains, which are frequently used in probability theory to acknowledge the potential for ‘absorption’ (here, mortality; Ross 2010). Our spatial absorbing Markov chain (SAMC) framework allows for probabilistic accounting of both movement behavior 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) predict connectivity over different time frames and provide both short- and long-term predictions; 2) incorporate population distribution and density into predictions of connectivity; and 3) quantify demographic parameters related to successful connectivity. We begin by introducing the SAMC framework for connectivity 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?

METHODS

The spatial absorbing Markov chain for complex landscapes

We start by considering successful movement across landscapes as a stochastic, probabilistic process that is driven by both movement behavior and mortality risk, each of which can be influenced by spatial heterogeneity in the landscape. The landscape can impact movement behavior and mortality risk in similar or different ways. For instance, areas of high mortality risk could be avoided during dispersal, but they could also be preferred if they provide a more direct route (Vasudev et al. 2015). In connectivity mapping, landscapes are generally considered as discrete representations of the environment via the use of raster maps; our framework assumes this discretization. We also treat time as a discrete variable, which matches the typical discretization of movement data.

Formally, we consider a stochastic process \( X_t \), which at each time is in one of 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 being in state \( i \) at time step \( t + 1 \) depends only on the state at time step \( t \). For a landscape divided into \( C \) cells (Fig. 2), we define a sparse, \( C \times C \) transition matrix, denoted \( Q \) (Note that 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”). The \((i,j)\)-th element of \( Q \), \( q_{ij} \), is the probability of an individual transitioning from cell \( i \) to \( j \) in
one time step, which is often formalized based on ‘cost’ or ‘friction’ maps that reflect matrix resistance to movement. Matrix $Q$ 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-neighbor 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 modeling (e.g., McRae et al. 2008). Absorbing Markov chains add one or more "absorbing" states to $Q$, 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, $P$, that contains both transition probabilities between transient states (i.e., landscape cells) and an absorbing state representing death (Fig. 2b). Matrix $P$ can be written as

$$
(P \quad R) \quad (0 \quad 1) \quad (2)
$$

where $R$ 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 $P$, denoted by $p_{ij}$ 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 $R$) 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. Matrix $P$ includes both habitat and matrix locations on the landscape, and so can readily accommodate within- and between-patch movement and
mortality (Reeve et al. 2008). 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 account for variation in movement velocity through landscapes (Hanks et al. 2011).

Parameterizing $\mathbf{P}$ 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 parameterize the diagonal of $\mathbf{Q}$ (Fig. 2); we do not focus on fidelity here and instead set $\text{diag}(\mathbf{Q}) = 0$ to emphasize dispersal behavior. To assure that $\sum_{j=1}^{C+1} p_{ij} = 1$, a normalization constant is needed, which may depend on the type of movement and mortality data used. A natural way to normalize $\mathbf{P}$ is to adjust $q_{ij}$ as

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

This normalization 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, 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 can be made across given time intervals, such as asking whether a location might be colonized 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 $\mathbf{P}^t$. In this way, temporally explicit predictions of movement and connectivity can be made for a time series.

Cumulative predictions over a time period can also be modeled. If an individual starts at location $i$, then the probability of ever visiting location $j, \neq i$, within $t$ or fewer steps can be obtained by transforming location $j$ into an absorbing state. To do so, we modify $\mathbf{P}$ as follows:

1. remove the $j$-th row and column, 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 $i \neq j$, all of which we store in vector $\mathbf{q}_j$ (i.e., $\mathbf{q}_j$ 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

$$
\begin{pmatrix}
\mathbf{Q}_j & \mathbf{R}_j & \mathbf{q}_j \\
\mathbf{0} & 1 & 0 \\
\mathbf{0} & 0 & 1
\end{pmatrix}.
$$

These modifications allow us to count the transitions that visit 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

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

where $\mathbf{I}$ is an $C \times C$ 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

$$
\mathbf{B}_t = \left( \sum_{n=0}^{t-1} \mathbf{Q}^n \right) \mathbf{R} = (1 - \mathbf{Q})^{-1} (1 - \mathbf{Q}^t) \mathbf{R},
$$
where $\mathbf{\tilde{R}}$ 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, interrelated but distinct metrics, 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 $\Psi$ is a $C \times 1$ vector whose $i$-th element, $\psi_i$, describes the probability that an individual is located at cell $i$ at time $t = 0$, then the $i$-th element of vector

$$
\mathbf{M}_t = \Psi^T \mathbf{Q}^t,
$$

(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 $\Psi$ 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, $\Psi^T \mathbf{\tilde{B}}_{jt}$ describes the unconditional probability of ever visiting location $j$ within $t$ or fewer steps. The $j$-th element of vector $\Psi^T \mathbf{\tilde{B}}_t$ is the total unconditional probability of experiencing mortality at location $j$ within $t$ or fewer steps, taking into account all possible initial locations.

**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 ($t \to \infty$; Table 1). Summing $\mathbf{Q}^t$ over all $t$ gives the “fundamental matrix”, $\mathbf{F}$, which can be written as

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

(8)
Matrix $\mathbf{F}$ has several important properties and provides a means for several extensions (Kemeny and 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 description of resource use by individuals moving across complex landscapes.

We extend time-specific predictions of $\mathbf{D}$ to long-term predictions of movement and dispersal. A key finding from probability theory (Kemeny and Snell 1976) is that the probability that location $j$ is visited starting from location $i$ is the $(i,j)$-th element of matrix

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

(9)

where $\mathop{\text{diag}}(\mathbf{F})$ is a matrix with diagonal elements from $\mathbf{F}$ and zeros otherwise. 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 probability distribution of ever visiting state $j$, taking into account the probability of each initial state, is given by the $j$-th element of $\mathbf{W}^T \mathbf{D}$. $\mathbf{D}$ provides a long-term approximation of the probability of movement between locations, and $D_{ij}$ 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, $\lim_{t \to \infty} \mathbf{D}_{j*}$ corresponds to the non-diagonal elements in the $j$-th column of $\mathbf{D}$.

The fundamental matrix also provides several ways in which demographic metrics can be calculated, both at location $j$ and across the entire landscape. For instance, the probability of suffering mortality in location $j$ if starting in location $i$, can be quantified as the $(i,j)$-th element of $\mathbf{B}$, where

$$\mathbf{B} = \mathbf{F} \mathbf{R}.$$ 

(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 $\Psi T B$ represents the unconditional probability of suffering mortality in location $i$. Consistent with the short-term analysis, $\lim_{t \to \infty} \tilde{B}_t = B$.

The expected 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 spatially varying movement and survival across landscapes (Acevedo et al. 2015b, Sefair et al. 2017). In this way, life expectancy if starting from location $i$ is defined as the $i$-th element of vector

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

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. Morality 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 $D$ and $B$ (eq. 9, 10) to map movement and mortality, respectively. We also illustrate how predictions change for $D$ when we vary the density of dispersing individuals leaving the two locations (ranging from 0-10 dispersers). Finally, we map time-specific mortality probabilities $\tilde{B}_t$ 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 modeling may be dependent, in part, on the grain and extent of the landscape of interest. Given the random walk nature of the model, time periods considered should be $\gg$ number of cells in the longest dimension of a map. We below plot a cumulative mortality risk map for dispersers over time, $\tilde{B}_t$, 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 central Florida, U.S.A. The cactus bug, *Chelinidea vittiger* (Hemiptera: Coreidae), is a pest insect that depends upon its hosts, prickly pear cacti (*Opuntia* spp.), across its life-cycle. 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 50 × 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 parameterizing the SAMC (see Supporting Information and Fletcher et al. 2018 for more details). 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 (12-94% patch loss; Fig. S1) to 12 landscapes, leaving three landscapes as controls. From March 2015-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 protonum. 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) (Schooley and Wiens 2005) and created maps of the matrix using ordinary kriging (Fig. 4a).

To parametrize 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 and Wiens 2004, Fletcher et al. 2014, Acevedo and Fletcher 2017); greater matrix vegetation height linearly increases resistance to movement (Fig. 4b). Here we use the inverse of matrix height to parameterize Q (eq.1, 3) and assumed no fidelity in the matrix so as to focus on movement (i.e., diag(Q) = 0). To parametrize 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 behavior, R may need to be re-scaled to account for variation in the time scale.
for data on resistance to movement and mortality risk because in the SAMC, these two processes are assumed to operate on the same time scale. 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 generalized 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 \(D_{ij}\) (eq. 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 and 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 (See Supporting Information). Finally, we calculated life expectancy of potential dispersers from cactus patches, \(\Psi^Tz\). 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 \(\Psi^T D\)), 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 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 $\tilde{B}_t$ 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. We used model selection to compare the ability of the SAMC, circuit theory, least cost distances, and simple Euclidean distances to predict observed movement across experimental landscapes, and support for the $D$ metric from the SAMC model was overwhelming (Table 2). 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 $\Psi^T D$ and $\Psi^T B$ 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, particularly circuit theory (McRae et al. 2008), is in how mortality risk is incorporated when predicting disperser success. 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 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 behavior and mortality have in their contribution to connectivity. The role of movement behavior 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, Robertson et al. 2013). Our results suggest a potential dispersal trap because of the conflicting effect of the matrix on mortality and movement behavior, where relatively open matrix environments are preferred for movement yet individuals suffer a higher risk of mortality there. Our framework permits one to ask how the relationship between movement behavior 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 modeling. Relative to least-cost and circuit theory approaches (McRae et al. 2008, Etherington 2016), the SAMC provides a probabilistic framework that distinguishes the role of landscapes altering mortality from altered movement behavior. By including mortality, it expands the range of problems that can be addressed in movement ecology. The probabilistic framework permits a wide range of short- and long-term metrics to be calculated (see Table 1).

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 and Snell (1984), Chandra et al. (1997), and Klein and Randic (1993) show that current, voltage, and resistance in electrical circuits have specific interpretations as Markov random walks. Mortality can be potentially be incorporated via inclusion of a ground (McRae et al. 2008) though in practice this issue has not oft been applied in connectivity modeling. 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, incorporates population distribution, and allows the mapping of movement and mortality processes (as in Fig. 5). Circuit theory may be considered a special case of SAMC, illustrating our suggestion that SAMC can be viewed as a unified framework for connectivity modeling.

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 modeling. One challenge is the appropriate estimation of the absorbing Markov chain matrix, \( P \). A second challenge is the fact that SAMC can be computationally more demanding than least-cost path and circuit theory modeling, because some of the metrics derived from SAMC require inverting large matrices (each dimension of which is at least the number of cells). With programming developments, we expect that SAMC will be able to be applied 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 and 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 parameterizing \( Q \).  

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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 (Peters et al. 2015, Hill et al. 2019). It should be useful in planning for underpasses and overpasses 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 and Lima 2005).

Third, because the SAMC explicitly accounts for variation in population abundance and distribution, this modeling 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 behavior and survival rate (Elliot et al. 2014) or to account for natal experience on connectivity (Fletcher Jr 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). Multi-individual extensions of SAMCs 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 and 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 behavioral and demographic processes, processes which can have drastically different effects on populations. Although it has long been emphasized that dispersal has major costs (Hamilton and May 1977), the demographic costs of dispersal in connectivity modeling has been less appreciated. Our framework provides a means to address this problem well grounded in probability theory. We expect our framework will provide new insight into connectivity in demographically variable, spatially complex landscapes.

ACKNOWLEDGMENTS

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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.
REFERENCES


Fletcher Jr, R. J., E. P. Robertson, R. C. Wilcox, B. E. Reichert, J. D. Austin, and W. K. Kitchens. 2015. Affinity for natal environments by dispersers impacts reproduction and


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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Equation</th>
<th>Interpretation/definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Short-term dynamics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Movement between locations</td>
<td>$P^t$</td>
<td>Element $(i, j)$ is the probability of being at location $j$ after $t$ steps if starting at</td>
</tr>
<tr>
<td></td>
<td></td>
<td>location $i$.</td>
</tr>
<tr>
<td>Disperser distribution at time $t$</td>
<td>$M_t = \Psi^T Q^t$</td>
<td>Element $i$ is the unconditional probability of finding an individual (or expected number</td>
</tr>
<tr>
<td></td>
<td></td>
<td>of individuals) in location $i$ after $t$ steps.</td>
</tr>
<tr>
<td>Cumulative mortality rate at time $t$</td>
<td>$\bar{B}<em>t = \left( \sum</em>{n=0}^{t-1} Q^n \right) \bar{R}$</td>
<td>Element $(i, j)$ is the probability of experiencing mortality at location $j$ within $t$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>or fewer steps if starting in location $i$.</td>
</tr>
<tr>
<td>Cumulative immigration rate at time $t$</td>
<td>$\bar{D}<em>{jt} = \left( \sum</em>{n=0}^{t-1} \bar{Q}^n \right) \bar{q}_j$</td>
<td>Element $k$ is the probability of ever visiting location $j$, if starting at location $i \neq j$, within $t$ or fewer steps. Note that $\bar{Q}$ is obtained by deleting the $j$-th row and column of $P$, thus $i$ is the location associated with the $k$-th row of $\bar{Q}$.</td>
</tr>
<tr>
<td>Cumulative disperser distribution at time $t$</td>
<td>$\Psi^T \bar{D}_{jt}$</td>
<td>Element $j$ is the unconditional probability of ever visiting (or the expected number of individuals that visited) location $j$ within $t$ or fewer steps.</td>
</tr>
<tr>
<td>Cumulative mortality distribution at time $t$</td>
<td>$\Psi^T \bar{B}_t$</td>
<td>Element $j$ is the unconditional probability of experiencing mortality at location $j$ within $t$ or fewer steps.</td>
</tr>
</tbody>
</table>
Long-term dynamics

Location use \[ F = (I - Q)^{-1} \] 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 \[ D = (F - I) \text{diag}(F)^{-1} \] Element \((i, j)\) is the probability that location \(j\) is visited when starting from location \(i\).

Spatially explicit mortality \[ B = F \tilde{R} \] Element \((i, j)\) is the probability of suffering mortality in location \(j\) if starting in location \(i\).

Life expectancy of dispersers \[ z = (I - Q)^{-1}1 = F \cdot 1 \] Element \(i\) is the expected amount of time that individuals survive when starting at location \(i\).

Dispersal distribution \[ \Psi^T D \] Element \(j\) is the unconditional probability distribution of ever visiting state \(j\), regardless of the initial state.

Mortality distribution \[ \Psi^T B \] Element \(j\) is the unconditional probability of suffering mortality in location \(j\), regardless of the initial state.

Overall life expectancy \[ \Psi^T z \] Expected time that any individual stays in the landscape before death, regardless of the initial location.
Table 2. The spatial absorbing Markov chain model explains the probability of movement of *C. vittiger* among patches in experimental landscapes undergoing habitat destruction better than least-cost paths, circuit theory or Euclidean distance.

<table>
<thead>
<tr>
<th>Model*</th>
<th>K</th>
<th>Log-likelihood</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial absorbing Markov chain, D</td>
<td>3</td>
<td>-3953.40</td>
<td>7912.80</td>
<td>0.00</td>
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<tr>
<td>Euclidean distance</td>
<td>3</td>
<td>-3979.10</td>
<td>7964.21</td>
<td>51.41</td>
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<tr>
<td>Least-cost distance-mortality*</td>
<td>3</td>
<td>-3985.93</td>
<td>7977.87</td>
<td>65.07</td>
</tr>
<tr>
<td>Least-cost distance</td>
<td>3</td>
<td>-3985.95</td>
<td>7977.90</td>
<td>65.10</td>
</tr>
<tr>
<td>Circuit theory-mortality*</td>
<td>3</td>
<td>-4004.35</td>
<td>8014.70</td>
<td>101.90</td>
</tr>
<tr>
<td>Circuit theory</td>
<td>3</td>
<td>-4004.39</td>
<td>8014.78</td>
<td>101.99</td>
</tr>
<tr>
<td>Intercept only</td>
<td>2</td>
<td>-4012.25</td>
<td>8028.50</td>
<td>115.70</td>
</tr>
</tbody>
</table>

*Model included information on movement resistance and results from the mortality experiment in the form of a mortality cost surface. See Supporting Information.*
Figure Captions

**Figure 1.** How the landscape can impact movement and connectivity. (a) Matrix resistance (darker gray indicates higher resistance) can alter movement behavior and trajectories across landscapes. Matrix resistance to movement is commonly assumed in connectivity mapping, with least-cost paths the most common approach to mapping corridors and connectivity. 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 not considered in connectivity predictions and mapping despite its clear importance for dispersal success across landscapes.

**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 neighbors based on ‘resistance’ of the matrix to movement (shown is an 8-neighbor rule). (b) Absorbing Markov chains can take each of these components to potential movement by be applied to this problem, which explicitly account for both movement (transition, $Q$, shown in orange) and mortality (absorption, $R$, shown in green) by adding absorbing column and row vectors to the transition matrix. Note that in this example, $P$ is a $9 \times 9$ matrix but only a portion is shown.

**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, $\tilde{B}_t$. For (c, d), both resistance to movement and mortality risk shown in (a) are included.

**Figure 4.** 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 an 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, $\Psi^T D$, and life expectancy, $\Psi^T z$).

**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.
Fig. 1

(a) Matrix effects on movement behavior

Impacts on:
Movement path
Search time
Immigration location

(b) Matrix effects on mortality

Impacts on:
Dispersal success
Survival of dispersers
Metapopulation demography
Fig. 2

(a) Fidelity | Cost to movement | Mortality risk

(b) $P = \begin{bmatrix} 0 & 0.2 & 0.5 & 0.2 & 0.1 & 0.5 & \ldots & 0 & 0.1 \\ 0.2 & 0.1 & 0.4 & 0.1 & 0.05 & 0.4 & \ldots & 0 & 0.05 \\ 0 & 0.2 & 0.5 & 0 & 0.1 & 0.3 & \ldots & 0 & 0.01 \\ 0.1 & 0.2 & 0.4 & 0.1 & 0.02 & 0.5 & \ldots & 0 & 0.2 \\ 0.1 & 0.11 & 0.5 & 0.1 & 0.03 & 0.3 & \ldots & 0 & 0.15 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$

$\begin{bmatrix} Q & R \end{bmatrix}$

- transient
- absorption
Fig. 3.

(a) Corridors with different resistance to movement and mortality

(b) Mapping long-term movement and mortality probability

Resistance due to:

- Movement
- Mortality
- Movement and mortality

(c) Variation in population distribution

(d) Mortality over time
Fig. 4.