Supporting Information for

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

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This Supporting Information includes: a) Supplementary Methods on the case study regarding connectivity and habitat loss; b) Supplementary Discussion on parameterizing the SAMC; c) Supplementary R code for running the SAMC; d) Supplemental Tables (Table S1); e) Supplementary Figures (Fig. S1, S2); and f) Supporting References.

**SUPPLEMENTARY METHODS**

We illustrate the SAMC with a model system where experiments can isolate the role of the matrix on movement and mortality and evaluate predictions of connectivity with observed movements across experimental landscapes. We conducted experiments at the Ordway-Swisher Biological Station (29.4°N, 82.0°W) in central Florida, U.S.A. The cactus bug, *Chelinidea vittiger* (Hemiptera: Coreidae), is dependent upon prickly pear cactus (*Opuntia* spp.), where it feeds, breeds, and aggregates on *Opuntia* throughout its life. In this area, *C. vittiger* uses *Opuntia humifusa* primarily occurring in relatively open, grass-dominated, old field and sandhill habitats that contain limited canopy cover. Adults are winged, but rarely fly; instead, adult cactus bugs typically walk between cactus patches through an unsuitable matrix. Movements of adults are thus relatively localized and can be easily measured via mark-recapture techniques and behavioral experiments (Fletcher *et al.* 2011; Fletcher *et al.* 2014; Acevedo & Fletcher 2017).

We evaluated the utility of the SAMC to predict observed movements of cactus bugs across 15 50 × 50 m landscapes (Fig. S1). 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, but see Fletcher et al. (2018) for more details.

In each landscape, we used a high-precision GPS (error ~30 cm) to map all cactus patches. Patches were defined as in Schooley and Wiens (2005), based on movement behaviors of *C. vittiger* near cactus boundaries. Landscapes were > 50 m apart. In May 2014, we first removed all in situ *C. vittiger* from landscapes. In June 2014, we released 100 individuals (50 males, 50 females) in each landscape. In February 2015, we randomly applied habitat loss treatments to 12 of the 15 landscapes, leaving 3 landscapes as controls. There were two types of habitat loss treatments (aggregated and random), but we do not focus on that aspect of the study design here. We used a regression-based treatment design, where habitat loss varied from approximately 12-94% patch removal (*n* = 2 for each amount of loss). In total, we removed 2088 cactus patches. From March 2015-April 2016, we surveyed all remaining patches within each landscape every 2 weeks except over winter, when bugs are dormant (19 total surveys), capturing approximately 3-4 generations. For adults, we marked all individuals with unique, three letter codes on their pronotum. With data collected from 2015-2016, we quantified observed movements between patches based on mark-resight data to estimate movement rates. Finally, we also measured variation in the matrix across landscapes. To assess variation in matrix resistance among landscapes, during fall 2015 we measured vegetation height (i.e., the maximum height) every 2 m (676 measurements/landscape). Using this information, we created resistance maps using ordinary kriging (Fig. 4a).

To parametrize the SAMC, we use information from prior experiments in both Florida and Colorado that suggest that the height of the matrix vegetation can influence movement in cactus bugs (Schooley & Wiens 2004, 2005; Fletcher *et al.* 2014; Acevedo & Fletcher 2017), where greater height of matrix vegetation increases resistance to movement. Vegetation height is also highly correlated with vegetation density in the study area (r = 0.80; Fletcher *et al.* 2014). Here we use the inverse of matrix height to parameterize (Fig. 4a, b). To parametrize mortality risk, , in the SAMC, we used a tethering experiment to quantify the daily rate of mortality under different matrix conditions. We attached individual cactus bugs to a nylon string (10 cm in length) anchored to a nail (*n* = 46). We placed tethered individuals across a stratified gradient of matrix height that captured observed variation in the matrix measured in the habitat fragmentation experiment of Fletcher et al. (2018). We then monitored mortality rates for 7 days, checking individuals at 0.5, 1, 2, 4, and 7 days. After 7 days, all remaining cactus bugs were removed and released. With these data, we used complementary log-log survival models to test for the influence of matrix height on daily mortality probabilities.

With this information, 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 and in the fragmentation experiment, the explanatory variable was , the -th element of and we included landscape as a random effect to account for non-independence within landscapes. When linking mortality risk to movement behavior, **R** may need to be adjusted to account for variation in the time scale for information used regarding 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 initially profiled across variation in absolute mortality risk estimated from the tethering experiment by altering the intercept of the complementary log-log model to populate **R**, selecting the value that best fit the observed movement data in Fletcher et al. (2018) based on model likelihoods (Fig. S2).

We contrasted to measures of simple Euclidean distance between patches, effective distances based on least-cost distance, and commute distance based on circuit theory (Marrotte & Bowman 2017). For the latter two effective distances, we used matrix height as a measure of resistance (Fletcher *et al.* 2014). As a consequence, these latter two effective distance metrics use the same information on resistance to movement as the SAMC but do not distinguish the problem of mortality in the matrix from movement behavior. We also considered a formulation of least-cost and commute distance that incorporated information on both resistance to movement and results from the mortality experiment, thereby using all of the information harnessed in the SAMC. In some applications of these algorithms, ‘resistance’ can reflect both aspects of movement behavior and also risk of mortality (Zeller *et al.* 2012; Watling & Braga 2015). Formally, we combine these to create a conductance (transition; ∝ **Q**) layer as:

We note that while risk layers can be incorporated into least-cost and circuit distance, the implicit assumption of the modeling framework is that these ‘risk’ areas will be avoided, rather than individuals suffering mortality and thus impacting dispersal failure. Consequently, while the incorporation of the mortality risk information in Eq S1 results in the least-cost and commute distance approaches using the same information as the SAMC, the way in which this information is used is fundamentally different.

Finally, we calculated life expectancy of potential dispersers from cactus patches, , where we set for cactus patch location and 0 otherwise. 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. Briefly, we estimated abundance of adult *C. vittiger* during survey time *t* at landscape *j*, , using the canonical estimator for capture-mark-recapture models to account for imperfect detection (Williams *et al.* 2002), , where is the number of marked adults captured at time *t* in landscape *j*, and is the estimated probability of capturing a marked adult at time *t* in landscape *j*. was obtained by model-averaging based on results from a set of Cormack-Jolly-Seber models that varied in allowing detection to change by landscape and by survey. See Fletcher et al. (2018) for more details on population size estimation. We then related population size estimates to the landscape average of . To determine if life expectancy from the SAMC could explain population variation in abundance across landscapes, we used a generalized linear mixed model, with a similar formulation as described above, but with a log link function and Poisson error distribution, adding an observation-level offset to account for overdispersion and weighting by the inverse of the population size SE (see Fletcher et al. 2018). Overall, **z** was a strong predictor of population abundance (β = 0.09 + 0.03 SE; *P* = 0.0003; Fig. 4d), consistent with conclusions in Fletcher et al. (2018) that treatments had a large effect on population connectivity.

**SUPPLEMENTARY DISCUSSION**

In our empirical example, we fit the SAMC framework to a tractable example where information about movement behavior and mortality risk were available. We used this example as a rigorous means to evaluate the utility of the SAMC to predict movement across complex landscapes and contrast it with other frameworks. In other applications, information on movement behavior and mortality risk may be less readily available. In addition, it may sometimes be unclear what the appropriate time step for implementation should be. Below, we provide some guidance, but we expect that the SAMC can be applied in a variety of ways, depending on the problem.

As in other applications that interpret 'resistance' for landscape connectivity, parameterizing the transition matrix that is used to interpret movement behavior can come from behavioral experiments, telemetry, habitat use, or expert opinion (Zeller *et al.* 2012). In particular, analysis of radio-telemetry data, such as the use of step-selection functions (Thurfjell *et al.* 2014; Avgar *et al.* 2016), provides a natural means to directly parameterize . In these ways, parameterizing of the SAMC is similar to that of least-cost and circuit theory approaches.

Information on mortality is less common. At one extreme, the SAMC can be used by assuming mortality risk is constant (and perhaps low) across the landscape. Mortality rates, , could then be treated as hypotheses regarding absolute risk (per time step) across the landscape. Alternatively, mortality rates could be derived based on organismal dispersal kernels (Koenig *et al.* 1996) or related information (Compton *et al.* 2007). For instance, if the mean dispersal distance for a species is known, could be tuned to derive dispersal distance estimates from the SAMC to equal known dispersal distances.

Variation in the risk of mortality could also be implemented in simple ways, such as assuming highways and interstates have a high risk of mortality but the remainder of the landscape has low mortality risk. Data from roadkill, areas of human-wildlife conflict such as the removal of problematic megafauna (Goswami *et al.* 2015), or poaching could be used to derive mortality risk layers using a variety of methods (e.g., point process models). In such situations, these maps may provide relative information on mortality risk but may be less reliable for interpreting absolute risk in the SAMC. Using independent data (as done here), or other auxiliary information (e.g., dispersal kernels) may help tune the model in such situations.

Finally, it may be unclear what the appropriate time step should be for deriving and implementing SAMC metrics. In some cases, movement data used to parameterize may be time-specific (e.g., fixed between GPS locations), or mortality data may be time-specific (e.g., monthly mortality rates taken from mark-recapture data), leading to clearly defined *t*. Yet when indirect data on movement (e.g., expert opinion) are used, interpreting *t* may be less clear. When performing time-specific analysis, the total number of time steps considered should be much greater than the number of cells in the longest dimension of the study area extent. The reason for this consideration is because in the standard formulation of the SAMC, individuals only move to adjacent cells in each time step (note that assumption could be relaxed). Consequently, the *minimum* number of time steps required to travel between locations *i* and *j* of a specific distance apart, *dij*, for a map with resolution *r*, is *dij*/*r*.

**SUPPLEMENTARY CODE**

We have developed an R package, samc, for the spatial absorbing Markov chain model. This package has ongoing active development. We illustrate the use of version 0.1.0 of samc package to recreate results shown in Figure 3 of the main text. We are continuing to expand this package to increase its utility and computational efficiency, which we will explore in detail elsewhere (Marx et al. *unpublished manuscript*).

## Installing the Package

This tutorial was written using version 0.1.0 of the samc package, which is available at https:/github.com/andrewmarx/samc. To ensure that you can run this example code, you can install version 0.1.0 directly using the following code. This requires the devtools package be installed on your system.

devtools::install\_github("andrewmarx/samc", ref = "0.1.0")

Note that the package and the example in this tutorial depend on several external packages. If these packages get updates that are inconsistent with our application it can potentially,affect how the example code runs. For your own work, it is recommend that you install the latest version using the instructions provided on https:/github.com/andrewmarx/samc.

## Loading Packages and Data

The samc package contains the required functions to construct the absorbing markov chain matrix and calculate the various metrics, **B**, **D**, and **z**, as well as the fundamental matrix, **F**. This tutorial illustrates how to implement the package using the small corridor landscape example from Fig. 3 in the main text with suggestions on how a user would use their own data.

First, we load the required packages for implementing the SAMC, using raster files, and plot the results.

library(samc)  
library(raster)  
library(ggplot2)

The primary function of the package is the samc() function. This function takes takes a RasterLayer with values for resistance to movement and a second RasterLayer with mortality probabilities for each cell. Some metrics presented in the main text involve calculating unconditional probabilities based on initial starting probabilities (e.g., species occurrence or abundance). The functions for these metrics require a RasterLayer with proportional occupancy values for the initial populations or abundance. Collectively, these are the only external data inputs needed to run all functions in the samc package. The first two RasterLayers, resistance and movement, would need to be created by the user to implement the SAMC and conditional probability metrics. The third RasterLayer is optional and only needed to calculate metrics for specific starting populations. Future versions will allow for point, polygon, and raster data for initial starting distributions. It will also allow for a RasterLayer describing potential fidelity (see Fig. 2 of main text).

Data are provided within the package as three sample layers for the corridor example presented in the main text (Fig. 3). The layers are stored in the package as matrices and must be converted to RasterLayer objects. The occupancy raster is given as a binary presence absence for each cell and must be converted to the starting occupancy probability by dividing by the total number of occupied cells as seen in the code below, generating a probability density function for the initial distribution.

res\_raster <- raster(samc::ex\_res\_data) # Resistance to movement  
mort\_raster <- raster(samc::ex\_mort\_data) # Mortality risk  
  
patch\_raster <- raster(samc::ex\_patch\_data) # Start location  
patch\_raster <- patch\_raster / cellStats(patch\_raster, sum) #pdf for patch

Similarly, a raster of abundances at starting locations could be used. Users have a number of options for this layer depending on what data available. Occupancy, abundance, or proportion of total population at each starting location can also be used. The package functions can take the starting locations as either a RasterLayer or as a vector representing each of the cells in the landscape.

Users can start with data already in RasterLayer form and directly input it into the samc() function or convert matrices to RasterLayers as above. Note that the function converts traditional resistance measures (positive integers) into transition probabilities.

Data or hypotheses on mortality across the landscape are needed to create the mortality layer to parameterize **R** in equation 2 of the main text. These data can come from direct measurements or created based on known mortality in corresponding areas of the landscape. For instance, one might hypothesize that mortality rates are high at interstates and highways in a landscape due to the potential for wildlife-vehicle collisions but low elsewhere. Mortality rates should be scaled to the probability of mortality in a single time step, which should be relative to the movements from one cell to an adjacent cell in the landscape. If no information is available on mortality risk, users can assume a constant, small value across the landscape.

The landscape shown in Fig 3a can be plotted by converting rasters to points and plotting with ggplot2 as:

res\_df <- data.frame(rasterToPoints(res\_raster))  
mort\_df <- data.frame(rasterToPoints(mort\_raster))

ggplot(res\_df, aes(x = x, y = y)) +  
 geom\_raster(aes(fill = layer)) +  
 scale\_fill\_gradient(limits = c(0, max(res\_df))) +  
 geom\_tile(data = res\_df,aes(x = x, y = y,fill = layer)) +  
 coord\_equal() + theme\_void()

ggplot(mort\_df, aes(x = x, y = y)) +  
 geom\_raster(aes(fill = layer)) +  
 scale\_fill\_gradient(limits = c(0, max(mort\_df$layer))) +  
 geom\_tile(data = mort\_df,aes(x = x, y = y,fill = layer)) +  
 coord\_equal() + theme\_void()

This landscape consists of two separate corridors connecting two ends. The res\_raster object is a RasterLayer object displaying the resistance values for this landscape. The resistance to movement is high () in the upper corridor and low () in the rest of the landscape. Without considering mortality, the lower corridor would be preferred in a random-walk based connectivity analysis.

Mortality probabilities are given in the second object, mort\_raster. In Fig. 3, we can see that mortality probability is high () in the upper corridor and an order of magnitude lower () everywhere else. Remember that the values for mortality are small as they are the probability per time step of dying in a time scale based around movement between cells.

The third object, patch\_raster, represents initial starting population for our example which can also be considered the starting patches. In our example, 32 raster cells are potentially occupied at the outset giving a percent occupancy for these cells of 0.031. Users can plot this data using similar code as above.

## SAMC Implementation

The samc()function itself takes two objects as input parameters. The resistance and absorption arguments seen in the example code below refer to the resistance and mortality in our example. While an absorbing markov chain can have multiple absorbing states, the current implementation of the samc() function allows for a single absorbing state (mortality). The latlong parameter argument is a true or false operator for whether the RasterLayer’s cell coordinates are given in latitude and longitude.

The samc()function utilizes the gdistance function transitionMatrix() to calculate the transition matrix and requires a correction for cell coordinates given in latitude and longitude. The samc() function calculates the transition matrix from this raster layer based on the equation for adjacent cells (if using the default method). Here is the total number of cells in the landscape.

samc\_p <- samc(resistance = res\_raster, absorption = mort\_raster, latlon =TRUE)  
str(samc\_p)

## List of 1  
## $ p:Formal class 'dgCMatrix' [package "Matrix"] with 6 slots  
## .. ..@ i : int [1:21613] 1 115 116 117 0 2 116 117 118 1 ...  
## .. ..@ p : int [1:2626] 0 4 9 14 19 24 29 34 39 44 ...  
## .. ..@ Dim : int [1:2] 2625 2625  
## .. ..@ Dimnames:List of 2  
## .. .. ..$ : NULL  
## .. .. ..$ : NULL  
## .. ..@ x : num [1:21613] 0.2945 0.1164 0.1151 0.0934 0.4176 ...  
## .. ..@ factors : list()  
## - attr(\*, "class")= chr "samc"

The code above returns an S3 object of the samc class which is functionally a sparse dgCMatrix. This is the transition probability () matrix consisting of the transient transition matrix () with the absorbing state constructed using the format,

where is the vector of site specific absorbing probabilities (see description of equation 2 in main text). The samc() function output is the input for subsequent functions covered in this tutorial. Users will need to successfully implement this function to proceed with the rest of the analyses shown (however, unconditional probabilities based on starting populations require the starting patch vector).

## Calculating Metrics

To get the matrix for the probability of mortality from site at within interval, , the matrix from above is inputted into the function with the number of time steps specified. Here we show the code for 4800 times steps. This function can take a while to run depending on your computer resources.

transB\_4800 <- calc\_trans\_b(amc = samc\_p, 4800)

In general, the appropriate time scales for consideration will be based on the question being considered and the landscape under consideration. If information regarding known dispersal distances are available, such information could be used to interpret meaningful time steps for consideration. For instance, if a species is known to disperse 10 km, and the resolution of the map being considered is 50 m, there would be a minimum of 200 pixels that would have to be traversed to successfully disperse this distance and 200 time steps would be the minimum amount of time required for an individual to disperse. In practice, the probable amount of time would be much greater than 200 time steps, but this would provide a lower bound for analysis.

The fundament matrix is calculated from the matrix using the fundamental function in the package. This matrix gives the asymptotic probabilties for the transition matrix as goes to infinity. The only input paramenter in the function is the sparse matrix output from samc().

samc\_fund <- fundamental(samc\_p)

Similarly, the matrix, which describes the probability that an individual in visits location , can be calculated using the function calc\_d(). This input for this function is the same matrix we used before.

disp\_metrics <- calc\_d(amc = samc\_p)

This matrix can be used to find the unconditional probability of ever visiting each site using a vector consisting of the probility of initial presence for each site, . This can be passed as either the starting probability raster or a vector of these same probabilities into the calc\_disp() function along with the samc object.

# Adjust D for starting locations  
disp\_patch <- calc\_disp(amc= samc\_p, pv = patch\_raster)

To plot the resulting probabilities in space, this vector needs to be turned into a RasterLayer and plotted with the following code.

# Map the results to RasterLayer objects  
disp\_ras <- res\_raster  
disp\_ras[!is.na(disp\_ras)] <- disp\_patch

This object can then be plotted in a similar way as described above (Fig. 3). The map shown in Fig. 3 shows the asymptotic probability of ever reaching those locations. The probability is high close to our starting point and decreases farther away. The high resistance and high mortality probabilities of the upper corridor lead to visiting probabilities of 0 within the corridor itself.

The asymptotic probability matrix for mortality at site from site , matrix is found by including the sparse matrix, returned from the samc()function, as a parameter in the function.

mort\_metrics <- calc\_b(amc=samc\_p)

The unconditional probability of mortality at site can be found in a similar way as we did for the matrix above. Here we can employ the built in function calc\_mort() with the matrix from samc() and the starting patch raster as parameter arguments. The argument can also take a vector of starting probabilities.

mort\_patch <- calc\_mort(amc=samc\_p,pv = patch\_raster)

We can plot mortality in the same way we did with the unconditional dispersal probability. We convert the mortality matrix to a RasterLayer and then make the appropriate plot using the following code.

# Plot mortality  
mortB\_ras <- res\_raster  
mortB\_ras[!is.na(mortB\_ras)] <- mort\_patch

mortB\_df <- data.frame(rasterToPoints(mortB\_ras))  
print(ggplot(mortB\_df, aes(x = x, y = y)) +  
 geom\_raster(aes(fill = layer)) +  
 scale\_fill\_gradient(limits = c(0,max(mortB\_df$layer))) +  
 coord\_equal() + theme\_void())

The resulting map in Fig. 3 shows the unconditional mortality probability for every site based on our initial starting occupancies. The mortality is more likely close to our starting locations and decreases farther away. Notice that mortality probability decreases in the upper corridor. This results from the high resistance and high mortality preventing individuals from making it to these areas to then die.

## Computational issues

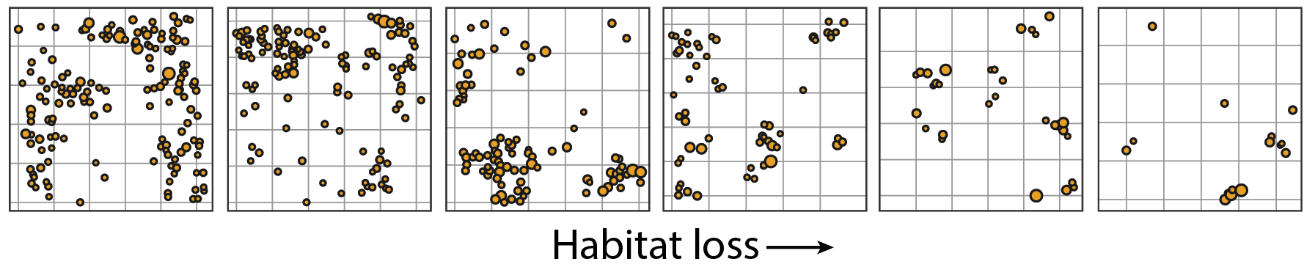
Different metrics vary in computational efficiency. In general, using the code provided, an average consumer grade computer with 8GB of RAM can calculate most of the metrics for landscapes with 10,000-20,000 cells. The number of patches (or start/end locations) are less influential for computation than the number of cells considered on raster grids. Optimizations and alternative approaches have recently been identified that allow landscapes with one to two order magnitudes more cells (>1M cells) to be used with most of the metrics in a reasonable amount of time using the same 8GB standard for consumer grade computers. These solutions are currently being implemented and evaluated as part of a more comprehensive and robust package framework that will be released at a future date (Marx et al. *unpublished manuscript*). So far, most of these optimized metrics appear to be similar or more computationally efficient than the related randomized shortest paths analysis in R (Saerens *et al.* 2009; Panzacchi *et al.* 2016) for >2M cells, but it is still less efficient than using circuit theory and least-cost metrics using the gdistance package (van Etten 2012). With these and other potential optimizations, we expect that our package will be able to be applied at scales comparable to that of circuit theory applications in R. Further improvements in computational performance may also be gained by transferring the framework outside of R, similar to Circuitscape.

**Table S1.** 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.

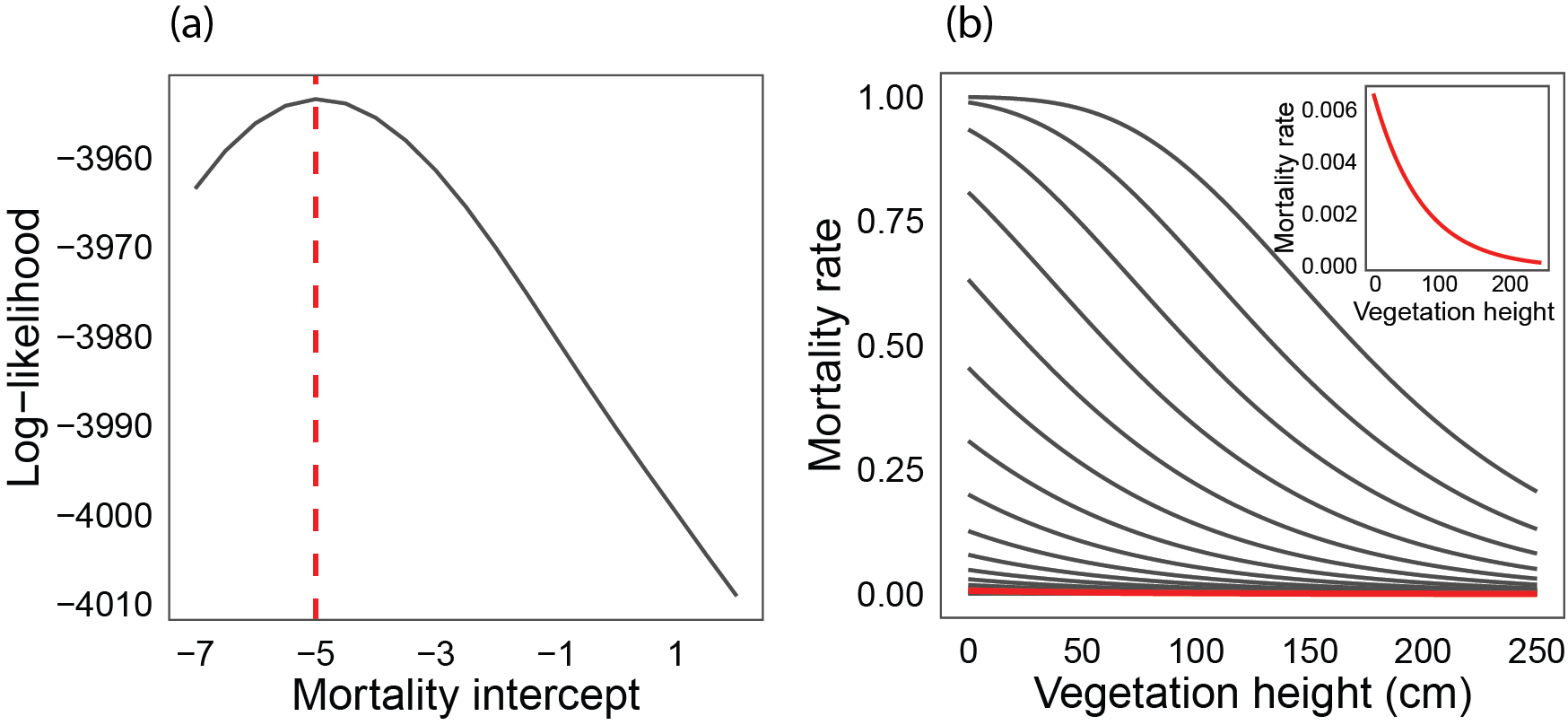
|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model\* | K | Log-likelihood | AICc | ΔAICc | Model  Weight\* |
| Spatial absorbing Markov chain, **D** | 3 | -3953.40 | 7912.80 | 0.00 | 1.0 |
| Euclidean distance | 3 | -3979.10 | 7964.21 | 51.41 | 0.0 |
| Least-cost distance-mortality\*\* | 3 | -3985.93 | 7977.87 | 65.07 | 0.0 |
| Least-cost distance | 3 | -3985.95 | 7977.90 | 65.10 | 0.0 |
| Circuit theory-mortality\*\* | 3 | -4004.35 | 8014.70 | 101.90 | 0.0 |
| Circuit theory | 3 | -4004.39 | 8014.78 | 101.99 | 0.0 |
| Intercept only | 2 | -4012.25 | 8028.50 | 115.70 | 0.0 |

\*AICc model weight ranges from 0 to 1 and is based on the relative differences in AICc.

\*\*Model included information on movement resistance and results from the mortality experiment in the form of a mortality cost surface. See Equation S1.



**Fig. S1**. The habitat loss gradient (11-94% patch loss; 150-15 patches remaining) considered in the experiment used to evaluate the SAMC. Shown are 50 × 50 m landscapes, where patches are in orange and background grid is 10 × 10 m.



**Fig. S2.** Tuning the SAMC. (a) The log-likelihood surface for fitting movement data to the SAMC, where the intercept of the mortality function is altered. The mortality function comes from a complementary log-log survival model fit to the tethering data. The red dashed line identifies the best-fit model, with an intercept = -5. (b) Estimated mortality rates as a function of vegetation height; grey lines show intercepts considered for tuning the SAMC and the best-fit intercept is shown in red. The inset also shows the best-fit function (with intercept = - 5).

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