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EDGE-1.0 - USER GUIDE

Autor: Lutz Tischendorf ELUTIS Modelling and Consulting Inc. in collaboration with Lenore Fahrig, Carleton University

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1 Overview

EDGE is a stochastic, spatially explicit, individual-based, multi-population model. Space is expressed as a two dimensional array (raster/grid) of cells (called landscape hereafter), whereas each cell can have a different categorical state, called landcover type. EDGE-1.0 supports two landcover types¹, which can be regarded as habitat and non-habitat (or matrix). Clusters of contiguous cells constitute patches, which are topological units of each landcover type. EDGE automatically generates patch topologies for each landcover type. EDGE allows to either generate artificial configurations of habitat and matrix or to import raster data in ASCII format. Habitat proportion and fragmentation can be controlled in artificially generated landcover configurations.

Individuals are independent units which operate within the spatial extent of a landscape. Each individual is located in space by one x, y coordinate pair, which also identifies the index of one cell in the landscape. The landcover type of an individual's current cell of residence determines its behavior, such as fecundity, survival and movement pattern. Movement changes the location of an individual. When the new cell of residence has a different landcover type than the previous cell, the individual encountered a boundary between two landcover types. Individuals may cross the boundary or return to the previous cell of residence depending on the corresponding boundary crossing probability. Individuals do not interact directly with each other. A population is a set of individuals with identical behavioral characteristics, whereas each individual still follows its own random movement path and therefore experiences a unique sequence of behavioral activities. EDGE-1.0 supports two populations², which indirectly interact by means of resource competition. Individuals of both populations may use resources differently and may also face a different density dependent mortality rate when available resources are exploited.

EDGE supports automatic execution of factorial or random parameter value combinations. Designated model parameters can be set with multiple values. In factorial mode, EDGE will carry out simulations for each of the resulting factorial parameter value combinations. In random mode, EDGE will execute a defined number of simulations with random parameter values within the given range. Each simulation may be repeated many times, which allows to calculate statistical measures across the resulting distributions of the recorded response variables. EDGE allows to configure the sequence and execution of reproduction, movement and mortality. EDGE can therefore be configured to simulate either movement, reproduction, mortality or any sequential or random combination of these.

Different aspects of the model state can be recorded during the course of simulations. EDGE allows to activate or disable a set of 'observers'. Observers exist outside of the actual model and collect information from the model during simulation. This information is stored across multiple repetitions of one simulation. Observers aggregate recorded distributions and can be configured to report statistical measures but also raw data. EDGE-1.0 allows to activate observers for recording population abundances, population abundances on habitat and/or matrix, extinction probability, patch immigration rates, cell immigration rates, search times, boundary crossing rates, dispersal distances and landscape indices. Recording intervals can be configured for active observers to reduce overall information output. Data in output files are organized in tabular structure with columns separated by ",". These CSV files can easily be imported into spreadsheet programs and statistical tools, such as EXCEL, SAS or STATISTICA.

EDGE is a generic framework for simulating population models in a spatially explicit environment. Its internal object oriented architecture facilitates incorporation of new features, such as roads and individual road behavior or individual genetic markers like loci and allele. EDGE is programmed in ANSI C++ and depends on different external libraries, such as STL. EDGE-1.0 is available for MS Windows and will shortly be available for Linux and Solaris operating systems.

² EDGE can principally support more than two populations, but is currently restricted to just two for reasons given in footnote 1.

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¹ EDGE is designed to support more than two landcover types, but is currently restricted to just two in order to reduce complexity of the model parameter file.

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2 Model Description

2.1 Landscape Model

In EDGE a landscape is defined by a two-dimensional array of cells. Each cell can have a different categorical state or landcover type. EDGE-1.0 supports two landcover types: habitat = 1 and matrix = 0. Consequently, the landcover type of each cell can be either 1 or 0 (see Figure 1).





Figure 1: ASCII data format and visualized image of a typical EDGE landscape. Adjacent cells constitute patches. When adjacency is defined for cell edges only, the above landscape consists of 6 habitat patches (dark cells). When adjacency is defined for cell edges and corners then the above landscape consists of 3 habitat patches.

In addition to a categorical landcover type, cells manage a scalar resource value (Model parameters beginning with MAX_RESOURCES_PER_CELL). Resource use by 'visiting' individuals decreases a cell's resource. If all resources are exploited in one cell, some of the 'visiting' individuals become subject to density dependent mortality, which will free resources for this cell (Model parameters REDUCTION_FACTOR).

Adjacent cells of the same landcover type constitute patches. A patch is a distinctive, topological unit in a landscape. EDGE allows to define adjacency either for cell edges only or for cell edges and corners (Model parameter CELL_ADJACENCY, see section 3.1). Latter results in fewer patches. Habitat patches are used for recording patch immigration rates and a variety of landscape indices.

Moving individuals can perceive landscape borders in three different ways: torus, absorb, reflect (Model parameter GRID_BORDER, see section 3.1). In 'torus' mode, individuals encountering a landscape border re-enter the landscape at the opposite border. In 'reflect' mode, individuals return into the landscape after having encountered a landscape border. Both, 'torus' and 'reflect' mode resemble a closed system, because individuals are forced to stay within the landscape. In 'absorb' mode, individuals encountering a landscape border are permanently removed from a population, which resembles an open system.

EDGE-1.0 supports landscapes based on grid sizes of up to 1000 x 1000 cells. EDGE can either generate artificial configurations of habitat and matrix or import one or a series of ASCII data files. The algorithm for distributing habitat across cells of the landscape controls the proportion and fragmentation of habitat (Model parameters HABITAT_AMOUNT and HABITAT_FRAGMENTATION), (see Figure 2).

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Figure 2: Flow chart of algorithm to distribute habitat (COV) across a grid of 200 x 200 cells. This algorithm generates habitat distributions as shown in Figure 3.



Figure 3: Exemplary distributions of habitat across a grid of 200 x 200 cells. The left figure shows a proportion of 10% habitat distributed with low fragmentation. The right figure shows a proportion of 20% habitat distributed with high fragmentation.

EDGE can import ASCII data files in the format shown in Figure 1. Hence, GIS maps may be used as landscape models for EDGE. If the model parameter GRID_FILE contains at least one filename, EDGE will try to read the corresponding ASCII file(s) from the local folder from which EDGE is executed. In this mode, the following model parameters: GRID_LENGTH, GRID_WIDTH, HABITAT_AMOUNT and HABITAT_FRAGMENTATION are ignored, since these parameters control the algorithm for artificial landscapes and are not needed when landscape models are read from external ASCII data files. If the model parameter GRID_FILE does not contain any values, EDGE will not try to read external ASCII files, but will use the above mentioned algorithm to generate artificial habitat configurations.

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EDGE allows to write landscapes into ASCII and GIF files. The data format of the written ASCII files conforms with the input data format, which allows to read these files again into subsequent simulations.

2.2 Population Model

The population model is composed of individuals. Individuals are independent units with a spatial reference to the landscape model. In EDGE-1.0 all individuals have the same gender and belong to one age class³. Individuals can either move, reproduce or die. EDGE allows to configure the sequence and execution of these three activities (Model parameter EVENT_CYCLE). If all three activities or events (move, repro, death) are listed for this parameter, then all individuals of the population will carry out these activities in the corresponding sequence, i.e. in this example, all individuals would first move, then reproduce and finally die with a certain probability. If only one event is listed, then all individuals of the population will carry out this activity only. Alternatively, if the model parameter EVENT_CYCLE is set to 'random', the sequence of all three activities will be random for each individual of the population.

Actual probabilities for an individual's movement, reproduction and death depend on the landcover type (habitat or matrix) of the individual's current location. The x, y coordinates are projected on the landscape model and identify the current cell of residence. For instance, if an individual's current location is defined by x=1.765, y=9.876, the individual's current cell of residence would be in the first row, ninth column of the array of cells. The landcover type of this cell will then define current probabilities for this individual's activities. Model parameters with relevance to behavioural activities therefore contain either HAB or MAT to indicate the landcover type (habitat and matrix respectively) for which they are valid.

When an individual reproduces, it creates a discrete number of new individuals at the same location as its own. The number of offspring per individual is drawn from poisson distribution. The model parameters starting with FECUNDITY_ define the expected mean value for this poisson distribution. For instance, a fecundity value of 1.2 would result in an average of 1.2 individuals offspring per reproducing individual, whereas each reproducing individual may have 0, 1, 2, 3 or more offspring individuals per time step. Reproduction may be scheduled or restricted to one out of max. 12 time steps. In EDGE, one year may be divided into max. 12 time steps (Model parameter YEAR_DIV). If YEAR_DIV is larger than one, parameters starting with REPRO_STEP_ define the time step within one YEAR at which reproduction can occur. IF YEAR_DIV is set to one, reproduction will occur at each time step. Movement and Death will always occur at each time step.

Each individual is located within the landscape model by one x, y coordinate pair. Movement steps are vectors defined by step length and turning angle. The unit of step length is relative to the grid of cells and corresponds to the neutral dimension of one cell. For instance, a step length of 200 would cover the distance of 200 adjacent cells. Step lengths are drawn from a negative exponential distribution. The model parameters starting with MOVE_DIST_ set the expected mean value for this negative exponential distribution for one time step. The turning angle is the difference between the direction of the previous and the next movement step. Turning angles are drawn from a symmetrical uniform distribution around 0 with a potential range of +/- π . The actual range of potential turning angles can be set with the model parameters starting with MOVE ANGLE .

When individuals move, they may encounter and cross boundaries between different landcover types. Before a movement step is completed, the landcover type of the new cell is compared to the landcover type of the previous cell. If both landcover types are different, the individual may either cross the boundary or return. This decision depends on the corresponding boundary crossing probability (Model parameters beginning with CROSS_). If an individual returns, its movement direction is reversed. To avoid missing boundaries or 'jumping' between non-adjacent cells with equal landcover types, EDGE traces each movement step at 0.5 length units. This ensures that a movement step of e.g. 5 length units will still detect

³ EDGE is designed to support female and male individuals in multiple age classes, but is currently restricted to just two in order to reduce complexity of the model parameter file.

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a boundary in between. If an individual encounters a landscape border, it may either return, re-enter the landscape at the opposite border or leave the landscape and the population permanently. This decision depends on the parameter GRID_BORDER, see section 2.1.

Individuals use resources maintained by each cell of the landscape. Resource use can be set differently for each population (Model parameters beginning with RESOURCES_FACTOR_). If all resources within each cell are exploited, EDGE will randomly remove individuals from both populations (only if two populations are initialised) until used resources are reduced below a defined threshold (Model parameters beginning with MAX_RESOURCES_PER_CELL_). The rate at which resources are being freed can be set differently for each population (Model parameters beginning with REDUCTION_FACTOR_). Resources of cells, the proportion of each landcover type and the resource use factors for each population define the overall carrying capacity of the landscape. To understand this, consider the following example.

| Model parameter | Explanation |
|--------------------------------|---|
| GRID_LENGTH = 10 | vertical dimension of the grid of cells |
| GRID_WIDTH = 10 | horizontal dimension of the grid of cells |
| HABITAT_AMOUNT = 0.3 | proportion of habitat cells in grid (30), implies 70 matrix cells |
| MAX_RESOURCES_PER_CELL_HAB = 3 | resources in habitat cells |
| MAX_RESOURCES_PER_CELL_MAT = 2 | resources in matrix cells |
| RESOURCES_FACTOR_1_HAB = 2 | resource use per individual in population 1 in habitat cell |
| RESOURCES_FACTOR_2_HAB = 1 | resource use per individual in population 2 in habitat cell |
| RESOURCES_FACTOR_1_MAT = 1 | resource use per individual in population 1 in matrix cell |
| RESOURCES_FACTOR_2_MAT = 1 | resource use per individual in population 2 in matrix cell |

The parameter settings of this example translate into the overall carrying capacity of the landscape model for population 1 as follows:

[30 (habitat cells) * 3 / 2 (resource use of population 1 in habitat)] + [70 (matrix cells) * 2 / 1] = 185

and for population 2 as follows:

[30 (habitat cells) * 3 / 1 (resource use of population 1 in habitat)] + [70 (matrix cells) * 2 / 1] = 230

Finally, individuals of each population can be initially distributed across habitat or matrix or across the entire landscape model (Model parameters INIT_1/INIT_2). Depending on the setting of this parameter, individuals are being placed randomly and uniformly across the areas of habitat or matrix or both⁴.

2.3 Simulation

One simulation calculates one or more response variables for one unique set of model parameter values. The results of a simulation are time series or trajectories of the response variables. Simulations are stochastic because they are based on random numbers. For instance, the probability that an individual dies depends on the value of a random variable. Results of stochastic simulations are always different. For this reason, simulations are usually repeated many times. In EDGE the number of repetitions can be set with the Model parameter RUNS. The results of multiple simulation runs are sets of trajectories (or distributions of response variables for each time step). One can either analyse those distributions or calculate statistical measures, such as mean, minimum/maximum value, variance and confidence interval. EDGE always produces statistical measures of response variables and can also write raw data (trajectories for each run) into separate output files.

The number of simulation or time steps is defined by the number of years and the number of steps within each year (Model parameters YEARS and YEAR_DIV). Years can be divided into 1 to 12 time steps. This

⁴ EDGE principally allows to seed populations into patches or single cells. This feature may become available in a later version of EDGE.

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mechanism allows to schedule reproduction into 1 out of max. 12 time steps (Model parameters beginning with REPRO_STEP_). If a year is divided into 1 time step, reproduction will take place at each time step together with movement and mortality. If a year is divided into e.g. 4 time steps, reproduction can be scheduled and restricted to e.g. time step 2. In this case, reproduction would occur only in the second step of each year or at each fourth time step.

Sensitivity analyses require a set of simulations with different parameter values. EDGE supports execution of factorial or random parameter value combinations. Therefore, designated model parameters (see section 3.1) can be set with multiple values. In factorial mode, EDGE will execute a set of simulation runs for each of the resulting factorial parameter combinations. For instance, if 2 parameters are set with 3 values each, the number of simulations would be 6. In random mode, EDGE will examine the lower and upper boundaries of parameter values and will draw actual parameter values for the simulations (Model parameter RANDOM_COMBINATIONS), each with a different set of parameter values drawn from random distributions. The question whether to use factorial or random simulation mode depends on the objective and scope of the simulation experiment. If the effects of many model parameters on response variables are of interest and those effects are being examined based on multiple regression or ANOVA, random mode may be preferential to factorial mode, simply to control and reduce the number of overall simulation experiments with known model parameter values are more suitable for factorial mode.

Finally, stochasticity can be controlled by the model parameter START_SEED. The value of this parameter defines the seed for all random generators used in the model. As long as START_SEED has a value different from 0, results will always be the same, because the sequence of random numbers will be identical throughout all simulation runs. Vice versa, if START_SEED is set to 0, the seed for all random generators will be determined based on the current computer time, which is always different. The results obtained from simulations with different random seeds will therefore also always be different. It is recommended to set START_SEED always to 0. A value different from 0 may be helpful for testing, i.e. comparing the output of different model versions against a result set obtained with a certain START_SEED value.

3 Model Input

3.1 Model Parameters

The following table lists and explains all parameters for EDGE-1.0. Values for multi value model parameters can be separated by, or empty spaces. For example, HABITAT_AMOUNT 0.1 0.2 0.3 0.4 indicates 4 values for this parameter and is identical to HABITAT_AMOUNT 0.1,0.2,0.3,0.4.

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| Parameter Name | Acronym | Multiple Values | Valid Range/Values | Explanation | | | |
|--|----------------------|-----------------|------------------------------|---|---|------------------------------|--|
| PARAMETER_MODE | n/a | no | 0/1 | factorial (0) or rand | om (1) mode | | |
| RANDOM_COMBINATIONS | n/a | no | 0 100.000 | number of combina | tions if PARAMETER_MODE | i = 1 | |
| START_SEED | n/a | no | 0 65000 | seed for random ge | enerators (0 = random, > 0 fix | ed seed) | |
| RUNS | n/a | no | 1 1000 | number of repetition | number of repetitions for each simulation | | |
| YEARS | n/a | no | 1 1000 | number of years | | | |
| YEAR_DIV | n/a | no | 1 12 | number of steps wit | thin each year | | |
| REPRO_STEP_1 | n/a | no | 1 YEAR_DIV | step for reproductio | on for population 1 | | |
| REPRO_STEP_2 | n/a | no | 1 YEAR_DIV | step for reproductio | on for population 2 | | |
| GRID_FILE | GRD_FILE | yes | valid file names | names for ascii ras | ter files | | |
| GRID_LENGTH | G_LENGTH | yes | 1 1000 | vertical dimension | of the landscape | | |
| GRID_WIDTH | G_WIDTH | yes | 1 1000 | horizontal dimensio | on of the landscape | | |
| GRID_BORDER | G_BORDER | yes | torus, absorb, reflect | defines individual b | ehaviour at the landscape bo | rder | |
| CELL_ADJACENCY | CELL_ADJ | yes | orthogonal, diagonal | defines cell adjacer | ncy for patch topology | | |
| HABITAT_AMOUNT | H_AMOUNT | yes | 0.01 0.9 | proportion of habitat in the landscape | | | |
| HABITAT_FRAGMENTATION | H_FRAG | yes | 0.01 1.0 | fragmentation of habitat | | | |
| MAX_RESOURCES_PER_CELL_H | AB H_CELRES | yes | 1 10000 | resource threshold per habitat cell | | | |
| MAX_RESOURCES_PER_CELL_M | IAT M_CELRES | yes | 1 10000 | resource threshold per matrix cell | | | |
| REDUCTION_FACTOR_HAB | H_REDFAC | yes | 0.0 1.0 | proportion of individuals to be removed from resource depleted habitat cell | | | |
| REDUCTION_FACTOR_MAT | M_REDFAC | yes | 0.0 1.0 | proportion of individ | luals to be removed from reso | ource depleted matrix cell | |
| START_NUM_1 | P1_START | yes | 0 100000 | initial size (number | of individuals) for population | 1 | |
| START_NUM_2 | P2_START | yes | 0 100000 | initial size (number | of individuals) for population | 2 | |
| INIT_1 | P1_INIT | yes | landscape, habitat, matrix | defines where indiv | iduals of population 1 are initi | ially distributed | |
| INIT_2 | P2_INIT | yes | landscape, habitat, matrix | defines where indiv | iduals of population 2 are init | ially distributed | |
| EVENT_CYCLE | EVENT | no | repro, death, move or random | execution and sequ | ence of individual activities, r | andom=all in random sequence | |
| The following paramete | rs relate to one tim | ne step | | | | | |
| RESOURCES_FACTOR_1_HAB | H_P1_RES | yes | 0 1000 | resource use factor | for individuals in population | 1 on habitat cells | |
| RESOURCES_FACTOR_2_HAB | H_P2_RES | yes | 0 1000 | resource use factor | for individuals in population | 2 on habitat cells | |
| RESOURCES_FACTOR_1_MAT | M_P1_RES | yes | 0 1000 | resource use factor for individuals in population 1 on matrix cells | | | |
| RESOURCES_FACTOR_2_MAT | M_P2_RES | yes | 0 1000 | resource use factor for individuals in population 2 on matrix cells | | | |
| SURVIVAL_1_HAB | H_P1_SUR | yes | 0.0 1.0 | survival probability for individuals in population 1 on habitat cells | | | |
| SURVIVAL_2_HAB | H_P2_SUR | yes | 0.0 1.0 | survival probability for individuals in population 2 on habitat cells | | | |
| SURVIVAL_1_MAT | M_P1_SUR | yes | 0.0 1.0 | survival probability | for individuals in population 1 | on matrix cells | |
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| Parameter Name | Acronym | Multiple Values | Valid Range/Values | Explanation | | | |
|----------------------|----------------------|-----------------|---|---|--|------------------------------------|--|
| SURVIVAL_2_MAT | M_P2_SUR | yes | 0.0 1.0 | survival probability | for individuals in population 2 | on matrix cells | |
| MOVE_DIST_1_HAB | H_P1_MOV | yes | 0.0 100.0 | expected mean mo | vement distance for individua | ls in population 1 on habitat | |
| MOVE_DIST_2_HAB | H_P2_MOV | yes | 0.0 100.0 | expected mean mo | vement distance for individua | ls in population 2 on habitat | |
| MOVE_DIST_1_MAT | M_P1_MOV | yes | 0.0 100.0 | expected mean mo | vement distance for individua | ls in population 1 on matrix | |
| MOVE_DIST_2_MAT | M_P2_MOV | yes | 0.0 100.0 | expected mean mo | vement distance for individua | ls in population 2 on matrix | |
| MOVE_ANGLE_1_HAB | H_P1_ANG | yes | 0.0 3.14159 | range of symmetric | al turning angle (0 = directed, | 3.14159 = random walk) | |
| MOVE_ANGLE_2_HAB | H_P2_ANG | yes | 0.0 3.14159 | range of symmetric | al turning angle (0 = directed, | 3.14159 = random walk) | |
| MOVE_ANGLE_1_MAT | M_P1_ANG | yes | 0.0 3.14159 | range of symmetric | al turning angle (0 = directed, | 3.14159 = random walk) | |
| MOVE_ANGLE_2_MAT | M_P2_ANG | yes | 0.0 3.14159 | range of symmetric | al turning angle (0 = directed, | 3.14159 = random walk) | |
| FECUNDITY_1_HAB | H_P1_FEC | yes | 0.0 1000.0 | expected mean nur | mber of offspring per individua | I in population 1 on habitat | |
| FECUNDITY_2_HAB | H_P2_FEC | yes | 0.0 1000.0 | expected mean nur | mber of offspring per individua | I in population 2 on habitat | |
| FECUNDITY_1_MAT | M_P1_FEC | yes | 0.0 1000.0 | expected mean nur | mber of offspring per individua | I in population 1 on matrix | |
| FECUNDITY_2_MAT | M_P2_FEC | yes | 0.0 1000.0 | expected mean nur | mber of offspring per individua | I in population 2 on matrix | |
| CROSS_1_HAB_MAT | HM_P1_CR | yes | 0.0 1.0 | probability to cross boundary from habitat to matrix for individual in populatio | | | |
| CROSS_1_MAT_HAB | MH_P1_CR | yes | 0.0 1.0 | probability to cross boundary from matrix to habitat for individual in population 1 | | | |
| CROSS_2_HAB_MAT | HM_P2_CR | yes | 0.0 1.0 | probability to cross | boundary from habitat to mat | rix for individual in population 2 | |
| CROSS_2_MAT_HAB | MH_P2_CR | yes | 0.0 1.0 | probability to cross boundary from matrix to habitat for individual in population 2 | | | |
| The following parame | ters control simulat | tion output | | | | | |
| SAVE_GIF_LANDSCAPES | n/a | no | 0/1 | turns on(1)/off(0) w | hether landscapes are saved | in GIF files | |
| SAVE_ASC_LANDSCAPES | n/a | no | 0/1 | turns on(1)/off(0) w | hether landscapes are saved | in ASCII files | |
| SAVE_DETAILS | n/a | no | 0/1 | turns on(1)/off(0) or | utput of raw data, i.e. time ser | ies for each run | |
| OBS_GAP | n/a | no | 1 YEARS * YEAR_DIV | observation interva | I, determines number of rows | in output files | |
| ABUNDANCE_1_OBS | AB_P1 | no | 0/1 | turns on(1)/off(0) re | cording of abundance for pop | oulation 1 | |
| ABUNDANCE_2_OBS | AB_P2 | no | 0/1 | turns on(1)/off(0) re | ecording of abundance for pop | oulation 2 | |
| EXTINCTION_1_OBS | EX_P1 | no | 0/1 | turns on(1)/off(0) re | ecording of extinction events for | or population 1 | |
| EXTINCTION_2_OBS | EX_P2 | no | 0/1 | turns on(1)/off(0) re | ecording of extinction events for | or population 2 | |
| ABUNDANCE_HAB_1_OBS | HA_P1 | no | 0/1 | turns on(1)/off(0) re | cording of abundance for pop | oulation 1 on habitat | |
| ABUNDANCE_HAB_2_OBS | HA_P2 | no | 0/1 | turns on(1)/off(0) re | ecording of abundance for pop | oulation 2 on habitat | |
| ABUNDANCE_MAT_1_OBS | MA_P1 | no | 0/1 | turns on(1)/off(0) re | turns on(1)/off(0) recording of abundance for population 1 on matrix | | |
| ABUNDANCE_MAT_2_OBS | MA_P2 | no | 0/1 | turns on(1)/off(0) recording of abundance for population 2 on matrix | | | |
| HAB_CELL_IMM_1_OBS | CI_P1 | no | 0/1 | turns on(1)/off(0) recording of cell immigration for population 1 | | | |
| HAB_CELL_IMM_2_OBS | CI_P2 | no | 0/1 | turns on(1)/off(0) re | cording of cell immigration for | r population 2 | |
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| Parameter Name | Acronym | Multiple Values | Valid Range/Values | Explanation | |
|---------------------|---------|-----------------|--------------------|---|--|
| HAB_PATCH_IMM_1_OBS | PI_P1 | no | 0/1 | turns on(1)/off(0) recording of patch immigration for population 1 | |
| HAB_PATCH_IMM_2_OBS | PI_P2 | no | 0/1 | turns on(1)/off(0) recording of patch immigration for population 2 | |
| SEARCH_TIME_1_OBS | ST_P1 | no | 0/1 | turns on(1)/off(0) recording of search time for population 1 | |
| SEARCH_TIME_2_OBS | ST_P2 | no | 0/1 | turns on(1)/off(0) recording of search time for population 2 | |
| DISPERSAL_1_OBS | DI_P1 | no | 0/1 | turns on(1)/off(0) recording of dispersal distances for population 1 | |
| DISPERSAL_2_OBS | DI_P2 | no | 0/1 | turns on(1)/off(0) recording of dispersal distances for population 2 | |
| CROSS HAB MAT 1 OBS | C1 HM | no | 0/1 | turns on(1)/off(0) recording of boundary crossings from habitat to matrix for population 1 | |
| CROSS_MAT_HAB_1_OBS | C1_MH | no | 0/1 | turns on(1)/off(0) recording of boundary crossings from matrix to habitat for population 1 | |
| CROSS_HAB_MAT_2_OBS | C2_HM | no | 0/1 | turns on(1)/off(0) recording of boundary crossings from habitat to matrix for population 2 | |
| CROSS_MAT_HAB_2_OBS | C2_MH | no | 0/1 | turns on(1)/off(0) recording of boundary crossings from matrix to habitat for population 2 | |
| LAND_INDICES_OBS | n/a | no | 0/1 | turns on(1)/off(0) recording of landscape indices | |

Table 1: Parameters for EDGE-1.0

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4 Model Output

4.1 Overview

EDGE writes simulation results to comma separated (CSV) output files. These files can be viewed with MS Excel or other spreadsheet programs. From here, output files can be converted into other data formats (e.g. dbase) and subsequently imported into statistic programs such as SAS, Statistica or SPSS. EDGE writes two types of output files for aggregated and raw data, respectively.

The aggregated output file contains statistical variables (mean, min, max, variance and confidence interval) for all activated observers (recorded response variables) together with values of all varied model parameters and the corresponding time step of the simulation. The following shows an exemplary record (row) in an aggregated output file:

| YEAR | STEP | H_AMOUNT | H_FRAG | AB_P1_AV | AB_P1_MI | AB_P1_MA | AB_P1_VA | AB_P1_KO |
|------|------|----------|--------|----------|----------|----------|----------|----------|
| 1 | 1 | 0.3 | 0.1 | 179 | 158 | 203 | 131 | 7.09 |

Columns YEAR and STEP show the actual time steps followed by a variable number of columns showing the values of the varied model parameters. In this example, habitat amount and habitat fragmentation (see Acronyms in Table 1) would have been set with multiple values in the parameter file and the values in this record (0.3 and 0.1) show the current values of those varied model parameters.⁵ Each response variable has 5 columns in the aggregated output file (except for extinction probability, which has only 3 columns, see 4.6). In this example, abundance for population 1 was recorded. The columns AB_P1_AV, AB_P1_MI, AB_P1_MA, AB_P1_VA and AB_P1_KO show the average, minimum, maximum, variance and confidence interval across all repetitions (runs) for this particular parameter combination and time step.

EDGE writes a separate raw data file for each recorded response variable if the model parameter SAVE_DETAILS was set to 1 (see Table 1 in section 3.1). Raw data files contain the actual values of the response variable for each simulation run. The following shows an exemplary record (row) in a raw data file.

| YEAR | STEP | H_AMOUNT | H_FRAG | RUN_1 | RUN_2 | RUN_3 | RUN_4 | RUN_5 | RUN_6 | RUN_7 | RUN_8 | RUN_9 | RUN_10 |
|------|------|----------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| 1 | 1 | 0.3 | 0.1 | 172 | 186 | 190 | 181 | 203 | 177 | 172 | 175 | 180 | 158 |

This record corresponds to the example record for the aggregated output file above, i.e. the minimum and maximum values shown above were recorded in RUN_10 and RUN_5 respectively.

4.2 Naming Conventions

The following naming conventions are applied to define the names of the output files, model parameters and response variables.

EDGE writes aggregated data for all response variables into one output file. The name of this file is composed of the base name of the parameter file extended with "_out.csv". For example, if the parameter file were named "test.par", the aggregated output file would be called "test_out.csv".

If the parameter SAVE_DETAILS is set to 1 in the parameter file, EDGE will write raw data files for each activated observer (response variable). The names of the raw data files are composed of the base name of the parameter file and the acronym of the observer (e.g. AB_P1 for ABUNDANCE_1_OBS, see Table 1). For example, if the parameter file were named "test.par", the corresponding raw output file would be called "test-AB_P1-raw.csv".

Acronyms (see Table 1, section 3.1) are also used to identify model parameters and response variables in the output files. Acronyms are no longer than 8 characters and conform with variable name requirements

⁵ Note that fixed model parameters (i.e. those with one value only) are not listed in the output files.

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of most statistical packages. Using acronyms therefore facilitates data processing and avoids problems when importing the output files into other programs.

4.3 Landscapes

EDGE may write generated or imported landscapes into ASCII or GIF files if the model parameters SAVE_ASC_LANDSCAPES or SAVE_GIF_LANDSCAPES are set to 1 in the parameter file. Names of the ASCII landscape files correspond to the following structure:

*basename*_land_w*X*_l*Y*_ha*M*_hf*N*.asc

The **basename** is the name of the parameter file without extension. **X** is the value of the parameter GRID_WIDTH, **Y** is the value of the parameter GRID_LENGTH, **M** is the value of the parameter HABITAT_AMOUNT and **N** is the value of the parameter habitat fragmentation. Based on this naming convention, landscapes of different dimensions and with different amounts and degrees of habitat fragmentation can be distinguished. GIF landscape files have identical file names with the extension .gif.

If EDGE imports landscapes as ASCII data files (parameter GRID_FILE), only gif files are written with the same basename as the imported landscape file extended with .gif.

4.4 **Population Abundance**

Abundance of populations over time are recorded when the model parameters ABUNDANCE_1_OBS or ABUNDANCE_2_OBS are set to 1. Response variables for population abundance will then be listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | AB_P1_AV | AB_P1_MI | AB_P1_MA | AB_P1_VA | AB_P1_KO |
| Population 2 | AB_P2_AV | AB_P2_MI | AB_P2_MA | AB_P2_VA | AB_P2_KO |

If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-**AB_P1**-raw.csv or *basename*-**AB_P2**-raw.csv)

4.5 Population Abundance on Habitat and/or Matrix

Population abundances on habitat or matrix are recorded when the model parameters ABUNDANCE_HAB_1_OBS, ABUNDANCE_MAT_1_OBS, ABUNDANCE_HAB_2_OBS or ABUNDANCE_MAT_2_OBS are set to 1 in the parameter file. Response variables for population abundance on habitat will then be listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | HA_P1_AV | HA_P1_MI | HA_P1_MA | HA_P1_VA | HA_P1_KO |
| Population 2 | HA_P2_AV | HA_P2_MI | HA_P2_MA | HA_P2_VA | HA_P2_KO |

Response variables for population abundance on matrix will then be listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | MA_P1_AV | MA_P1_MI | MA_P1_MA | MA_P1_VA | MA_P1_KO |
| Population 2 | MA_P2_AV | MA_P2_MI | MA_P2_MA | MA_P2_VA | MA_P2_KO |

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If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-**HA_P1**-raw.csv, *basename*-**HA_P2**-raw.csv, *basename*-**MA_P1**-raw.csv or *basename*-**MA_P2**-raw.csv).

4.6 Extinction Probability

When population abundance becomes zero during simulation, the population is extinct. EDGE may record the time steps of population extinctions and generate a frequency distribution and cumulative extinction rates across all runs when the model parameters EXTINCTION_1_OBS or EXTINCTION_2_OBS are set to 1. Extinction will be reported by three columns for each population in the aggregated output file.

- 1. EX_P1_CT/ EX_P2_CT are counters of population extinctions across all simulation runs.
- 2. EX_P1_RE/ EX_P2_RE are extinction rates, i.e. counters divided by the number of simulation runs.
- 3. EX_P1_CU/ EX_P2_CU are the cumulative extinction rates. A value of 1 indicates that the population always went extinct at this particular time step.

There is no raw output file for extinction probability.

4.7 Landscape Connectivity

EDGE supports three different measures for landscape connectivity. Patch immigration rate and search time are based on movements between habitat patches. Cell immigration rate is based on movements between habitat cells and considers inter-patch as well as intra-patch movements.

4.7.1 Patch Immigration Rate

Patch immigration rate across all habitat patches at a give time step is the ratio between all cumulated immigration events and the maximum recorded population size. An immigration event occurs when an individual enters a habitat patch for the first time (e.g. the individual started in the matrix) or when it comes from another habitat patch, i.e. successfully moved between two habitat patches. If, for example, 145 immigration events were recorded across all habitat patches and the maximum recorded population size was 45, the patch immigration rate would be 3.22. Patch immigration rates will be recorded if the model parameters HAB_PATCH_IMM_1_OBS or HAB_PATCH_IMM_2_OBS are set to 1 in the parameter file. Response variables for patch immigration rates will be listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | PI_P1_AV | PI_P1_MI | PI_P1_MA | PI_P1_VA | PI_P1_KO |
| Population 2 | PI_P2_AV | PI_P2_MI | PI_P2_MA | PI_P2_VA | PI_P2_KO |

If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-**PI_P1**-raw.csv or *basename*-**PI_P2**-raw.csv). The raw data output file provides an approximate transition matrix between all habitat patches at the end of each time series of each parameter combination.

| Patch Immigra | tion Matrix | | | | |
|---------------|-------------|--------|--------|--------|------|
| | P1_21 | P2_719 | P3_115 | P4_143 | P5_2 |
| P1_21 | 0 | 0 | 0 | 0 | 0 |
| P2_719 | 0 | 0 | 0 | 0 | 5.5 |

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| P3_115 | 0 | 0 | 0 | 0.78571427 | 0 |
|--------|---|------------|------|------------|---|
| P4_143 | 0 | 0.06395349 | 0.44 | 0 | 0 |
| P5_2 | 0 | 0.03197674 | 0 | 0 | 0 |

The numbers in these matrices are average habitat patch immigrations across all simulation runs divided by the average population size of the patches of origin (left column). Due to using average population sizes across time and simulation runs, transition rates may actually be larger than 1. If transition matrices are of interest, it is recommended to run the model in movement mode only (Model parameter EVENT_CYCLE move) to avoid large fluctuations in patch population sizes due to fecundity and survival. Patches are identified by an id and patch size. For example, P1_21 identifies patch #1 with a size of 21 cells. Patch size should facilitate identification of the corresponding patches in GIF landscape maps.

4.7.2 Cell Immigration Rate

Cell immigration rate corresponds to the total number of immigration events into all habitat cells in the landscape, divided by the maximum recorded population size and the number of habitat cells. Only the first visit of an individual in a habitat cell is counted as immigration event. Cell immigration rates will be recorded if the model parameters HAB_CELL_IMM_1_OBS or HAB_CELL_IMM_2_OBS are set to 1 in the parameter file. Response variables for cell immigration rates are listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | CI_P1_AV | CI_P1_MI | CI_P1_MA | CI_P1_VA | CI_P1_KO |
| Population 2 | CI_P2_AV | CI_P2_MI | CI_P2_MA | CI_P2_VA | CI_P2_KO |

If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-**CI_P1**-raw.csv or *basename*-**CI_P2**-raw.csv).

4.7.3 Search Time

Search time corresponds to the average number of movement steps between all pairs of habitat patches in the landscape. The average is calculated over all successful movements of all individuals between any two different habitat patches. Search time will be recorded if the model parameters SEARCH_TIME_1_OBS or SEARCH_TIME_2_OBS are set to 1 in the parameter file. Response variables for search time are listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | ST_P1_AV | ST_P1_MI | ST_P1_MA | ST_P1_VA | ST_P1_KO |
| Population 2 | ST_P2_AV | ST_P2_MI | ST_P2_MA | ST_P2_VA | ST_P2_KO |

If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-**ST_P1**-raw.csv or *basename*-**ST_P2**-raw.csv).

4.8 Dispersal Distance

Dispersal distance corresponds to the average straight movement distance of all individuals. Dispersal distances are calculated from individual's starting locations to their current location (at the time step of observation) or to their final location (when an individual dies). Dispersal distances will be recorded if the model parameters DISPERSAL_1_OBS or DISPERSAL_2_OBS are set to 1 in the parameter file. Response variables for dispersal distance are listed in the aggregated output file with the following column names:

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| | Average | Minimum | Maximum | Variance | Confidence Interval |
|--------------|----------|----------|----------|----------|---------------------|
| Population 1 | DI_P1_AV | DI_P1_MI | DI_P1_MA | DI_P1_VA | DI_P1_KO |
| Population 2 | DI_P2_AV | DI_P2_MI | DI_P2_MA | DI_P2_VA | DI_P2_KO |

If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-**DI_P1**-raw.csv or *basename*-**DI_P2**-raw.csv).

4.9 Boundary Crossing Rate

The boundary crossing rate is the number of all individual boundary crossings between any two different landcover types (i.e. habitat -> matrix or matrix -> habitat in EDGE-1.0) divided by the number of all individual movement steps. Boundary crossing rates will be recorded if the model parameters CROSS_HAB_MAT_1_OBS, CROSS_MAT_HAB_1_OBS, CROSS_HAB_MAT_2_OBS or CROSS_MAT_HAB_2_OBS are set to 1 in the parameter file. Response variables for boundary crossing rates are listed in the aggregated output file with the following column names:

| | Average | Minimum | Maximum | Variance | Confidence Interval |
|----------------------------------|----------|----------|----------|----------|---------------------|
| Population 1 : Habitat -> Matrix | C1_HM_AV | C1_HM_MI | C1_HM_MA | C1_HM_VA | C1_HM_KO |
| Population 1 : Matrix -> Habitat | C1_MH_AV | C1_MH_MI | C1_MH_MA | C1_MH_VA | C1_MH_KO |
| Population 2 : Habitat -> Matrix | C2_HM_AV | C2_HM_MI | C2_HM_MA | C2_HM_VA | C2_HM_KO |
| Population 2 : Matrix -> Habitat | C2_MH_AV | C2_MH_MI | C2_MH_MA | C2_MH_VA | C2_MH_KO |

If SAVE_DETAILS is set to 1 in the parameter file, EDGE will write a raw data output file for each response variable (*basename*-C1_HM-raw.csv, *basename*-C1_MH-raw.csv, *basename*-C2_HM-raw.csv or *basename*-C2_MH-raw.csv).

4.10 Landscape Indices

EDGE may also calculate and report a few landscape indices if the model parameter LAND_INDICES_OBS is set to 1 in the parameter file. The following landscape indices will be reported in the aggregated output file:

| Name | Acronym | Comment |
|---------------------------|----------|---------------------------|
| Degree of Fragmentation | F_GRAD | developed by J. Jaeger |
| Density of Fragmentation | F_DENSIT | developed by J. Jaeger |
| Fragmentation index | F_INDEX | developed by J. Jaeger |
| Effective Meshsize | MESHSIZE | developed by J. Jaeger |
| Habitat Patch Cohesion | PTCH_COH | developed by M. Schumaker |
| Number of Habitat Patches | PATCHES | |
| Habitat Edge/Cover Ratio | EDG/COV | |
| Total Habitat Edge | EDGE | |
| Total Habitat Amount | COVER | |

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5 Model Operation

5.1 Running EDGE-1.0

Copy the following files into one folder on your computer:

- edge1.exe
- parameter file (e.g. test.par)
- ASCII landscape files (if defined in parameter GRID_FILE)

Open a DOS or Unix shell on your computer and navigate to the folder where the above mentioned files are stored. Execute EDGE-1.0 by typing "edge1.exe test.par" after the DOS or Unix prompt in your shell. Adjust the name of the parameter file if it differs from this example. EDGE-1.0 will write output to the screen indicating progress of execution.

INFO [02/15/2005 12:18:31] (1/128)

INFO [02/15/2005 12:19:12] (2/128)

The first number in the () bracket shows the current parameter combination and the second number shows the total number of parameter combinations. In this example the factorial simulation experiment would consist of 128 parameter combinations.

After successful completion, the output files as described in section 4 can be viewed and further processed.

5.2 Important Considerations

When running EDGE, consider the following suggestions:

- activate only observers for response variables, which are needed, recording response variables and writing data to output files uses computation time and slows down overall execution speed
- increase recording intervals (parameter OBS_GAP) to reduce simulation output, if time series are not needed and a large number of parameter combinations are executed, MS Excel can read files up to 65.000 lines only
- avoid very large grids/landscapes, grid sizes of 200x200 cells are usually sufficient for most experiments
- calculate and adjust carrying capacity of the landscape (see section 2.2) to avoid exponential population growth, large populations use more memory and slow down simulation speed
- avoid Cell Immigration and Patch Immigration observers with grid sizes larger than 100.000 cells, observers themselves use memory and slow down simulation speed

5.3 License

EDGE is released under the GNU General Public License. This means, EDGE is free software and will be released with the source code to allow for free and unrestricted redistribution and/or modification under the terms of the GNU General Public License. This particular license is inherited from third party libraries EDGE is build on.

5.4 System Requirements

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EDGE-1.0 should run on any MS Windows OS, such as NT, ME, 98, 2000, XP⁶. EDGE-1.0 has been tested on Windows XP. The program edge1.exe requires about 600 KB free space on the hard drive, but may need much more during operation and for storing results. One should have 1 GB free space available on the hard drive when running edge1.exe. EDGE-1.0 will use up to 50 MB of RAM, but may use much more, in particular when using large grids and large populations.

⁶ EDGE-1.0 will shortly be available for Linux and Solaris operating systems.

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5.5 Logging

EDGE writes detailed information into a file named 'edge.log'. This file will be rotated after exceeding 10 MB. Logging information is useful for the author and will help to track and to identify potential errors or problems with EDGE.

5.6 Trouble Shooting

EDGE-1.0 has been thoroughly tested under the Windows XP operating system, in particular with respect to memory leaks, functional stability and functional accuracy. If, for some reason, EDGE-1.0 does not 'behave' as described in this user guide, first verify the parameter file and the data format in the ASCII landscape files (if used). If you believe to have detected a problem, please send a short description together with the edge.log file and all input data to the author.

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6 Appendix

6.1 Sample Parameter File

/* input mode: 0 for factorial combination, 1 for random selection between min und max settings*/ PARAMETER_MODE 0

/* sets the number of combinations for random selection [1 .. 100000] */ RANDOM COMBINATIONS 1000

/* random number seed, 0=system time (pseudo random) or > 0, fixed random seed */ START_SEED 0

/* replications for factorial combination or random selection mode [1 .. 1000] */ RUNS 50

/* total number of years in the simulation [1 .. 1000] */ YEARS 50

/* number of divisions per year, the maxium is [1 .. 12] */ YEAR_DIV 6

/* marks YEAR_DIV step of reproduction, [1 .. YEAR_DIV] */ REPRO_STEP_1 2 REPRO_STEP_2 4

/*** provide filenames for ASCII raster files (habitat=1, matrix=0) in the same folder */ GRID_FILE

/*** grid width and length [1..1000] */ GRID_LENGTH 100 GRID_WIDTH 100

/*** border types for moving individuals [torus, absorb, reflect] */ GRID_BORDER torus

/*** adjacent cells belong to one patch [orthogonal, diagonal] */ CELL_ADJACENCY diagonal

/*** percentage of habitat cells in the grid [0.01 .. 0.9] */ HABITAT_AMOUNT 0.1 0.2

/* probability of a cell becoming habitat if neighbouring*/ /*** cells are matrix [0.01 .. 1.0] */ HABITAT_FRAGMENTATION 0.01

/*** maximium number of resources available per cell [1 .. 10000] */ MAX_RESOURCES_PER_CELL_HAB 2 MAX_RESOURCES_PER_CELL_MAT 2

/* reduction value when the cell reaches maximum capacity */ /* For example, if the maximum capacity is 100 and the */ /* reduction value is 0.1, then once a cell reaches 100 individuals, it */ /*** would be reduced down to 10 individuals [0.0 .. 1.0] */ REDUCTION_FACTOR_HAB 0.3 REDUCTION_FACTOR_MAT 0.1

/*** starting number of populations [0 .. 100000] */ START_NUM_1 100 START_NUM_2 100

/*** initial distribution of populations [landscape, habitat, matrix] */ INIT_1 habitat INIT_2 landscape

/*** resources factor for each population in habitat (factor * individuals = resources used in a cell) [0.0 .. 1000.0] */ RESOURCES_FACTOR_1_HAB 3 RESOURCES_FACTOR_2_HAB 2

/*** resources factor for each population in non-habitat (factor * individuals = resources used in a cell) [0.0 .. 1000.0] */ RESOURCES_FACTOR_1_MAT 1 RESOURCES_FACTOR_2_MAT 1

/*** probability of survival per individual per step in habitat [0.0 .. 1.0] */ SURVIVAL_1_HAB 0.7 0.8 SURVIVAL_2_HAB 0.8 0.9

/*** probability of survival per individual per step in matrix [0.0 .. 1.0] */

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| SURVIVAL_1_M SURVIVAL_2_M | A <i>T 0.4</i> | | | |
| /*** mean distanc MOVE_DIST_1_I MOVE_DIST_2_I | HAB 2 | ibution per movement step in habitat [0.0 1 | 00.0] */ | |
| /*** mean distanc MOVE_DIST_1_I MOVE_DIST_2_I | MAT 6 | bution per movement step in matrix [0.0 10 | 00.0] */ | |
| /*** range of sym MOVE_ANGLE_ MOVE_ANGLE_2 | 1_HAB 3.14159 | ovement step in habitat [0.0 3.14159] */ | | |
| /*** range of sym MOVE_ANGLE_ MOVE_ANGLE_2 | 1_MAT 1 2 | ovement step in matrix [0.0 3.14159] */ | | |
| /*** mean numbe FECUNDITY_1_F FECUNDITY_2_F | | Poisson) [0.0 1000.0] */ | | |
| /*** mean numbe FECUNDITY_1_I FECUNDITY_2_I | | Poisson) [0.0 1000.0] */ | | |
| /*** boundary cro CROSS_1_HAB_ CROSS_1_MAT_ CROSS_2_HAB_ | HAB 0.7 | ion 1 and 2 [0.0 1.0] */ | | |
| CROSS_2_MAT_ | HAB 0.5 | | | |
| | ience [random, or combination repro death move | n of: repro and/or move and/or death] */ | | |
| SAVE_GIF_LANL SAVE_ASC_LAN SAVE_DETAILS /* Recording inter | IDSCAPES 1 | . YEARS * YEAR DIV] */ | | |
| OBS_GAP 10 | | | | |
| ABUNDANCE_1 ABUNDANCE_2 EXTINCTION_1_ EXTINCTION_2_ | OBS 1 OBS 1 | | | |
| ABUNDANCE_H, ABUNDANCE_H, ABUNDANCE_M ABUNDANCE_M | AB_2_OBS 1 IAT_1_OBS 1 | | | |
| HAB_CELL_IMM HAB_CELL_IMM HAB_PATCH_IM HAB_PATCH_IM SEARCH_TIME_ SEARCH_TIME_ | _2_OBS 1 M_1_OBS 1 M_2_OBS 1 1_OBS 1 | | | |
| DISPERSAL_1_0 DISPERSAL_2_0 | | | | |
| CROSS_HAB_M. CROSS_MAT_H. CROSS_HAB_M. CROSS_MAT_H. | AB_1_OBS | | | |
| LAND_INDICES_ | OBS 1 | | | |
| | | | | |
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| Lutz Tischendorf | ELUTIS – Modelling and Consulting Inc. 681 Melbourne Avenue, Ottawa, Ontario, K2A 1X4, CANADA | 20 of 20 |