Ecography

Supplementary material

Appendix 1

Model description

The model used in this study is based on empirical knowledge on the ecology and population dynamics of the hairy-footed gerbil (Ascaray and McLachlan 1990; Ascaray et al. 1991; Perrin and Boyer 1996; Skinner and Chimimba 2005 and references therein; Blaum et al. 2007) and has been validated by own empirical investigations (Blaum et al. 2007; Blaum and Wichmann 2007).

This model description follows the ODD protocol (overview, design concepts, and details) for describing individual- and agent-based models (Grimm et al. 2005; Grimm et al. 2006) and consists of seven elements. The first three elements provide an overview, the fourth element explains general concepts underlying the model's design, and the remaining three elements provide details. Please also refer to Figure 1 in the main text.

1) Purpose

The purpose of the model is to analyse how the intensity of interannual variation in rainfall affects the genetic difference between two subpopulations of a Kalahari rodent in two neighbouring pristine savannah habitats that are separated by an inhospitable shrub matrix.

2) Entities, state variables, and scales

The model consists of two neighbouring subpopulations (SP) of a rodent species and an inhospitable matrix between them. The model species is diploid and has one locus with two alleles, A and B.

The SPs are simulated spatially implicit and are characterized by their population size and by the frequencies of individuals with allele compositions AA, AB and BB.

The matrix is simulated spatially explicit by a grid of 84 ha (24 by 35 cells) with a cell size of 0.1 ha corresponding to an average male home range size (Ascaray and McLachlan 1990). The SPs border on the opposite short edges of the matrix along 8 grid cells where animals can cross between the matrix and the SPs. Thus, the distance between the SPs is 1.155 m.

The population processes in the matrix are simulated individual based. Each matrix cell can contain up to 6 reproducing individuals that differ by their sex, age, pair status (unpaired or paired with another individual) and genotype (AA, AB or BB).

The model environment is characterized by the amount of rainfall in a time step that affects the population processes in the SPs and in the matrix. The changing habitat quality of the matrix is defined by a variable that describes the food availability (mainly grass biomass) in the matrix in a time step and that is dependent on rainfall.

The model proceeds in three months time steps, corresponding to the generation time of gerbils (Ascaray et al. 1991). A simulation run lasts 100 years.

3) Process overview and scheduling

In each time step, the population dynamics is simulated in the order: population dynamics in the SPs, emigration of individuals from the SPs into the matrix, population dynamics in the matrix, and immigration of individuals from the matrix into the SPs.

Population dynamics in the SPs - The population dynamics in each subpopulation i is simulated in two steps. First, the new population size N_i^{t+1} in the next time step is determined by a commonly used density dependent population model (Maynard-Smith and Slatkin 1973) that includes environmental stochasticity caused by the variation in rainfall and demographic stochasticity. Then individual numbers of emigrating individuals, dying individuals, and newborn individuals are calculated in a way that the

targeted subpopulation size N_{it+1} is met. The emigrating, dying and new born individuals are assigned a random genotype with probabilities equal to the ratio of the genotypes at the beginning of each of these processes, and the genetic structure of the subpopulation is updated. Simulating death and birth in the subpopulations in this way ensures a certain degree of population turnover and thus a change in the genetic structure of the subpopulations during one time step.

Emigration into the matrix - Individuals emigrating from the subpopulations enter the matrix and are assigned a random sex and age and carry a genotype as determined before.

Population dynamics in the matrix - In the matrix, the food availability is updated in the beginning and at the end of a time step. Individuals move between grid cells, mate if they meet individuals of the opposite sex in a grid cell, reproduce, age and may die. These processes are scheduled in the named order. For scheduling individual movement and mating, grid cells containing individuals are picked in a random order, and all individuals in a grid cell move and mate one after another in a random order. One individual finishes moving and mating before the next individual moves.

Immigration into the SPs - Individuals that had left the matrix at the border to one of the SPs during movement enter the SP.

4) Design concepts

i) Emergence: The model was designed to let the genetic difference between the two SPs emerge from the effect of rainfall on the population dynamics in the subpopulations and in the matrix, and on the population exchange between the three. As gene flow between the two SPs is driven by successful survival, reproduction and dispersal in the matrix, we focussed the model design on a detailed implementation of the processes in the matrix.

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ii) Sensing: Individuals in the matrix move, reproduce and survive randomly or driven by the environment. Only the presence of conspecifics while mating is perceived.

iii) Interactions: Intraspecific competition and density dependence are considered in the SPs and in the matrix. In the SPs, population growth and emigration are density dependent. In the matrix the number of individuals that can reproduce in a grid cell is ceiled.

iv) Stochasticity: The model is mostly driven by environmental stochasticity given by the amount of rainfall in a time step. Demographic stochasticity is considered in all demographic processes. Characteristics and decisions of individuals are modelled stochastically on an individual basis.

v) Observations: Following the objective of the model, we observed the genetic difference between the two SPs, measured as Fst in the last year of a model run. To explain the emergence of the genetic difference, we observed the frequency of gene flow between the SPs averaged over a model run, the population size in the matrix averaged over a model run, the number of years without individuals in the matrix in a model run, and the frequency distribution of rainfall. All quantities are observed at the end of a time step.

5) Initialisation

Each SP is initialised with 75 individuals corresponding to the mean carrying capacity of the SPs. All individuals are homozygous for the simulated locus with AA in SP1, and BB in SP2, resulting in $F_{ST} = 1.0$. The matrix does not harbour any individuals. The food resource in the matrix is set equal to the mean rainfall in a time step.

6) Input

The model is driven by the amount of rainfall e_t in a three month time step that affects

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population growth of the SPs and reproduction and survival of individuals in the matrix. The amount of rainfall e_t is determined by first drawing the annual amount of rainfall from a truncated normal distribution with mean and CV systematically varied by the simulation scenarios (see main text). The normal distribution is truncated between zero and twice its mean to avoid both, values below zero and unrealistically high values. The annual rainfall values are transformed into quarterly values (corresponding to the time step of the model) by distributing the total amount of annual rainfall equally over the 6 months rainy season while rainfall in the 6 months dry season is set to zero.

7) Submodels

A   POPULATION DYNAMICS IN SPS

Population size

1. The population size N_{it} of subpopulation i is determined by a commonly used density dependent population model (Maynard-Smith and Slatkin 1973) that includes environmental and demographic stochasticity. The expected population size at certain environmental conditions is given by:

$$E(N_{t+1} \mid N_t, K_t) = N_t \cdot \frac{R}{1 + (R-1) \cdot \left(\dfrac{N_t}{K_t}\right)^b}$$

   where R is the population growth rate fixed at 1.2, K_t is the carrying capacity subject to environmental stochasticity, and b is a competition parameter fixed at 1.8.

2. Environmental stochasticity is introduced by letting the carrying capacity K_t deviate from the mean carrying capacity $K_m = 75$ according to the deviation of the current precipitation e_t from its mean e_m: $K_t = K_m \cdot e_t / e_m$. In addition, the carrying capacity K_t is truncated between 0.33 and 3 K_m in order to avoid population extinction and unrealistically high population sizes.

3. Demographic stochasticity is introduced by drawing the population size N_{t+1} from a Poisson distribution with the expectation $E(N_{t+1}| N_t, K_t)$.

4. The population size N_{it+1} is targeted by the following processes emigration, mortality and birth.

Emigration

1. Individuals of the population of size N_{it} leave the subpopulation i with a density dependent probability if the population size at the beginning of the emigration process exceeds 50% of the carrying capacity K_t. The emigration probability of an individual j is given by

$$pE_{itj} = min\left(2 \cdot \left(\frac{N_{sbDj}}{K_t}\right)^2, 1\right) \; if \; \left(N_{sbDj} > 0.5 \cdot K_t\right); \; else: 0$$

where N_{itj} is population size as perceived by disperser j that is updated after every individual decision, starting at population size N_{it}.

2. Emigrating individuals are assigned a random genotype with probabilities equal to the ratio of genotypes before emigration.

Mortality and birth

1. The remaining individuals after emigration die with a probability of 0.75. If the number of individuals after emigration and mortality is still larger than the target population size N_{it+1} the surplus individuals leave the population as additional emigrants.

2. The number of newborn individuals is set in a way that emigrating and dying individuals are replaced and the target population size N_{it+1} is met.

3. Dying and newborn individuals are assigned a random genotype with probabilities equal to the ratio of genotypes before the respective process.

B   EMIGRATION FROM THE SUBPOPULATIONS INTO THE MATRIX

1. Emigrants from the SPs enter the matrix as dispersers at a random point in a transition zone that borders their origin SP. Two transition zones are located at the eight middle cells of the matrix edges next to the SPs. New dispersers move between one and three spatial steps into the matrix, the number of steps being randomly chosen.

2. The new dispersers are assigned a random sex following a sex ratio of 1:1, a mating status "unpaired", and a random age chosen from a realistic age structure with probabilities:

Age (time steps)	Probability
2	0.5
3	0.25
4	0.125
5	0.125

C   POPULATION DYNAMICS IN THE MATRIX

Food availability

1. The grass biomass in the matrix depends on the grass biomass in the previous time step and on the current primary production driven by rainfall. Thus the food availability in the matrix was modelled in arbitrary units as $food_t = food_{t-1} + e_t$ where e_t is the amount of rainfall in the current time step.

2. During each time step food is eaten by the study species and by other species. At the end of a time step $food_t$ is decreased as follows:

> if $(food_t \leq 50)$ $food_t = 5$;
> if $(50 < food_t \leq 75)$ $food_t = -35 + 0.8 * food_t$;
> if $(75 < food_t \leq 100)$ $food_t = 25$;
> if $(100 < food_t \leq 150)$ $food_t = -75 + food_t$;
> if $(food_t > 150)$ $food_t = 75$;

Movement

1. Individuals can move 5 spatial steps per time step. One spatial step refers to a move from the current matrix cell to one of the four neighbouring cells (or beyond the matrix edge).

2. Individuals favour reproduction over continuing dispersal. They do not continue to move if (a) they form a potentially reproducing pair in the current cell, (b) they get paired in this cell in the current time step.

3. Density regulation: Individuals that can only reach cells that are occupied at their carrying capacity (6 reproductive individuals) are removed.

4. Individuals leaving the matrix from a transition zone to a SP enter this SP (see D). Individuals leaving the matrix outside of a transition zone are lost from the system.

5. Movement directions are simulated in a correlated random walk. The correlated random walk is realized by defining a variable *dr* ranging between 0 and 11 that determines the direction of the current spatial step as:

dr	results in matrix movement towards
11, 0, 1	up
2, 3, 4	right
5, 6, 7	down
8, 9, 10	left

Values for *dr* are drawn from a Gaussian distribution with mean *dr* of the previous step and variance $v = 2.368$. If numbers >11 or <0 are drawn 11 is subtracted or added, respectively. Using three different values of *dr* for a certain direction results in different probabilities to move into the same or into a different direction as in the previous step. E.g., $dr = 3$ results in a high probability to move into the same direction while $dr = 4$ or 2 results in a high probability to change direction.

Mating

1. Unpaired individuals of opposite sex that meet in cells that are occupied below the carrying capacity do mate (and according to C2 stay in current cell).

2. The mating system is polygynous. Males may mate with an unlimited number of females being in the same cell (maximum 5 due to carrying capacity) whereas females can only mate with one male.

3. Only a limited number of dominant males can mate. The longest inhabitant of a cell has first priority to mate.

Reproduction

1. Each mated female produces a litter with 0 to 6 offspring (Ascaray et al 1991). The actual litter size depends on the food availability in the matrix. The mean litter size yg_t in a time step is determined by a function f of $food_t$ (taking into account potentially eaten food in the current time step $food_e$=75).

$$f(food_t) = -0.0991 + 6.8072 \cdot \left[1 - e^{-0.009 \cdot (food_t - food_e)}\right]$$

$$yg_t = min\left(max\left(f\left(food_t\right); 0\right); 6\right)$$

The litter size of a female is drawn from a binomial distribution with $N = 6$ and $p = yg_t / 6$.

2. Offspring inherit the alleles A and B from their parents. The assignment of the offspring's genotype (AA, AB or BB) is stochastic following Mendel's laws.

Aging

1. After movement and reproduction the age of each individual is incremented by one.

Mortality

Individuals survive with an age specific survival probability which is low for offspring and higher for adults but then subject to senescence. The maximum age of an individual is 20 time steps i.e. 5 years (Ascaray et al 1991). The age specific survival probabilities are set to (Ascaray et al 1991):

$surv[1] = 0.05$; $surv[2] = 0.5$; $surv[3] = 0.85$; $surv[4] = 0.85$;

$surv[5] = 0.8$; $surv[6] = 0.8$; $surv[7] = 0.8$; $surv[8] = 0.8$;

$surv[9] = 0.75$; $surv[10] = 0.75$; $surv[11] = 0.75$; $surv[12] = 0.75$;

$surv[13] = 0.7$; $surv[14] = 0.7$; $surv[15] = 0.7$; $surv[16] = 0.7$;

$surv[17] = 0.65$; $surv[18] = 0.65$; $surv[19] = 0.65$; $surv[20] = 0.0$;

In addition, the survival probability is dependent on the food availability in the matrix by adding $surv'[age]_t = surv[age] + food_t / e_m$ and truncating surv'[age]t between 0 and 1.

D   IMMIGRATION FROM THE MATRIX INTO THE SUBPOPULATIONS

1.   Individuals that had left the matrix from a transition zone (see B) during movement enter the bordering SP.

2.   The population sizes and the frequencies of genotypes in the SPs are updated accordingly.

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