Ecography

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Cobben, M. M. P., Verboom, J., Opdam, P. F. M., Hoekstra, R. F., Jochem, R., Arens, P. and Smulders, M. J. M. 2011. Projected climate change causes loss and redistribution of genetic diversity in a model metapopulation of a medium-good disperser. – Ecography 34: xxx–xxx.

Appendix 1

Detailed model description

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom et al. 2001, Vos et al. 2001). The model has been extended to allow for stochastic temperature zone shifts by Schippers et al. (2011). Here a new extension provided each individual in this study with a genome of 10 unlinked diploid genes (for more detailed information see Appendix 2).

Neutral population genetics in our model is the result of population demography. There is no reciprocal effect of genetics on demography. The yearly metapopulation demography is simulated based on four events: reproduction, dispersal, survival and aging, in this order. Reproduction, dispersal and survival are based on population density and habitat quality. Habitat quality is controlled by time and location specific temperature. As such we simulate the effect of stochastic temperature zone shifts on neutral genetic diversity.

Landscape

The landscape we used in the model had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape. The landscape contained 3000 circular habitat patches of 50 ha each, so consisted of a total of 5% habitat. When generating the landscape, patches were placed in random positions in the landscape, yet only allowed if they were at a minimum distance of 150 m from existing patches. Five landscape variants with different habitat positions were randomly generated in this way.

Species

We modelled a woodland bird, parameterised as the middle spotted woodpecker *Dendrocopus medius*. Parameters were based on biological information (Pettersson 1985a, b, Hagemeijer and Blair 1997, Pasinelli 2000, Kosenko and Kaigorodova 2001, Michalek and Winkler 2001, Kosinski et al. 2004, Kosinski and Ksit 2006) and on the interpretation by Schippers et al. (2011) (Table 1). The model distinguishes 2 sexes and 2 lifestages: adults and juveniles. The yearly life cycle consists of recruitment, dispersal, and survival, in this order. Lastly, all juveniles age to adults. Recruitment, dispersal and survival are all dependent of life stage, population density (PD) and habitat quality (HQ).

PD = I/CC

with I: number of individuals in patch, CC: carrying capacity of patch, and HQ: see section Climate in this appendix.

Recruitment function

The number of nests in a patch in each generation is equal to the number of unique adult pairs of opposite sex in this patch, with a maximum of 10. The number of offspring per nest is then found with:

$$N_{\rm O} = N_{\rm O_PD0HQ1} * (1 - (1 - N_{\rm O_PD0HQ0} / N_{\rm O_PD0HQ1}) * (1 - HQ)) * (1 - (1 - N_{\rm O_PD1HQ1} / N_{\rm O_PD0HQ1}) * PD)$$

with N_{O_PD0HQ1} : survival rate at population density (PD) = 0 and habitat quality (HQ) =1, and similar for N_{O_PD0HQ0} and N_{O_PD1HQ1} ; Table 1.

Dispersal function

Determines for each individual the yearly chance that it leaves its patch to go on dispersal, P_D.

$$P_{\rm D} = P_{\rm D_PD0HQ\,1} * (1 - (1 - P_{\rm D_PD0HQ\,0} / P_{\rm D_PD0HQ\,1}) * (1 - HQ)) * (1 - (1 - P_{\rm D_PD1HQ\,1} / P_{\rm D_PD0HQ\,1}) * PD)$$

with P_{D_PD0HQ1} : dispersal rate at population density (PD) = 0 and habitat quality (HQ) =1, and similar for P_{D_PD0HQ0} and P_{D_PD1HQ1} ; Table 1.

Survival function

Determines for each individual the chance that it survives the current year, P_s.

$$P_{S} = P_{S_PD0HQ1} * (1 - (1 - P_{S_PD0HQ0} / P_{S_PD0HQ1}) * (1 - HQ)) * (1 - (1 - P_{S_PD1HQ1} / P_{D_PD0HQ1}) * PD)$$

with P_{S_PDOHQ1} : survival rate at population density (PD) = 0 and habitat quality (HQ) =1, and similar for P_{S_PDOHQ0} and P_{S_PDOHQ0} ; Table 1. If an individual disperses, we need to determine where it goes. From their origin patch individuals can go in every direction, along a straight line. Connectivity to other patches is determined by destination patch radius (r) and distance to there (d). So the chance to disperse from patch A to patch B is:

$$P_{AB} = \frac{2 * arcsin\left(\frac{r_B + 1}{d_{AB}}\right)}{2\pi}$$

with l is 150 m, the maximum distance from where an individual can detect suitable habitat. The maximum dispersal distance is 15 km, so habitat patches that are separated by more than this distance are not connected at all. Our model does not allow dispersers to ignore a nearer patch, so more distant patches are located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and is then allowed to disperse again. Should it fail to reach a habitable patch within a total of three dispersal rounds, it dies.

Climate

Climate is incorporated in the model through habitat quality. Where climate is optimal for the species, habitat quality equals 1, and where climate is unsuitable for the species, habitat quality is 0 (see equation HQ below). Climate change scenarios are based on temperature increase predictions (I °C yr⁻¹) by the Hadley Centre of 0.0167 and 0.0333 °C yr⁻¹, and we also included a scenario with a temperature increase of 0.084 °C yr⁻¹. Besides, the used scenarios include weather variability increase assumptions as temporal stochasticity in the temperature (the current standard deviation of the average temperature $\sigma_{\rm t}$ (°C), 0.59 °C (Schippers et al. 2011). Climate in our model is thus defined as the temperature in year t and at location Y. Climate change is then the speed with which temperature isoclines travel north (T km yr⁻¹) and the yearly fluctuation of these lines ($\sigma_{\rm d}$ km). We use a climatic gradient from south to north of G (°C km⁻¹) to get to:

$$T = I/G$$

and

$$\sigma_{d} = \sigma_{r} / G$$

This results in a current yearly fluctuation of the temperature isoclines σ_d of 140 km, and we further included scenarios with yearly fluctiations σ_d of 0 km and 280 km. We can then calculate the location of the optimal temperature in north-south direction (Y_{opt}) in a certain year as:

$$Y_{opt,t} = Y_{opt,0} + T * t + \sigma_d * N_t$$

with N_t is the yearly random number drawn from a standard normal distribution.

We obtain a normal habitat quality distribution with this optimal coordinate Y_{oot} in its centre by defining habitat quality (HQ) as

$$HQ_{patch,t} = exp \left\lceil \frac{-0.695(Y_{opt,t} - Y_{patch})^2}{H^2} \right\rceil$$

H is an indicator of the temperature tolerance of the species, and defined as the distance from the temperature optimum at which habitat quality is 0.5; Table 1.

Initialisation

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles per locus for 10 different, unlinked loci (for more detailed information see Appendix 2). The climate optimum Y_{opt} was initialised at 400 km from the southern landscape edge.

Burn-in

After initialisation the model was run for 3000 generations, thus 3000 yr (for more detailed information see Appendix 2). During these 3000 yr burn-in, the model runs with temperature isocline speed T equaling 0 in the equation for $Y_{opt,t}$. After this burn-in we started our experiments.

Experiments

In the experiments the temperature isoclines were simulated to move northward for 600 yr, under the different scenarios in Table 1. Each parameter setting was run twice in each landscape variant (10 runs in total). For studying trends in numbers of individuals and alleles, we averaged these per parameter setting. For individuals we averaged over the two runs of the five landscape variants, for alleles we also averaged over the 10 loci.

Appendix 2

Genetic make-up and protocol

The model species is diploid and its DNA consists of 10 unlinked loci (representing 1 locus at each of 10 different chromosomes). At initialisation of the model, each individual was randomly given 2 alleles per locus. All alleles are neutral and thus have no effect on individual performance. The mutation rate per generation in the model is 10^{-4} , equal to the estimated mutation rate for medium-sized microsatellites per haplotype per generation (Whittaker et al. 2003).

Since we wanted to monitor the level and distribution of genetic diversity under climate change, we first needed to establish equilibrium population genetics in the metapopulation. We regarded three aspects of population genetics: 1) the number of unique alleles, 2) the population structure, which is represented by the average differentiation among populations within the metapopulation, F_{SP} and 3) the frequency distribution of the alleles.

- 1) In search for the number of alleles this metapopulation can contain under stable conditions, we tried various initialisations (see Initialisation and Burn-in in Appendix 1). When we tried burn-ins of several hundreds generations initialised with 250, 100, and 50 unique alleles, randomly distributed among the initial individuals, we observed that the numbers of unique alleles steadily declined during these simulations. We then initialised with only 20 unique alleles and gave new alleles created through mutation a value between 21 and 50 in order to be able to observe them. In a simulated 1000 generations burn-in the equilibrium level of unique alleles was established after approximately 500 generations at approximately 33. When we tried to generate this equilibrium level of approximately 33 alleles by starting with a single allele, this took much longer, > 20 000 generations.
- 2) For a stable population structure we ran a burn-in of 20 000 generations and observed that the average F_{ST} value stabilised already after 2000 generations.
- 3) During burn-in runs, the allele frequency distribution tended towards a lognormal decline in allele frequencies from the most common to the least common allele (comparative to Ewens (1972) for the situation θ >>1, where he observes a comparatively large number of low-frequency alleles). At most loci this distribution established after approximately 2000 generations. When we initialised with a single allele, this distribution establishment was not found within 20 000 generations of burn-in.

Based on these results we decided to initialise each model run with unique allele numbers ranging from 1 to 20. Mutations were given values between 21 and 50, to be able to distinguish between initial alleles and newly mutated alleles. We then allowed before each experiment a generous burn-in of 3000 generations, which established equilibrium F_{ST} values and allele frequency distributions.

Appendix 3

Extra figures

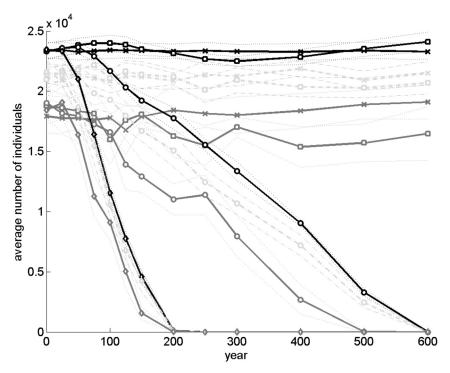


Figure A3-1a. Average number of individuals per year for all combined temperature isocline speeds 0 (-x–), 2 ($-\Box$ –), 4 ($-\Box$ –), and 8 ($-\Diamond$ –) km yr⁻¹, and random weather variabilities of 0 (black), 140 (light gray) and 280 (dark gray) km. Dotted lines indicate confidence intervals.

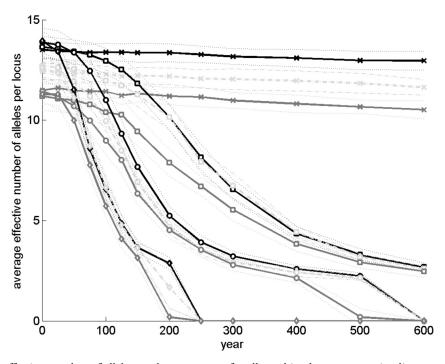


Figure A3-1b. Average effective number of alleles per locus per year for all combined temperature isocline speeds 0 (-x–), 2 ($-\square$ –), 4 ($-\square$ –), and 8 ($-\square$ –) km yr⁻¹, and random weather variabilities of 0 (black), 140 (light gray) and 280 (dark gray) km. Dotted lines indicate confidence intervals.