The evolution of local adaptation

Background

Most species are not uniform entities, where each individual shares the same genotype. Instead, species show intra-specific genetic variation. One example of genetic variation is local adaptation, when locally adapted individuals have a higher fitness in their home patch as compared to incoming individuals from other patches. Local adaptation is a widespread phenomenon, with pronounced fitness differences between residents and incoming individuals, and is of considerable interest for nature conservation, agriculture, or forestry. More generally, local adaptation is one adaptive strategy to cope with spatially heterogeneous environment when local genetic adaptations allow individuals to increase fitness in certain habitat patches. The evolution of local adaptation, however, is rarely perfect and many processes can limit its scope.

The population

Consider a single species that inhabits two habitat patches (indexed 1 and 2). The species shows constant carrying capacities in both patches (N_1 and N_2) where both carrying capacities are identical (when N_1=N_2). Within patches, we assume random mating. Dispersal between patches happens by individuals, not gametes. The two patches differ in some environmental parameter (e.g., temperature, rainfall, pH, …) that demands different genetic adaptations to maximize local survival and reproduction. We model a diploid species where a single locus sets the fecundity of each individual, and controls the evolution of local adaptation. At this locus, two alleles segregate (allele *A* and *B*, a classic one-locus-two-alleles scenario). Allele *A* allows to adapt to patch *1* (e.g, promotes adaptation to hot and dry conditions), allele *B* is favored in patch *2* (e.g., cold and humid conditions). In the first year, both alleles occur at the same frequencies in both patches (p_A = 0.5, p_B = 0.5).

The annual events

In this project, you will study the evolution of local adaptation over the course of years. Each year, the following events unfold consecutively:

1. dispersal

At the beginning of each year, adult individuals disperse to the respective other patch with probability *m*, and stay in their home patch with probability *1-m*.

2. gamete production

Each adult individual produces a large number of haploid gametes that stay in the local patch. The gamete production depends on the match between the genotype of the adult and the environment in the local patch. The fitness of adults follows the classic population genetic formalism (see Table 1).

The selection coefficient (*s*) describes how strongly selection acts against maladapted genotypes. For instance, an adult that is homozygous for *A* (with an *AA* genotype) in patch 2 produces on average f_{max} *(1 – s)* gametes. The larger the selection coefficient, the smaller is the gamete production of maladapted genotypes. Instead, maximum fecundity is reached with a selection coefficient of $s = 0$.

The dominance coefficient *h* determines the fate of heterozygote individuals. Here, we assume that h=0.5 and fitness being additive such that heterozygote individual has exactly a fitness (f_{max} *(1 - 0.5 s)*) inbetween the adapted genotype (f_{max}) and the maladapted genotype (f_{max} *(1-s)*). With *h=1*, the *B* allele is dominant and the *AB* genotype would have the same fitness as the *BB* genotype. Instead, the *A* allele is dominant with $h=0$ when *AA* and *AB* have the same fitness. However, we only consider the additive model with $h=0.5$ in the baseline scenario.

Specifically, individual gamete production is set as

Table 1: The individual gamete production as a function of the patch, the genotype, the selection coefficient s, and the dominance coefficient h.

patch	**adult genotype**	**avg. gamete production per adult**
1	*AA*	$f_{max}\ (1)$
	AB	$f_{max}\ (1 - h\ s)$
	BB	$f_{max}\ (1 - s)$
2	*AA*	$f_{max}\ (1 - s)$
	AB	$f_{max}\ (1 - (1-h)\ s)$
	BB	$f_{max}\ (1)$

3. fusion of gametes

Haploid gametes fuse randomly within patches and form exactly N_1 offspring individuals in patch *1* and N_2 offspring in patch *2*. All gametes other than those that form offspring die. We therefore assume that f_{max} is large and there are always enough gametes to produce N_1 and N_2 individuals. After gamete fusion, all adults die and the offspring become adults.

4. storage of summary statistics

At the end of each year, store meaningful summary statistics. For instance, you could collect the allele frequency for each allele (p_A and p_B) in each patch (1 and 2). In addition, you should compute the divergence in allele frequencies between patches ($d_A = p_{A1} – p_{A2}$).

Study the evolution of local adaptation systematically

After coding and debugging your simulation code, study the evolution of local adaptation systematically and explore the parameter space. How does the dispersal probability and the selection coefficient affect the evolution of local adaptation?