Exercise

The evolution of local adaptation in face of phenotypic plasticity

The topic

Local adaptation describes genetic adaptations to local environmental conditions such that local individuals have higher survival and/or reproduction than incoming individuals from other habitat. Local adaptation is a widespread pattern, a key component of intra-specific genetic diversity, and relevant for agriculture, forestry, and nature conservation.

The evolution of local adaptation depends on a couple of processes, for instance dispersal (large dispersal between patches acts against genetic divergence between them), the strength of selection (strong selection puts strong pressure on adapting locally), or the response to selection (e.g., additive genetic variance, heritability).

An additional key determinant is phenotypic plasticity. With plasticity, genotypes can express different phenotypes in different environments. Plasticity thus is an alternative strategy to local adaptation, and feeds back on the course of genetic evolution.

The ecological scenario

The species

You will study a diploid species with two stage classes, offspring and adults. Within a year, offspring become adults, reproduce, and then die (i.e. the species has an annual life history, lines 14-16 of the ini-file). The focal species occupies two habitat patches (line 13 of the ini-file) where individuals could disperse between patches. Patches differ from each other in an environmental parameter (e.g., temperature, pH, etc.) and selection favors different phenotypes to adapt to the local conditions (e.g., different morphologies).

Annual events

Each year, a couple of events happen consecutively (lines 18-27 of the ini-file):

1) Reproduction

All hermaphroditic adults mate at random within each patch (line 33), and produce offspring by sexual reproduction (line 20). Here, each adult has the same <u>average</u> fecundity while individual fecundity is picked from a Poisson distribution (leading to demographic stochasticity, line 32).

2) Dispersal

Offspring disperse to the other patch with probability *m*, and stay in their natal patch with probability *1-m* (lines 35-38). We assume that there is no mortality during dispersal.

3) Phenotype expression

Each offspring expresses a single phenotype (line 44) following

$$z = g_0 + g_1 * e$$

where the trait value z is expressed based on the individuals' breeding value (g_0, the intercept of the reaction norm), the degree of plasticity (g_1, the slope of the reaction norm), and the local environmental cue (e). For simplicity, we assume that the degree of plasticity g_1 is constant for all individuals and does not evolve over time (line 42). Instead, the intercept g_0 is a quantitative trait such that the reaction norm could evolve up- or down-wards. We assume that the environmental cues differ between patches with e_1=-1 and e_2=+1 (line 48).

The trait value g_0 is controlled by 10 loci (line 50) with additive effects (all effect size at the 10 loci and both homologous copies are summed up to get g_0). Mutations at each allele contributing to the intercept occur with probability μ=0.001 (line 51), mutational effects are drawn from normal distribution with mean=0 and variance=0.01 (line 52), and these effects are then added to the existing allelic effect.

4) Viability selection

During this event, those offspring individuals that are not well adapted to their local environmental condition die (line 57). The survival probability *W(z)* follows a Gaussian function (line 58) and varies with the match between the individuals trait value z and the local phenotypic optimum θ as

$$W(z) = exp(\frac{(z-\theta)^2}{2\omega^2})$$

We assume that the phenotypic optima differ between both patches (θ_1=10, θ_2=12; line 59), which installs divergent selection and favors phenotypic and (potentially) genetic divergence. The variance of the survival function is ω^2=10 (line 60), and inversely proportional to the selection strength.

5) Aging

All adults die and offspring become adults (lines 14-16).

6) Regulation

The new generation of adults experiences a step of density regulation (ceiling regulation, line 66) when adults are randomly removed until only 1000 adults are left within each patch (line 67).

6) Summary statistics

To study the evolution of local adaptation in face of plasticity, we record a couple of summary statistics for each patch (as set by line 73):

- the avg. breeding value g_0 (*adlt.g0.p1* and *adlt.g0.p2*)
- the avg. plasticity level g_1 (*adlt.g1.p1* and *adlt.g1.p2*)
- the avg. environmental cue e (*adlt.e1.p1* and *adlt.e1.p2*)
- the avg. phenotypic value z (*adlt.z1.p1* and *adlt.z1.p2*)

and eventually use them to compute

- genetic divergence between patches (D_g = *adlt.g0.p2 – adlt.g0_p1*)
- phenotypic divergence between patches (D_p = *adlt.z1.p2 – adlt.z1.p1*)

Exercises

1. The evolution of local adaptation

Before studying the effect of plasticity on genetic and phenotypic divergence, we first recommend to study the evolution of local adaptation in absence of plasticity (when g_1=0). To do this, run the ini-file “*Exercise_Phenotypic_plasticity.ini*”, and study the simulation results using the first part of the R-Script “*Exercise_Phenotypic_plasticity.R*” (lines 1-75 of the R-script).

1.1 How does gene flow shape the evolution of local adaptation?

After plotting the basic simulations, change the dispersal probability (line 37 of the ini-file), rerun the simulations, and study the effect on the evolution of genetic divergence. We recommend to study both, dispersal larger and smaller than m=0.1 (where $0 \leq m \leq 0.5$).
→ *What happens with smaller dispersal?*
→ *What is the effect of larger dispersal?*

1.2 How does the selection strength shape the evolution of local adaptation?

Reset the dispersal to m=0.1 (line 37 of the ini-file) and change the variance of the survival function (line 60 of the ini-file), rerun the simulations, and study the effect on genetic divergence via the R plots. We recommend to study both, stronger selection ($0<\omega^2<10$) and weaker selection ($\omega^2>10$).
→ *What happens with stronger selection?*
→ *What is the effect of weaker selection?*

2. The evolution of local adaptation with phenotypic plasticity

In a second step, we ask you to study the role of phenotypic plasticity ($g_1 \neq 0$) when plasticity is either adaptive ($g_1>0$) or maladaptive ($g_1<0$). Beside creating the four graphs in the first part of the R script (lines 1-75 of the R script), also have a look at the second part (lines 75-110 of the R script). Here, you plot genetic and phenotypic divergence for two levels of plasticity.

Recall that you should reset the dispersal to m=0.1 (line 37 of the ini-file) and selection strength to $\omega^2=10$ (line 60 of the ini-file).

2.1 How does adaptive phenotypic plasticity shape the evolution of local adaptation?

Extend the degree of plasticity for more positive values (for instance adding $0<g_1<1$ in steps of 0.25, line 47 of the ini-file), rerun the simulations, and study the effect on the evolution of divergence D_g and D_P. To extend the last plots (lines 75-110 of the R script) for more plasticity values, adapt line 89 of the R-script for the newly simulated values.

2.2 How does maladaptive phenotypic plasticity shape the evolution of local adaptation?

Change (or better extend) the degree of plasticity for negative values (for instance adding $-1<g_1<0$ in steps of 0.25, line 47 of the ini-file), rerun the simulations, and study the effect on the evolution of divergence (D_g and D_P).

Bonus:

How does the timing of phenotype expression and/or dispersal shape local adaptation? To this end, change the order of annual events (lines 19-28 of the ini-file).