Exercise

Competition for resources

The topic

Resources are key for every living organism. The ability of an organism to consume resources critically relies on its so called *consumer traits* which need to fit to the resource properties. For instance, the beak morphology of bird needs to match with the respective seed morphologies. When diversity in resources is present, diversity in consumer traits might evolve. When competition for resources is present, diversity might even evolve in absence of spatial separation, in sympatry.

The scenario

The consumer species & resource distribution

You will study a diploid species with two stage classes, offspring and adults. Within a year, offspring become adults, reproduce, and then die (lines 13-18 of the ini-file). The consumer species (e.g., a fish species) occupies two habitat patches (line 13) and individuals could disperse between patches (when the lake are connected in some way).

Each patch (e.g., lake) is characterized by its resource composition (e.g., the plankton community). More precisely, each patch harbors a set of discrete resource types j (e.g., planktonic species) that differ in their resource property q_j (e.g., size, line 44) and occur with a certain frequency p_j (e.g., the proportion of the plankton species, line 46). When resource types differ from each other in their property, we find within-patch resource variation

$$\sigma_w^2 = \sum p_j (q_j - \bar{q})^2 \qquad (1).$$

At the beginning of each year, all the resource types fully regrow to the same resource distribution.

Annual events

Each year, a couple of events consecutively shape the consumer population (lines 21-26):

1) Resource consumption & Cloning

Adults produce offspring by clonal reproduction (line 22). Clones are perfect copies of their parents unless their genotypes mutate. The fecundity of each adult depends on how many resources it could exploit during this event. Resource consumption here is controlled by a single consumer trait with continuous trait value z (e.g, gill raker morphology). The trait is controlled by 10 loci with additive effects. Mutations follow a continuum-of-allele model and occur with frequency μ=0.0001 and variance $\sigma_m{}^2$=0.1 (lines 30-38).

The rate with which a consumer individual with trait value z_i feeds on a resource of type j is

$$\alpha(z_i, q_j) = \exp\left(\frac{(z_i - q_j)^2}{2g^2}\right) \qquad (2)$$

The feeding rate is maximized ($\alpha(z_i, q_j) = 1$) when the consumer trait z matches the property of resource type j ($z = c_j$, when the gill morphology matches the plankton size). With increasing mismatch between consumer trait and resource property, the feeding rate declines. How much $\alpha(z_i,q_j)$ declines depends on the degree of resource generalism g^2 (the variance of the α-function, line 43). A large resource generalism (i.e. a large variance) allows to feed on a broad range of resources with large rates.

How much the consumer species exploits resources each year has strong consequences for the course of evolution. We consider two scenarios:

a) Highly abundant resources:

When only a tiny fraction of all available resources are exploited in the course of the season, the individual fecundity function becomes

$$f_i = f_{max} \sum_{j=1}^{R} p_j \, \alpha(z_i, q_j) \qquad (3)$$

Here, fecundity f_i is a summation over all resource types j, where the frequency q_j is multiplied by the feeding rate $\alpha(z_i,q_j)$ on the respective type. The maximum fecundity f_{max} (line 43) is reached when the individual is perfectly adapted to all resource (and all $\alpha(z_k,q_j)=1$). This scenario is modelled when setting line 40 to "*resource_consumption_soft*".

b) Resource scarcity:

When in turn all resources are exploited by the consumer species (e.g, when exploitation time is long), the individual fecundity function then becomes

$$f_i = f_{max} \sum_{j=1}^{R} p_j \frac{\alpha(z_i, q_j)}{\sum_{k=1}^{N} \alpha(z_k, q_j)} \qquad (4)$$

Such a fecundity function is also called a contest success function where the fecundity f_i of individual i is not only a function of its own feeding rate $\alpha(z_i,q_j)$, but also varies with the feeding rates of all other patch members $\sum \alpha(z_k,q_j)$. The maximum fecundity f_{max} is reached when the individual is perfectly adapted to all resource and competition is absent (when all $\alpha(z_i,q_j)=1$ and the feeding rate of all competitors is $\alpha(z_k,q_j)=0$). This scenario is modeled when setting line 43 to "*resource_competition_soft*".

Fecundity function (2) leads to exploitation competition and negative frequency-dependent selection when the specialization on a rarely used resource type could offer fecundity benefit. In other words, there is a fecundity reward when having a consumer trait z that allows to maximize consumption of a resource that most other patch members can hardly exploit and $\sum \alpha(z_k,q_j)$ is small.

We will study the consequences of both scenarios, when competition is present or absent, and how they might shape diversity at the consumer level.

2) Dispersal

After resource consumption and reproduction, the resulting offspring can disperse to the other patch with probability m, and stay in the natal patch with probability $1-m$ (lines 50-53).

3) Aging

After dispersal, all adults die and offspring become adults. See matrix population model (line 15).

4) Summary statistics

To study the evolution of consumer diversity, we record a couple of summary statistics (as set by line 56):

- the avg. consumer trait value within each patch (*adlt.q1.p1* and *adlt.q1.p2*)
- the mean genetic variance in consumer trait within each patch (*adlt.Va.q1.p1* and *adlt.Va.q1.p2*)

In addition, we also export the genotype table of the entire population to study the distribution of trait values (line 37-38).

Exercises

We want to study the evolution of the consumer trait (avg. value and variance) depending on resource variation within patches (σ_w^2) and the degree of resource generalism (g^2). Run simulations with ***nemoage0.32.1*** using the ini-file "*Exercise_Resource_competition.ini*". To plot the simulation results, run the R-script "*Exercise_Resource_competition.R*".

The evolution of consumer traits

1 Where does the avg. consumer trait value evolve to?

a) Change the mean of the resource properties of the first scenario (line 44 of the ini-file), rerun the simulations, and study the effect on the average consumer trait. For instance, we suggest to increase or decrease all q_j-values by the same amount (e.g., change the first entry of line 44 to "{{2,3,4,5,6}{2,3,4,5,6}}"). Then, adapt the R script for these new values (in particular lines 20 and 21 of the R-script) and redo the plots.
b) Can you predict the endpoint of average trait evolution?
c) Do such changes affect the variance in the consumer trait?

2 Under which conditions does resource polymorphism evolve?

a) Study the additive genetic variance within patches for different levels of resource variation. As a first step, do the same three plots for the alternative scenario with "{{1,2,3,4,5}{1,2,3,4,5}}" (adapt lines 23 and 24 of the R script).
b) In a second step, extend line 44 in the ini-file for new resource property matrices. Ideally, you should add new matrices that lead both to smaller and larger σ_w^2 levels than "{{1,2,3,4,5}{1,2,3,4,5}}".
b) How does the distribution of trait values change with σ_w^2.
c) Can you predict when consumer diversity will evolve, or not? To answer this question, extend section "*PLOT equilibrium conditions*" in the R-script (lines 77-102) for the newly simulated resource properties.

3 How does the evolution of resource polymorphism depend on competition?

a) What happens when competition is absent?
(change the entry of line 40 of the ini-file to *resource_consumption_soft* to switch to fecundity function 4, rerun the simulations, and redo the plots)

Bonus:

a) What happens with sexual reproduction? How does the trait distribution within a patch change? (to this end, replace all instances of "*cloning** in the the ini-file to "*breed*", for instance "*cloning_model*" to "*breed_model*")
b) What is the effect of between-patch resource variation on consumer trait evolution? Which is a stronger driver of diversity, divergent or frequency-dependent selection?