Stage-Structure and Evolution in Age/Stage-Structured Populations

A. Stage-structured populations: the Lefkovitch matrix

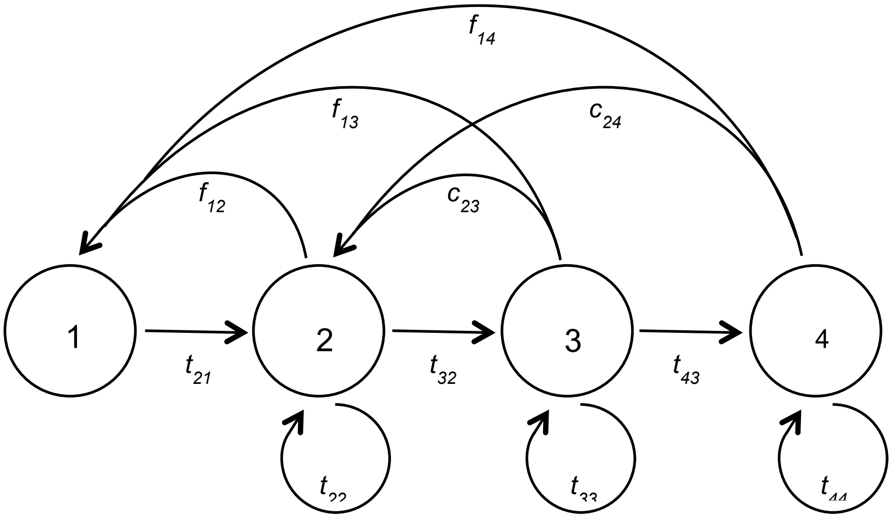
$$\mathbf{n}(t+1) = \mathbf{A}\,\mathbf{n}(t)$$

$$n_i(t+1) = \sum_{i=1}^{n} a_{ij} n_i(t+1)$$

$\mathbf{n}(t)$ can generally be a vector of *stage* abundances (the n_i), and the life-cycle graph can include more than just survival from stage i to stage $i + 1$ and fecundities (production of stage 1 individuals).

Example: stage-structured population with both sexual and clonal reproduction

For the life-cycle graph, each a_{ij} is the coefficient on the arc from stage j to i.



Lefkovitch matrix model for this example:

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \begin{pmatrix} 0 & f_{12} & f_{13} & f_{14} \\ t_{21} & t_{22} & c_{23} & c_{24} \\ 0 & t_{32} & t_{33} & 0 \\ 0 & 0 & t_{43} & t_{44} \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}$$

$$n_1(t+1) = f_{12}n_2(t) + f_{13}n_3(t) + f_{14}n_4(t)$$
$$n_2(t+1) = t_{21}n_1(t) + t_{22}n_2(t) + c_{23}n_3(t) + c_{24}n_4(t)$$
$$n_3(t+1) = t_{32}n_2(t) + t_{33}n_3(t)$$
$$n_4(t+1) = t_{43}n_3(t) + t_{44}n_4(t)$$

General form of the characteristic equation

$$\mathbf{n}(t) = \sum_i \lambda_i^t \, \boldsymbol{w}_i c_i$$

where $\boldsymbol{w}_i$ is the right eigenvector of $\mathbf{A}$ corresponding to λ_i and the c_i are coefficients determined by the initial conditions. We can also write

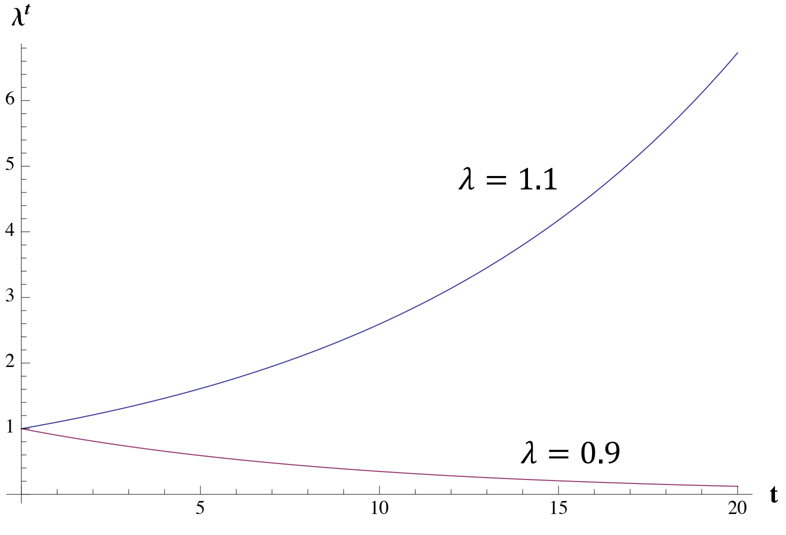
$$\mathbf{n}(t) = \sum_i \lambda_i^t \, \boldsymbol{w}_i \boldsymbol{v}_i^* \, \mathbf{n}(0)$$

where $\boldsymbol{v}_i^*$ is the complex conjugate transpose of the left eigenvector corresponding to λ_i; $\boldsymbol{v}_i^* \, \mathbf{n}(0)$ gives a scalar and is equivalent to c_i (Caswell 2001).

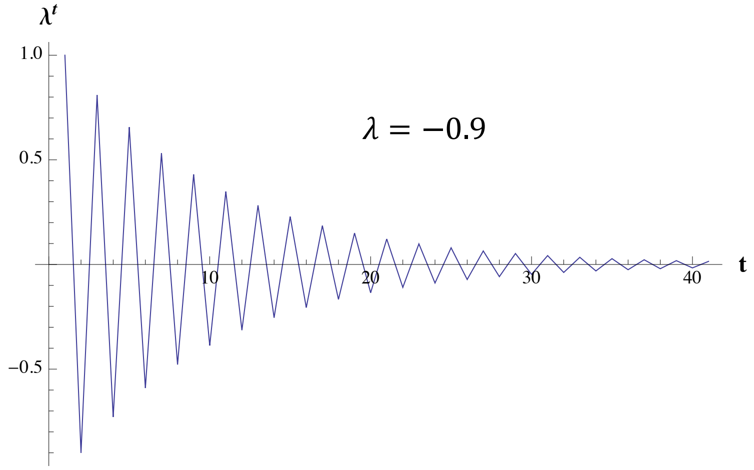
Effects of eigenvalues

The long-term behavior of $\mathbf{n}(t)$ depends on the eigenvalues λ_i as they are raised to higher and higher powers; the eigenvalues are the solutions to the characteristic equation, which is a polynomial in λ; thus they can be real or complex.

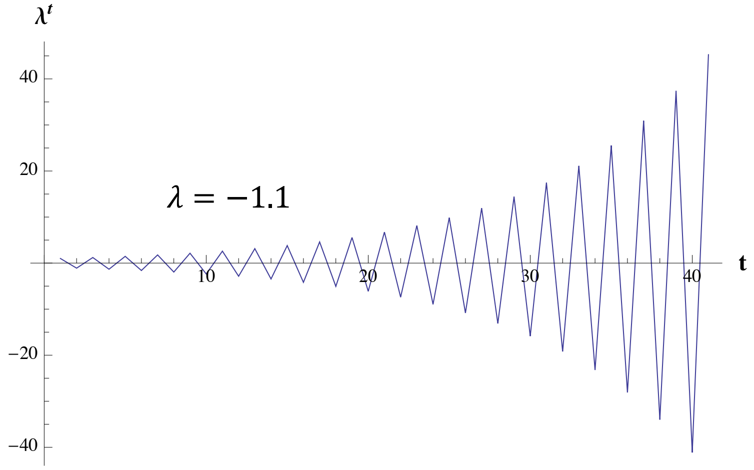
- $\lambda_i > 0$: λ_i^t produces exponential growth if $\lambda > 1$, exponential decay if $\lambda < 1$



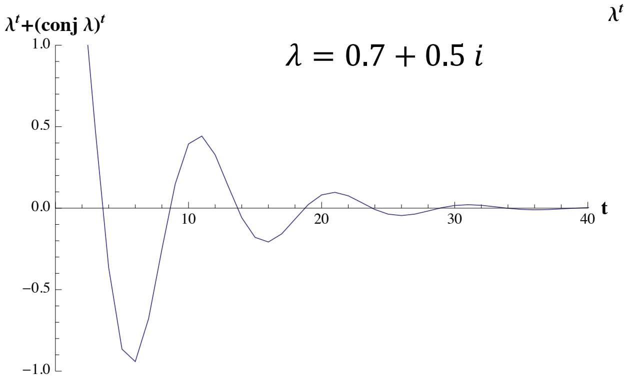
- $-1 < \lambda_i < 0$: λ_i^t exhibits damped oscillations with a period equal to 2

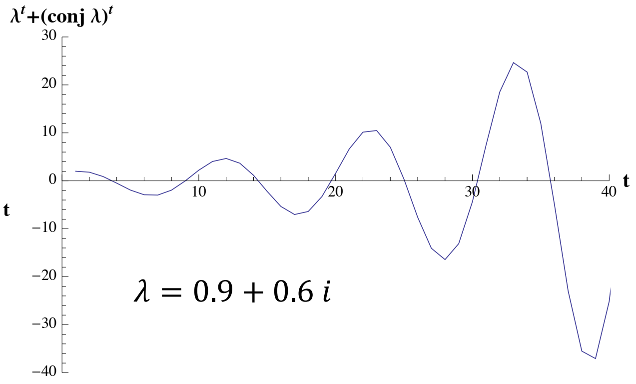


- $\lambda_i < -1$: λ_i^t exhibits diverging oscillations with a period equal to 2



- $\lambda_i = a + bi$: complex eigenvalues produce oscillations; boundary between population increase and population decrease comes at $|\lambda_i| = 1$





B. Selection in age-structured populations

We now allow for a genotype specific transition matrix $\mathbf{A}_{ij}$ that allows us to project the number of A_iA_j individuals of age *x* at time *t*, $N_{ij}(x,t)$.

$$N_{ij}(x,t) = B(t-x)p_i(t-x)p_j(t-x)l_{ij}(x,t)$$

$$B(t) = \sum_i \sum_j \sum_x B(t-x)\, p_i(t-x)p_j(t-x)k_{ij}(x,t)$$

where $k_{ij}(x,t) = l_{ij}(x,t)m_{ij}(x,t)$ and *B*(*t*) gives the number of newborn individuals at time *t* (Charlesworth 1980).

At genetic equilibrium for an age-structured populations, the allele frequencies at any particular locus are $p_i(t) = \hat{p}_j$, and we can write

$$1 = \sum_j \hat{p}_j \sum_x \frac{B(t-x)}{B(t)} k_{ij}(x,t)$$

$$B(t) = \sum_i \sum_j \sum_x B(t-x)\hat{p}_i\hat{p}_j\, k_{ij}(x,t)$$

At some time t', the population reaches demographic equilibrium, and each age class will grow at the same rate as the whole population. We can then write

$$\frac{B(t'-x)}{B(t')} = \lambda_1^{-x}$$

where λ_1 is the geometric rate of increase of the equilibrium population.

This then gives the following equilibrium fitness measure for A_iA_j individuals for $t \geq t'$, letting $\hat{r} = \ln(\lambda_1)$:

$$w_{ij} = \sum_x e^{-\hat{r}x}\, k_{ij}(x,t)$$

Under weak selection, we can write the change in allele frequency due to selection as:

$$\Delta p_i T(\hat{r}) = p_i[w_i(\hat{r}) - 1] + O(\varepsilon^2)$$

where $T(z) = \sum_x xe^{-zx} \sum_i \sum_j p_i \, p_j k_{ij}(x)$ gives a measure of the generation time of the population at time *t* and $w_i(z) = \sum_j p_j \, w_{ij}(z)$ is the marginal fitness.

> Note:
> In Lecture #1, we noted that $T = \sum_{x=1}^{n} x l_x m_x \lambda_1^{-x} = \sum_{x=1}^{n} x \lambda_1^{-x} k_x = \sum_{x=1}^{n} xe^{-rx} k_x$ gave a measure of generation time for age-structured populations; this the equivalent function taken over all genotypes.

Approximating $w_{ij}(\hat{r})$ using Taylor's theorem allows the change in allele frequency to be written as

$$\Delta p_i = p_i(r_i - \bar{r}) + O(\varepsilon^2)$$

where $r_i = \sum_j p_j \, r_{ij}$, r_{ij} gives the instrinsic rate of increase for a population of $A_i A_j$ individuals at the steady age distribution, and $\bar{r} = \sum_i \sum_j p_i \, p_j r_{ij}$ [see Charlesworth 1980 for detailed derivations].

> Note:
> For unstructured diploid populations with 2 alleles under selection, $\Delta p = \frac{pq[p(w_{11} - w_{12}) + q(w_{12} - w_{22})]}{\bar{w}} = \frac{p(\bar{w}_1 - \bar{w})}{\bar{w}}$, where $\bar{w}_1 = pw_{11} + qw_{12}$.

C. Selection in stage-structured populations

In the stage-structured case, we can similarly allow for a genotype specific transition matrix $\mathbf{A}^{\langle i,j \rangle}$ that allows us to project the number of $A_i A_j$ individuals of stage *x* at time *t*, $N_{(x,t)}^{\langle i,j \rangle}$.

$$N_{(x,t)}^{\langle i,j \rangle} = \sum_{\tau=1}^{\infty} h_{(x,\tau)}^{\langle i,j \rangle} p_i(1, t-\tau) \, p_j(1, t-\tau) B(1, t-\tau)$$

$$B(1,t) = \sum_i \sum_j \sum_x a_{1x}^{\langle i,j \rangle} \, N_{(x,t-1)}^{\langle i,j \rangle}$$

where $h_{(x,\tau)}^{\langle i,j \rangle}$ gives the probability of moving from stage 1 (newborn) to stage *x* (without going through stage 1) in exactly time τ steps (see Orive 1995 and 2001),

$p_i(x,t)$ gives the frequency of allele A_i in individuals of stage x at time t, and $B(1,t)$ gives the number of newborn individuals at time t, for density- and frequency-independent population demographics, letting $N_{(x,t)}^{\langle i,j\rangle} = N_{(x,t)}^{\langle j,i\rangle}$

The equilibirum fitness can be defined as

$$w_{ij}(\bar{\lambda}) = \sum_x a_{1x}^{\langle i,j\rangle} \sum_\tau \bar{\lambda}^{-(\tau+1)} h_{(x,\tau)}^{\langle i,j\rangle}$$

(equation A2 from Orive 1995), where $\bar{\lambda}$ is the leading nonunit eigenvalue of the **A** matrix for the population at the equilibrium allele frequencies, $p_i(x,t) = \hat{p}_i(x)$.

This gives the contribution of the A_iA_j genotype at the newborn stage to the reproductive value of the whole population. We follow allele frequencies in the newborn stage ($x = 1$), and ask how selection affects these allele frequencies.

Following a similar approach as for age-structured populations, we can show that, under weak selection, the change in allele frequency is

$$\Delta p_i(1,t) S_i(\bar{\lambda}) = p_i(1,t)\left[w_i(\bar{\lambda}) - 1\right] + O(\varepsilon^2)$$

where $w_i(\bar{\lambda}) = \sum_j p_j(1,t) w_{ij}(\bar{\lambda})$, $S_i(\bar{\lambda}) = \sum_j p_j(1,t) S_{ij}(\bar{\lambda})$, and $S_{ij}(\bar{\lambda})$ is the *meiotic generation time* (Orive 1993); the mean number of time units since a parent of a newborn individual was itself a newborn.

Approximating $w_i(\bar{\lambda})$ using Taylor's theorem allows the change in allele frequency to be written as

$$\Delta p_i(1,t) = p_i(1,t)\left(\frac{\lambda_i}{\bar{\lambda}}\right) + O(\varepsilon^2)$$

where $\lambda_i = \sum_j p_j \lambda_{ij}$, λ_{ij} gives the geometric rate of increase for a population of A_iA_j individuals at the steady age distribution, and $\bar{\lambda} = \sum_i \sum_j p_i p_j \lambda_{ij} + O(\varepsilon^2)$.

For a locus with two alleles, A_1 and A_2, A_2 will increase in frequency if $\lambda_2 > \bar{\lambda}$, or

$$p_1\lambda_{12} + p_2\lambda_{22} > p_1(p_1\lambda_{11} + p_2\lambda_{12}) + p_2(p_1\lambda_{12} + p_2\lambda_{22})$$

$$p_1(\lambda_{12} - \lambda_{11}) + p_2(\lambda_{12} - \lambda_{12}) > 0$$

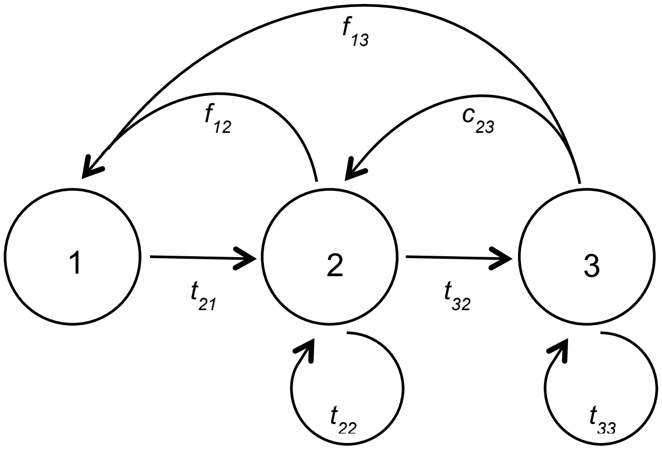
or, approximately,

$$p_1\left[\sum_{x,y\in S}\left(a_{xy}^{\langle 1,2\rangle}-a_{xy}^{\langle 1,1\rangle}\right)\frac{\partial\lambda_{11}}{\partial a_{xy}^{\langle 1,1\rangle}}\right]+p_2\left[\sum_{x,y\in S}\left(a_{xy}^{\langle 2,2\rangle}-a_{xy}^{\langle 2,1\rangle}\right)\frac{\partial\lambda_{12}}{\partial a_{xy}^{\langle 1,2\rangle}}\right]>0$$

for alleles affecting a set of life-history parameters, *S* (Orive 1995).

In-Class Activities: Lecture #2 - Part C

Exercise 1



$$\mathbf{A}=\begin{pmatrix}0 & f_{12} & f_{13}\\ t_{21} & t_{22} & c_{23}\\ 0 & t_{32} & t_{33}\end{pmatrix}=\begin{pmatrix}0 & 10 & 200\\ 0.005 & 0.7 & 0.2\\ 0 & 0.1 & 0.6\end{pmatrix}$$

Using *Mathematica*, we find $\lambda_1 = 1.025$, $\boldsymbol{w}_1 = (0.9783, 0.01758, 0.00413)$, and $\boldsymbol{v}_1 = (0.00129, 0.2653, 0.7334)$.

Using $\frac{\partial\lambda}{\partial a_{xy}} = \frac{v_x w_y}{\langle \boldsymbol{w},\boldsymbol{v}\rangle}$ (from Lecture #1), we can find the sensitivities of this transition matrix, as follows:

$$\begin{pmatrix}\dfrac{\partial\lambda}{\partial a_{11}} & \dfrac{\partial\lambda}{\partial a_{12}} & \dfrac{\partial\lambda}{\partial a_{13}}\\ \dfrac{\partial\lambda}{\partial a_{21}} & \dfrac{\partial\lambda}{\partial a_{22}} & \dfrac{\partial\lambda}{\partial a_{23}}\\ \dfrac{\partial\lambda}{\partial a_{31}} & \dfrac{\partial\lambda}{\partial a_{32}} & \dfrac{\partial\lambda}{\partial a_{33}}\end{pmatrix}\approx\begin{pmatrix}0.141 & 0.00254 & 0.0006\\ 28.95 & 0.5204 & 0.1224\\ 80.04 & 1.439 & 0.3383\end{pmatrix}$$

Note: Calculate $\frac{\partial\lambda}{\partial a_{11}}$ and $\frac{\partial\lambda}{\partial a_{23}}$ by hand and check that you get approximately 0.141 and 0.1224.

Imagine an allele A_2 that affects survival rates for life-history stages 1 and 2, increasing survival for stage 2 but decreasing survival in stage 1:

	Genotype		
Survival rates	A_1A_1	A_1A_2	A_2A_2
t_{32}	$t_{32}^{\langle 1,1\rangle}$	$t_{32}^{\langle 1,1\rangle} + \alpha$	$t_{32}^{\langle 1,1\rangle} + 2\alpha$
t_{21}	$t_{21}^{\langle 1,1\rangle}$	$t_{21}^{\langle 1,1\rangle} - \beta$	$t_{21}^{\langle 1,1\rangle} - 2\beta$

Find the conditions under which allele A_2 will increase when rare (you can assume that the frequency of A_2 is approximately zero).