

Supporting File 1

Aging asexual lineages and the evolutionary maintenance of sex.

Constant Rate of Senescence

■ Preliminaries

Sexual species diversify at rate e^S and produce asexual species into age-class 0 at rate $e^U \ll 1$. The net growth of sexual species per time step is then equal to $e^S - e^U$ and assumed to be larger than 1. Asexual species progress through age-classes, x , where $0 \leq x < \infty$ and possess diversification rates $e^{A-2\alpha x}$, where $\alpha \geq 0$. α describes the rate that diversification rates senesce in aging asexual lineages.

Below, we construct a linear system of equations to describe the abundance of sexual and asexual species.

We first construct a system with a finite number of asexual age-classes. By normalizing all species abundance to that of the sexual species, we find an analytical formula to describe the relative frequency of asexual species in age-class x . By induction, we extend the model to accomodate any number of age-classes, which is used for the paper.

■ Linear System with 21 asexual age-classes

Sexual species produce asexual species in to age-class 0 at rate e^U .

The diversification rate of asexual age-classes follow the function $e^{A-2\alpha x}$.

By limiting the number of age-classes to 21, we assume that species in age-classes subsequent to 21 do not exist or have negligible abundance. The parameters values that allow for this is restrictive but our goal with considering a finite number of age-classes is to explore the properties of this model. We show below that extension to large number of age-classes relieves some of these restrictions.

```
DivRateAsex[x_] := Exp[A] Exp[-2 α x];
DivRate20Classes = Table[DivRateAsex[x], {x, 0, 20}]
```

$$\{e^A, e^{A-2\alpha}, e^{A-4\alpha}, e^{A-6\alpha}, e^{A-8\alpha}, e^{A-10\alpha}, e^{A-12\alpha}, e^{A-14\alpha}, e^{A-16\alpha}, e^{A-18\alpha}, e^{A-20\alpha}, e^{A-22\alpha}, e^{A-24\alpha}, e^{A-26\alpha}, e^{A-28\alpha}, e^{A-30\alpha}, e^{A-32\alpha}, e^{A-34\alpha}, e^{A-36\alpha}, e^{A-38\alpha}, e^{A-40\alpha}\}$$

$\vec{x}(t+1) = M \vec{x}(t)$ represents the recursion equation for the linear system.

$\vec{x}(t) = \{N_S(t), N_{A,1}(t), N_{A,2}(t), \dots, N_{A,21}(t)\}$ is the vector containing the abundance of sexual species, $N_S(t)$, and asexual species in age-class x , $N_{A,x}(t)$, at time point t .

M represents the transition matrix (shown below).

The diagonal of M contains the transition rate of one class into itself. The sub-diagonal of M contains the transition rate of one to class to the next.

In our model, only sexual species diversify into their own class and thus the diagonal of M only contains $e^S - e^U$, which represents the net growth of sexual species per time step.

Sexual species produce into age-class 0 asexual species at rate e^U and all asexual species diversify into subsequent age-classes. These transition rates are contained in the sub-diagonal of M .

```

TMatrixSubDiagonal = Join[{E^U}, DivRate20Classes];
TMatrix = DiagonalMatrix[TMatrixSubDiagonal, -1];
TMatrix[[1, 1]] = E^S - E^U;
TMatrix

{ {eS - eU, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {eU, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, eA, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, eA-2α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, eA-4α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, eA-6α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, eA-8α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, eA-10α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, eA-12α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, eA-14α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, eA-16α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-18α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-20α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-22α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-24α, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-26α, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-28α, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-30α, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-32α, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-34α, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-36α, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-38α, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, eA-40α, 0} }

```

■ Solve for the stationary distribution of species abundance

We find the equilibrium stationary distribution of species abundance by finding the sole eigenvalue of the system, $e^S - e^U$, and the corresponding eigenvector.

Then we normalize all species abundance to that of the sexual species and obtain the relative frequency of asexual species in all 21 age-classes.

```

SexualAbundance = Eigenvectors[Matrix][[-1]][[1]];
EigenvectorNormalizedToSexualAbundance = Eigenvectors[Matrix][[-1]] / SexualAbundance;
AsexFrequency21Classes = Delete[EigenvectorNormalizedToSexualAbundance, 1]

```

$$\left\{ \frac{e^U (e^S - e^U)^{21}}{(-e^S + e^U)^{22}}, \frac{e^{A+U} (e^S - e^U)^{20}}{(-e^S + e^U)^{22}}, \frac{e^{2A+U-2\alpha} (e^S - e^U)^{19}}{(-e^S + e^U)^{22}}, \frac{e^{3A+U-6\alpha} (e^S - e^U)^{18}}{(-e^S + e^U)^{22}}, \right.$$

$$\frac{e^{4A+U-12\alpha} (e^S - e^U)^{17}}{(-e^S + e^U)^{22}}, \frac{e^{5A+U-20\alpha} (e^S - e^U)^{16}}{(-e^S + e^U)^{22}}, \frac{e^{6A+U-30\alpha} (e^S - e^U)^{15}}{(-e^S + e^U)^{22}}, \frac{e^{7A+U-42\alpha} (e^S - e^U)^{14}}{(-e^S + e^U)^{22}},$$

$$\frac{e^{8A+U-56\alpha} (e^S - e^U)^{13}}{(-e^S + e^U)^{22}}, \frac{e^{9A+U-72\alpha} (e^S - e^U)^{12}}{(-e^S + e^U)^{22}}, \frac{e^{10A+U-90\alpha} (e^S - e^U)^{11}}{(-e^S + e^U)^{22}}, \frac{e^{11A+U-110\alpha} (e^S - e^U)^{10}}{(-e^S + e^U)^{22}},$$

$$\frac{e^{12A+U-132\alpha} (e^S - e^U)^9}{(-e^S + e^U)^{22}}, \frac{e^{13A+U-156\alpha} (e^S - e^U)^8}{(-e^S + e^U)^{22}}, \frac{e^{14A+U-182\alpha} (e^S - e^U)^7}{(-e^S + e^U)^{22}},$$

$$\frac{e^{15A+U-210\alpha} (e^S - e^U)^6}{(-e^S + e^U)^{22}}, \frac{e^{16A+U-240\alpha} (e^S - e^U)^5}{(-e^S + e^U)^{22}}, \frac{e^{17A+U-272\alpha} (e^S - e^U)^4}{(-e^S + e^U)^{22}},$$

$$\frac{e^{18A+U-306\alpha} (e^S - e^U)^3}{(-e^S + e^U)^{22}}, \frac{e^{19A+U-342\alpha} (e^S - e^U)^2}{(-e^S + e^U)^{22}}, \frac{e^{20A+U-380\alpha} (e^S - e^U)}{(-e^S + e^U)^{22}}, \frac{e^{21A+U-420\alpha}}{(-e^S + e^U)^{22}} \left. \right\}$$

- The normalized frequency of asexual species can be described by the analytical function: $fx =$

$$e^U e^{-\alpha x^2 + (A+\alpha)x} (e^S - e^U)^{-(x+1)}$$

```

fx[x_] := Exp[U] Exp[(A + α) x] Exp[-α x^2] (Exp[S] - Exp[U]) ^ -(x + 1)
AnalyticalAsexFrequency21Classes = Table[fx[x], {x, 0, 21}] // Simplify;
AnalyticalAsexFrequency21Classes == AsexFrequency21Classes // Simplify
True

```

- Extension to k age-classes to approximate system with infinite age-classes

We can approximate a system with infinite age-classes using one with a large finite number of age-classes, k , by ensuring that asexual lineages will eventually decrease to negligible frequencies at some age. In our model, this condition is met when asexual species diversify at lower rates than sexuals, $e^A / (e^S - e^U) < 1$, or when diversification rates senesce with age, $\alpha > 0$. Given that the k -th age-class is negligible in frequency, their descendants will also be negligible. We make the simplifying assumption that the k -th age-class leave no descendants and truncate the matrix at the k -th age-class.

Under these conditions, we can approximate an infinite age-class model with a k age-class model by taking the limit of k approaching infinity. We can utilize the analytical function shown above to describe the frequency of asexual species in age-class x because of our truncation at the k -th age-class.

- Total frequency of asexual species (F)

- Classic model with no senescence in diversification rate, $\alpha = 0$, and $e^A / (e^S - e^U) < 1$; Equation [3]

Without senescence in diversification rates, $\alpha = 0$, coexistence between sexual and asexual species require that the diversification rate of all asexual species be lower than that of sexuals, $e^A / (e^S - e^U) < 1$. If $e^A / (e^S - e^U) \geq 1$, asexual species will diversify faster than sexuals, thus dominating the system.

$$F_{\text{Const}} = \frac{e^U}{-e^A + e^S - e^U} = \frac{e^U}{e^S - e^U} \frac{1}{1 - e^A / (e^S - e^U)}$$

Sum[fx[x] /. $\alpha \rightarrow 0$, {x, 0, Infinity}]

$$\frac{e^U}{-e^A + e^S - e^U}$$

■ **Strong senescence model, $\alpha \gg 1$; Equation [4]**

With sufficiently strong senescence in diversification rates, $\alpha \gg 1$, only age-class 0 and 1 contribute significantly to the total frequency of asexual species. All sub-sequent age-classes have negligible rates of diversification.

$$F_{\text{Senesce}} = \frac{e^U (e^A + e^S - e^U)}{(e^S - e^U)^2} = \frac{e^U}{e^S - e^U} \left(1 + \frac{e^A}{e^S - e^U} \right)$$

Sum[fx[x], {x, 0, 1}] // Simplify

$$\frac{e^U (e^A + e^S - e^U)}{(e^S - e^U)^2}$$

■ **Weak senescence model, $1 > \alpha > 0$; Equation [5]**

Let $B = \ln(e^S - e^U)$ and substitute into fx[x] to make fx2[x].

fx2[x_] := Exp[U] Exp[(A + α) x] Exp[- α x^2] Exp[B (-x - 1)] ;

We use an integral approximation to obtain an analytical experssion for F_{Senesce} .

F_{Senesce}

$$= \frac{e^{\frac{1}{4} \left(2A - 6B + 4U + \frac{(A-B)^2}{\alpha} + \alpha \right)} \sqrt{\pi} \left(1 + \text{Erf} \left[\frac{A-B+\alpha}{2\sqrt{\alpha}} \right] \right)}{2\sqrt{\alpha}} = e^{U-B} \frac{e^{\frac{(\alpha+A-B)^2}{4\alpha}} \sqrt{\pi} \left(1 + \text{Erf} \left[\frac{\alpha+A-B}{2\sqrt{\alpha}} \right] \right)}{2\sqrt{\alpha}} = \frac{e^U}{e^S - e^U} \frac{e^{\frac{\left(\alpha + \ln \left(\frac{e^A}{e^S - e^U} \right) \right)^2}{4\alpha}} \sqrt{\pi} \left(1 + \text{Erf} \left[\frac{\alpha + \ln \left(\frac{e^A}{e^S - e^U} \right)}{2\sqrt{\alpha}} \right] \right)}{2\sqrt{\alpha}}$$

Simplify[Integrate[fx2[x], {x, 0, Infinity}], Assumptions -> Re[α] > 0]

$$\frac{e^{\frac{1}{4} \left(2A - 6B + 4U + \frac{(A-B)^2}{\alpha} + \alpha \right)} \sqrt{\pi} \left(1 + \text{Erf} \left[\frac{A-B+\alpha}{2\sqrt{\alpha}} \right] \right)}{2\sqrt{\alpha}}$$

If $e^A / (e^S - e^U) \geq 1$, asexual species initially possess higher diversification rates than sexual species. With senescence, asexual lineages will reach an age-class, x^* , possessing a diversification rate equal to that of sexual species (i.e. $e^{A-2\alpha x^*} = e^S - e^U$). That is, asexual species in age-classes younger than $x^* = (A-B) / (2\alpha)$ all diversify at higher rates than sexual species, where $B = \ln(e^S - e^U)$.

We find that the proportion of asexual species that possess diversification rates higher than sexual species is approxi-

$$\text{mately } \frac{\text{Erf} \left[\frac{A-B+\alpha}{2\sqrt{\alpha}} \right] - \text{Erf} \left[\frac{\sqrt{\alpha}}{2} \right]}{1 + \text{Erf} \left[\frac{A-B+\alpha}{2\sqrt{\alpha}} \right]} = \frac{\text{Erf} \left[\frac{\ln \left(\frac{e^A}{e^S - e^U} \right) + \alpha}{2\sqrt{\alpha}} \right] - \text{Erf} \left[\frac{\sqrt{\alpha}}{2} \right]}{1 + \text{Erf} \left[\frac{\ln \left(\frac{e^A}{e^S - e^U} \right) + \alpha}{2\sqrt{\alpha}} \right]}; \text{Equation [6]}$$

Simplify[Integrate[fx2[x], {x, 0, (A - B) / (2 α)}] / (Integrate[fx2[x], {x, 0, Infinity}]), Assumptions -> Re[α] > 0]

$$- \frac{\text{Erf} \left[\frac{-A+B-\alpha}{2\sqrt{\alpha}} \right] + \text{Erf} \left[\frac{\sqrt{\alpha}}{2} \right]}{1 + \text{Erf} \left[\frac{A-B+\alpha}{2\sqrt{\alpha}} \right]}$$

■ **Mean diversification rate of asexual species relative to sexual species when $1 > \alpha > 0$, (\bar{R}); Equation [7]**

Here we find the average diversification rate of asexual species relative to the net growth of sexual species ($e^S - e^U$)

when senescence is present but weak.

$$\bar{R} = \frac{1}{e^S - e^U} \sum_{x=0}^{\infty} \frac{f_x D_x}{F_{\text{Senesce}}} \approx \frac{1}{e^S} \int_0^{\infty} \frac{f_x D_x}{F_{\text{Senesce}}} = \frac{\text{Erfc}\left[\frac{-A+B+\alpha}{2\sqrt{\alpha}}\right]}{1 + \text{Erf}\left[\frac{A-B+\alpha}{2\sqrt{\alpha}}\right]} = \frac{1 + \text{Erf}\left[\frac{\ln\left(\frac{e^A}{e^S - e^U}\right) - \alpha}{2\sqrt{\alpha}}\right]}{1 + \text{Erf}\left[\frac{\ln\left(\frac{e^A}{e^S - e^U}\right) + \alpha}{2\sqrt{\alpha}}\right]}$$

Simplify[**Integrate**[**DivRateAsex**[**x**] **fx2**[**x**], {**x**, 0, Infinity}] *

$$\frac{1}{2\sqrt{\alpha}} e^{\frac{1}{4}\left(2A-6B+4U+\frac{(A-B)^2}{\alpha}+\alpha\right)} \sqrt{\pi} \left(1 + \text{Erf}\left[\frac{A-B+\alpha}{2\sqrt{\alpha}}\right]\right) * 1/e^B, \text{Assumptions} \rightarrow \text{Re}[\alpha] > 0$$

$$\frac{\text{Erfc}\left[\frac{-A+B+\alpha}{2\sqrt{\alpha}}\right]}{1 + \text{Erf}\left[\frac{A-B+\alpha}{2\sqrt{\alpha}}\right]}$$

Variable Rates of Senescence

■ Preliminaries

Suppose an asexual lineage can experience n changes in senescence rate as it ages. Age-classes can be divided into intervals, each experiencing a constant senescence rate differing from that of the preceding interval. Senescence rate, α_i , can be described by a step function of age-class x , containing $n+1$ intervals.

$$\alpha_i = \begin{cases} \alpha_0 & y_0 = 0 \leq x < y_1 \\ \alpha_1 & y_1 \leq x < y_2 \\ \alpha_2 & y_2 \leq x < y_3 \\ \vdots & \vdots \\ \alpha_n & y_n \leq x < y_{n+1} = \infty \end{cases}$$

y_i represents the threshold age-class where senescence rate changes for the i^{th} time, from α_{i-1} to α_i ; senescence remains at rate α_i for the interval $y_i \leq x < y_{i+1}$.

We define $\alpha_i = \alpha_0 + \sum_{j=1}^i \delta_j$, such that $\delta_j = \{\delta_1, \delta_2, \dots, \delta_n\}$ denote effects of the i^{th} change in senescence rate.

D_x is a continuous piecewise function to describe diversification rate in asexual species. The i^{th} sub-function governs the diversification rate following the i^{th} change in senescence rate and over the age-class interval $y_i \leq x < y_{i+1}$, analogous to the senescence rate step function. Let $\Delta_i = \sum_{j=1}^i \delta_n(x - (y_i - 1))$.

$$D_x = \begin{cases} e^{A-2\alpha_0 x} & y_0 = 0 \leq x < y_1 \\ e^{A-2(\alpha_0 x + \Delta_1)} & y_1 \leq x < y_2 \\ e^{A-2(\alpha_0 x + \Delta_2)} & y_2 \leq x < y_3 \\ \vdots & \vdots \\ e^{A-2(\alpha_0 x + \Delta_n)} & y_n \leq x < y_{n+1} = \infty \end{cases}$$

Below, we examine a model with finite number of age-classes where senescence rate changes twice during the life time of asexual lineages. Afterwards, we extend the model to accomodate any number of age-classes.

■ System with 21 age-classes and 2 senescence rate changes

Sexual species diversify at rate e^S and produce asexual species into age-class 0 at rate $e^U < 1$. The net growth of sexual species per time step is then equal to $e^S - e^U$ and assumed to be larger than 1.

We construct the piecewise function to describe diversification rate of asexual species in the three intervals.

We define the range of the three intervals below and construct the list of diversification rates for 20 asexual age-classes.

Age-class 0 to 4, 5 to 9, 10 to 20 experience senescence rates of α_0 , α_1 and α_2 , respectively.

```

y1 = 5; y2 = 10; y3 = 20;
PiecewiseDx := Piecewise[{
  {Exp[A] Exp[- $\alpha_0$  (2 x)], 0 ≤ x < y1},
  {Exp[A] Exp[-( $\alpha_0 + \delta_1$ ) (2 x) + 2  $\delta_1$  (y1 - 1)], y1 ≤ x < y2},
  {Exp[A] Exp[-( $\alpha_0 + \delta_1 + \delta_2$ ) (2 x) + 2  $\delta_1$  (y1 - 1) + 2  $\delta_2$  (y2 - 1)], y2 ≤ x < y3}
}]
Dx20Classes = Table[PiecewiseDx, {x, 0, 19}]

{eA, eA-2  $\alpha_0$ , eA-4  $\alpha_0$ , eA-6  $\alpha_0$ , eA-8  $\alpha_0$ , eA+10 (- $\alpha_0 - \delta_1$ ) + 8  $\delta_1$ , eA+12 (- $\alpha_0 - \delta_1$ ) + 8  $\delta_1$ , eA+14 (- $\alpha_0 - \delta_1$ ) + 8  $\delta_1$ ,
eA+16 (- $\alpha_0 - \delta_1$ ) + 8  $\delta_1$ , eA+18 (- $\alpha_0 - \delta_1$ ) + 8  $\delta_1$ , eA+8  $\delta_1$  + 20 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 22 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ ,
eA+8  $\delta_1$  + 24 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 26 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 28 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 30 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ ,
eA+8  $\delta_1$  + 32 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 34 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 36 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ , eA+8  $\delta_1$  + 38 (- $\alpha_0 - \delta_1 - \delta_2$ ) + 18  $\delta_2$ }

```

$\vec{x}(t+1) = M \vec{x}(t)$ represents the recursion equation for the linear system.

$\vec{x}(t) = \{N_S(t), N_{A,1}(t), N_{A,2}(t), \dots, N_{A,21}(t)\}$ is the vector containing the abundance of sexual species, $N_S(t)$, and asexual species in age-class x , $N_{A,x}(t)$, at time point t .

M represents the transition matrix which is shown below.

The diagonal of M contains the transition rate of one class into itself. The sub-diagonal of M contains the transition rate of one to class to the next.

In our model, only sexual species diversify into their own class and thus the diagonal of M only contains $e^S - e^U$, which represents the net growth of sexual species per time step.

Sexual species produce into age-class 0 asexual species at rate e^U and all asexual species diversify into subsequent age-classes. These transition rates are contained in the sub-diagonal of M .

To continue we let $B = \text{Log}(e^S - e^U)$

```

TMatSubDiagonal = Join[{E^U}, Dx20Classes];
TMat = DiagonalMatrix[TMatSubDiagonal, -1];
TMat[[1, 1]] = E^B;
TMat

```

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{ {e^B, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {e^U, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, e^A, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, e^{A-2 \alpha_0}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, e^{A-4 \alpha_0}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, e^{A-6 \alpha_0}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, e^{A-8 \alpha_0}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, e^{A+10 (-\alpha_0-\delta_1)+8 \delta_1}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, e^{A+12 (-\alpha_0-\delta_1)+8 \delta_1}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, e^{A+14 (-\alpha_0-\delta_1)+8 \delta_1}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+16 (-\alpha_0-\delta_1)+8 \delta_1}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+18 (-\alpha_0-\delta_1)+8 \delta_1}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+20 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+22 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+24 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+26 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+28 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+30 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+32 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+34 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+36 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0, 0},
  {0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, e^{A+8 \delta_1+38 (-\alpha_0-\delta_1-\delta_2)+18 \delta_2}, 0} }

```

■ Solve for the stationary distribution of species abundance

We find the equilibrium stationary distribution of species abundance by finding the sole eigenvalue of the system, $e^S - e^U$, and the corresponding eigenvector. We normalize all species abundance to that of the sexual species and obtain the relative frequency of asexual species in all 21 age-classes.

```

Eigenvalues[TMat];
SexualAbundance = Eigenvectors[TMat][[-1]][[1]];
EigenvectorNormalizedToSexualAbundance = Eigenvectors[TMat][[-1]] / SexualAbundance;
AsexFrequency21Classes = Delete[EigenvectorNormalizedToSexualAbundance, 1]

```

```

{e^{-B+U}, e^{A-2 B+U}, e^{2 A-3 B+U-2 \alpha_0}, e^{3 A-4 B+U-6 \alpha_0}, e^{4 A-5 B+U-12 \alpha_0}, e^{5 A-6 B+U-20 \alpha_0}, e^{6 A-7 B+U-30 \alpha_0-2 \delta_1},
  e^{7 A-8 B+U-42 \alpha_0-6 \delta_1}, e^{8 A-9 B+U-56 \alpha_0-12 \delta_1}, e^{9 A-10 B+U-72 \alpha_0-20 \delta_1}, e^{10 A-11 B+U-90 \alpha_0-30 \delta_1},
  e^{11 A-12 B+U-110 \alpha_0-42 \delta_1-2 \delta_2}, e^{12 A-13 B+U-132 \alpha_0-56 \delta_1-6 \delta_2}, e^{13 A-14 B+U-156 \alpha_0-72 \delta_1-12 \delta_2}, e^{14 A-15 B+U-182 \alpha_0-90 \delta_1-20 \delta_2},
  e^{15 A-16 B+U-210 \alpha_0-110 \delta_1-30 \delta_2}, e^{16 A-17 B+U-240 \alpha_0-132 \delta_1-42 \delta_2}, e^{17 A-18 B+U-272 \alpha_0-156 \delta_1-56 \delta_2},
  e^{18 A-19 B+U-306 \alpha_0-182 \delta_1-72 \delta_2}, e^{19 A-20 B+U-380 \alpha_0-248 \delta_1-38 (-\alpha_0-\delta_1-\delta_2)-128 \delta_2}, e^{20 A-21 B+U-380 \alpha_0-240 \delta_1-110 \delta_2}}

```

- The normalized frequency of asexual species can be described by a continuous piecewise function:

$$(e^U / (e^S + e^U))^{-1} f_x = \begin{cases} (e^S - e^U)^{-x} e^{-\alpha_0 x^2 + (A + \alpha_0)x} & y_0 = 0 \leq x \leq y_1 \\ (e^S - e^U)^{-x} e^{-\alpha_1 x^2 + (A + \alpha_1)x + L_1 x + M_1} & y_1 < x \leq y_2 \\ (e^S - e^U)^{-x} e^{-\alpha_2 x^2 + (A + \alpha_2)x + L_2 x + M_2} & y_2 < x \leq y_3 \\ \vdots & \vdots \\ (e^S - e^U)^{-x} e^{-\alpha_n x^2 + (A + \alpha_n)x + L_n x + M_n} & y_n < x < y_{n+1} = \infty \end{cases}$$

, where $L_i = \sum_{j=1}^i 2 \delta_j (y_j - 1)$ and $M_i = \sum_{j=1}^i -\delta_j y_j (y_j - 1)$

```
AnalyticalPiecewisefx := Piecewise[{
  {Exp[U - B] Exp[-α0 x^2] Exp[(A - B + α0) x], 0 ≤ x ≤ y1},
  {Exp[U - B] Exp[-(α0 + δ1) x^2]
    Exp[(A - B + α0 + δ1) x] Exp[2 δ1 (y1 - 1) x] Exp[-δ1 y1 (y1 - 1)], y1 < x ≤ y2},
  {Exp[U - B] Exp[-(α0 + δ1 + δ2) x^2] Exp[(A - B + α0 + δ1 + δ2) x] Exp[2 δ1 (y1 - 1) x]
    Exp[2 δ2 (y2 - 1) x] Exp[-δ1 y1 (y1 - 1)] Exp[-δ2 y2 (y2 - 1)], y2 < x ≤ y3}
}]
```

```
AnalyticalAsexFrequency21Classes = Table[AnalyticalPiecewisefx, {x, 0, 20}] // Simplify
AnalyticalAsexFrequency21Classes == AsexFrequency21Classes // Simplify
```

```
{e^{-B+U}, e^{A-2 B+U}, e^{2 A-3 B+U-2 α0}, e^{3 A-4 B+U-6 α0}, e^{4 A-5 B+U-12 α0}, e^{5 A-6 B+U-20 α0}, e^{6 A-7 B+U-30 α0-2 δ1},
e^{7 A-8 B+U-42 α0-6 δ1}, e^{8 A-9 B+U-56 α0-12 δ1}, e^{9 A-10 B+U-72 α0-20 δ1}, e^{10 A-11 B+U-90 α0-30 δ1},
e^{11 A-12 B+U-110 α0-42 δ1-2 δ2}, e^{12 A-13 B+U-132 α0-56 δ1-6 δ2}, e^{13 A-14 B+U-156 α0-72 δ1-12 δ2}, e^{14 A-15 B+U-182 α0-90 δ1-20 δ2},
e^{15 A-16 B+U-210 α0-110 δ1-30 δ2}, e^{16 A-17 B+U-240 α0-132 δ1-42 δ2}, e^{17 A-18 B+U-272 α0-156 δ1-56 δ2},
e^{18 A-19 B+U-306 α0-182 δ1-72 δ2}, e^{19 A-20 B+U-342 α0-210 δ1-90 δ2}, e^{20 A-21 B+U-380 α0-240 δ1-110 δ2}}
```

True

- Extension to k age-classes to approximate system with infinite age-classes

We can approximate a system with infinite age-classes using one with a large finite number of age-classes, k , by ensuring that asexual lineages will eventually decrease to negligible frequencies at same age (relative to the total abundance of asexuals). In the variable senescence rate model, this condition is met when asexual species diversify at lower rates than sexuals after the n^{th} change in senescence rate, $e^{A+L_n} / (e^S - e^U) < 1$, or when diversification rates senesce with age after the n^{th} change in senescence rate, $\alpha_n > 0$. Given that the k -th age-class is negligible in frequency, their descendants will also be negligible in frequency. We make the simplifying assumption that they leave no descendants and truncate the matrix at the k -th age-class.

Under these conditions, we can approximate an infinite age-class model with a k age-class model by taking the limit of k approaching infinity. We can still utilize the analytical piecewise function shown above to describe the frequency of asexual species in age-class x because of our truncation at the k -th age-class.

- Total frequency of asexual species (F_{Senesce}); Equation [11]

We first make the assumption that senescence rates at each interval falls between $0 \leq \alpha_i \leq 1$. As in equation [5], this ensures that senescence is either absent or weak and we can apply an integral approximation to find the sum of asexual frequencies for each interval where senescence rate is constant, F_i .

$$F_{\text{Senesce}} = \sum_{x=0}^{\infty} f_x \approx \sum_{i=0}^n F_i, \text{ where } F_i = \int_{y_i}^{y_{i+1}} f_x dx = \int_{y_i}^{y_{i+1}} e^{U-B-\alpha_i x^2 + (A-B+\alpha_i)x + L_i x + M_i} dx.$$

$L_i = \sum_{j=1}^i 2 \delta_j y_j$ and $M_i = \sum_{j=1}^i -\delta_j y_j^2$ are slightly different when assuming age-classes are continuous. F_i has two distinct forms depending on whether α_i is equal to or larger than 0.

$$\ln \left(\frac{e^A}{e^S - e^U} \right) \frac{e^U}{e^S - e^U}$$

- When

$$\begin{aligned}
& \alpha_i > 0, F_i = \frac{1}{2\sqrt{\alpha_i}} \\
& e^{\frac{(A-B)^2 + L_i^2 + 2(A-3B+2U+2M_i)\alpha_i + \alpha_i^2 + 2L_i(A-B+\alpha_i)}{4\alpha_i}} \sqrt{\pi} \left(-\text{Erf}\left[\frac{-A+B-L_i + (-1+2Y_i)\alpha_i}{2\sqrt{\alpha_i}}\right] + \text{Erf}\left[\frac{-A+B-L_i + (-1+2Y_{i+1})\alpha_i}{2\sqrt{\alpha_i}}\right] \right) = \\
& e^{U-B} e^{\left(\frac{A-B+\alpha_i+L_i}{2\sqrt{\alpha_i}}\right)^2 + M_i} \frac{\sqrt{\pi}}{2\sqrt{\alpha_i}} \left(\text{Erf}\left[\frac{A-B+L_i - (2Y_i-1)\alpha_i}{2\sqrt{\alpha_i}}\right] - \text{Erf}\left[\frac{A-B+L_i - (2Y_{i+1}-1)\alpha_i}{2\sqrt{\alpha_i}}\right] \right) = \\
& \frac{e^U}{e^S - e^U} e^{\left(\frac{\ln\left(\frac{e^A}{e^S - e^U}\right) + \alpha_i + L_i}{2\sqrt{\alpha_i}}\right)^2 + M_i} \frac{\sqrt{\pi}}{2\sqrt{\alpha_i}} \left(\text{Erf}\left[\frac{\ln\left(\frac{e^A}{e^S - e^U}\right) + L_i - (2Y_i-1)\alpha_i}{2\sqrt{\alpha_i}}\right] - \text{Erf}\left[\frac{\ln\left(\frac{e^A}{e^S - e^U}\right) + L_i - (2Y_{i+1}-1)\alpha_i}{2\sqrt{\alpha_i}}\right] \right) \\
& \text{Integrate}\left[e^{U-B-\alpha_i x^2 + (A-B+\alpha_i+L_i)x + M_i}, \{x, Y_i, Y_{i+1}\}\right] \\
& \frac{1}{2\sqrt{\alpha_i}} e^{\frac{(A-B)^2 + L_i^2 + 2(A-3B+2U+2M_i)\alpha_i + \alpha_i^2 + 2L_i(A-B+\alpha_i)}{4\alpha_i}} \sqrt{\pi} \\
& \left(-\text{Erf}\left[\frac{-A+B-L_i + (-1+2Y_i)\alpha_i}{2\sqrt{\alpha_i}}\right] + \text{Erf}\left[\frac{-A+B-L_i + (-1+2Y_{i+1})\alpha_i}{2\sqrt{\alpha_i}}\right] \right) \\
& \blacksquare \text{ When } \alpha_i = 0, F_i = \frac{e^{-B+U+M_i}(-e^{(A-B+L_i)Y_i} + e^{(A-B+L_i)Y_{i+1}})}{A-B+L_i} = e^{U-B} \frac{e^{M_i}(e^{(A-B+L_i)Y_{i+1}} - e^{(A-B+L_i)Y_i})}{A-B+L_i} = \\
& \frac{e^U}{e^S - e^U} \frac{e^{M_i} \left(e^{\left(\ln\left(\frac{e^A}{e^S - e^U}\right) + L_i\right)Y_{i+1}} - e^{\left(\ln\left(\frac{e^A}{e^S - e^U}\right) + L_i\right)Y_i} \right)}{\ln\left(\frac{e^A}{e^S - e^U}\right) + L_i} \\
& \text{Integrate}\left[e^{U-B-\alpha_i x^2 + (A-B+\alpha_i+L_i)x + M_i} / . \alpha_i \rightarrow 0, \{x, Y_i, Y_{i+1}\}\right] \\
& \frac{e^{-B+U+M_i} \left(-e^{(A-B+L_i)Y_i} + e^{(A-B+L_i)Y_{i+1}} \right)}{A-B+L_i}
\end{aligned}$$

■ Mean diversification rate of asexual species relative to sexual species (\bar{R}); Equation [12]

We assume senescence rates at each interval falls between $0 \leq \alpha_i \leq 1$, as in equation [11]. \bar{R} can be broken down as a weighted sum of the average diversification rate relative to sexual species at each age-class interval where senescence rate is constant, \bar{R}_i .

$$\bar{R} = \frac{1}{e^S - e^U} \sum_{x=0}^{\infty} \frac{f_x D_x}{F_{\text{Senesce}}} \approx \frac{1}{e^S - e^U} \sum_{i=0}^n \int_{Y_i}^{Y_{i+1}} \frac{f_x D_x}{F_{\text{Senesce}}} = \sum_{i=0}^n \frac{F_i}{F_{\text{Senesce}}} \bar{R}_i, \text{ where } \bar{R}_i = \frac{1}{e^S - e^U} \int_{Y_i}^{Y_{i+1}} \frac{f_x D_x}{F_i} dx$$

\bar{R}_i has two distinct forms depending on whether α_i is equal to or larger than 0.

$$\blacksquare \text{ When } \alpha_i = 0, R_i = \left(\text{Erf} \left[\frac{-A+B-L_i+\alpha_i+2 Y_i \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{-A+B-L_i+\alpha_i+2 Y_{i+1} \alpha_i}{2 \sqrt{\alpha_i}} \right] \right) /$$

$$\left(\text{Erf} \left[\frac{-A+B-L_i+(-1+2 Y_i) \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{-A+B-L_i+(-1+2 Y_{i+1}) \alpha_i}{2 \sqrt{\alpha_i}} \right] \right) =$$

$$\left(\text{Erf} \left[\frac{A+B+L_i-(2 Y_i+1) \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{A+B+L_i-(2 Y_{i+1}+1) \alpha_i}{2 \sqrt{\alpha_i}} \right] \right) /$$

$$\left(\text{Erf} \left[\frac{A+B+L_i-(2 Y_i-1) \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{A+B+L_i-(2 Y_{i+1}-1) \alpha_i}{2 \sqrt{\alpha_i}} \right] \right) =$$

$$\left(\text{Erf} \left[\frac{\ln \left(\frac{e^A}{e^S-e^U} \right) + L_i - (2 Y_i+1) \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{\ln \left(\frac{e^A}{e^S-e^U} \right) + L_i - (2 Y_{i+1}+1) \alpha_i}{2 \sqrt{\alpha_i}} \right] \right) /$$

$$\left(\text{Erf} \left[\frac{\ln \left(\frac{e^A}{e^S-e^U} \right) + L_i - (2 Y_i-1) \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{\ln \left(\frac{e^A}{e^S-e^U} \right) + L_i - (2 Y_{i+1}-1) \alpha_i}{2 \sqrt{\alpha_i}} \right] \right)$$

$$\text{Integrate} \left[e^{U-B-\alpha_i x^2 + (A-B+\alpha_i+L_i) x + M_i} e^{A-2 \alpha_i x+L_i}, \{x, Y_i, Y_{i+1}\} \right] * \\ 1 / \text{Integrate} \left[e^{U-B-\alpha_i x^2 + (A-B+\alpha_i+L_i) x + M_i}, \{x, Y_i, Y_{i+1}\} \right] * 1 / e^B // \text{Simplify}$$

$$\left(\text{Erf} \left[\frac{-A+B-L_i+\alpha_i+2 Y_i \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{-A+B-L_i+\alpha_i+2 Y_{i+1} \alpha_i}{2 \sqrt{\alpha_i}} \right] \right) /$$

$$\left(\text{Erf} \left[\frac{-A+B-L_i+(-1+2 Y_i) \alpha_i}{2 \sqrt{\alpha_i}} \right] - \text{Erf} \left[\frac{-A+B-L_i+(-1+2 Y_{i+1}) \alpha_i}{2 \sqrt{\alpha_i}} \right] \right)$$

$$\blacksquare \text{ When } \alpha_i = 0, R_i = e^{A-B+L_i} = e^{\ln \left(\frac{e^A}{e^S-e^U} \right) + L_i}$$

$$\text{Integrate} \left[e^{U-B-\alpha_i x^2 + (A-B+\alpha_i+L_i) x + M_i} e^{A-2 \alpha_i x+L_i} /. \alpha_i \rightarrow 0, \{x, Y_i, Y_{i+1}\} \right] * \\ 1 / \text{Integrate} \left[e^{U-B-\alpha_i x^2 + (A-B+\alpha_i+L_i) x + M_i} /. \alpha_i \rightarrow 0, \{x, Y_i, Y_{i+1}\} \right] * 1 / e^B // \text{Simplify}$$

$$e^{A-B+L_i}$$

Constant Rate of Senescence with Linear Senescence Function

■ Preliminaries

This model has the same structure as the constant senescence rate model above except that we use a linear, rather than an exponential, function for senescence.

Sexual species diversify at rate e^S and produce asexual species into age-class 0 at rate $e^U \ll 1$. The net growth of sexual species per time step is then equal to $e^S - e^U$ and assumed to be larger than 1. Asexual species progress through age-classes, x , where $0 \leq x < \infty$ and possess diversification rates $e^A / (1 + \alpha x)$, where $\alpha \geq 0$. α describes the rate that diversification rates senesce in aging asexual lineages.

Below, we construct a linear system of equations to describe the abundance of sexual and asexual species.

We first construct a system with a finite number of asexual age-classes. By normalizing all species abundance to that of the sexual species, we find an analytical formula to describe the relative frequency of asexual species in age-class x . By induction, we extend the model to accommodate any number of age-classes.

■ Linear System with 21 asexual age-classes

Sexual species produce asexual species into age-class 0 at rate e^U .

The diversification rate of asexual age-classes follow the function $e^A / (1 + \alpha x)$.

By limiting the number of age-classes to 21, we assume that species in age-classes subsequent to 21 do not exist or have negligible abundance. The parameter values that allow for this is restrictive but our goal with considering a finite

number of age-classes is to explore the properties of this model. We show below that extension to large number of age-classes relieves some of these restrictions.

```
DivRateAsex[x_] := Exp[A] / (1 + α x);
DivRate20Classes = Table[DivRateAsex[x], {x, 0, 20}]
```

$$\left\{ e^A, \frac{e^A}{1+\alpha}, \frac{e^A}{1+2\alpha}, \frac{e^A}{1+3\alpha}, \frac{e^A}{1+4\alpha}, \frac{e^A}{1+5\alpha}, \frac{e^A}{1+6\alpha}, \frac{e^A}{1+7\alpha}, \frac{e^A}{1+8\alpha}, \frac{e^A}{1+9\alpha}, \frac{e^A}{1+10\alpha}, \frac{e^A}{1+11\alpha}, \frac{e^A}{1+12\alpha}, \frac{e^A}{1+13\alpha}, \frac{e^A}{1+14\alpha}, \frac{e^A}{1+15\alpha}, \frac{e^A}{1+16\alpha}, \frac{e^A}{1+17\alpha}, \frac{e^A}{1+18\alpha}, \frac{e^A}{1+19\alpha}, \frac{e^A}{1+20\alpha} \right\}$$

$\tilde{x}(t+1) = M \tilde{x}(t)$ represents the recursion equation for the linear system.

$\tilde{x}(t) = \{N_S(t), N_{A,1}(t), N_{A,2}(t), \dots, N_{A,21}(t)\}$ is the vector containing the abundance of sexual species, $N_S(t)$, and asexual species in age-class x , $N_{A,x}(t)$, at time point t .

M represents the transition matrix (shown below).

The diagonal of M contains the transition rate of one class into itself. The sub-diagonal of M contains the transition rate of one to class to the next.

In our model, only sexual species diversify into their own class and thus the diagonal of M only contains $e^S - e^U$, which represents the net growth of sexual species per time step.

Sexual species produce into age-class 0 asexual species at rate e^U and all asexual species diversify into subsequent age-classes. These transition rates are contained in the sub-diagonal of M .

```
TMatrixSubDiagonal = Join[{E^U}, DivRate20Classes];
TMatrix = DiagonalMatrix[TMatrixSubDiagonal, -1];
TMatrix[[1, 1]] = E^S - E^U;
TMatrix
```

$$\begin{aligned} & \left\{ \{e^S - e^U, 0\}, \right. \\ & \left\{ e^U, 0\}, \right. \\ & \left\{ 0, e^A, 0\}, \right. \\ & \left\{ 0, 0, \frac{e^A}{1+\alpha}, 0\}, \right. \\ & \left\{ 0, 0, 0, \frac{e^A}{1+2\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left\{ 0, 0, 0, 0, \frac{e^A}{1+3\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left\{ 0, 0, 0, 0, 0, \frac{e^A}{1+4\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left\{ 0, 0, 0, 0, 0, 0, \frac{e^A}{1+5\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left\{ 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1+6\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left\{ 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1+7\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1+8\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \\ & \left. \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1+9\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0\}, \right. \right. \end{aligned}$$

$$\begin{aligned}
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 10\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 11\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 12\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 13\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 14\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 15\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 16\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 17\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 18\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 19\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}, \\
& \left\{ 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, \frac{e^A}{1 + 20\alpha}, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0 \right\}
\end{aligned}$$

■ Solve for the stationary distribution of species abundance

We find the equilibrium stationary distribution of species abundance by finding the sole eigenvalue of the system, $e^S - e^U$, and the corresponding eigenvector.

Then we normlize all species abundance to that of the sexual species and obtain the relative frequency of asexual species in all 21 age-classes.

```

SexualAbundance = Eigenvectors[TMatrix][[-1]][[1]];
EigenvectorNormalizedToSexualAbundance = Eigenvectors[TMatrix][[-1]] / SexualAbundance;
AsxFrequency21Classes = Delete[EigenvectorNormalizedToSexualAbundance, 1]

```

$$\left\{ \frac{e^U (e^S - e^U)^{21}}{(-e^S + e^U)^{22}}, \frac{e^{A+U} (e^S - e^U)^{20}}{(-e^S + e^U)^{22}}, \frac{e^{2A+U} (e^S - e^U)^{19}}{(-e^S + e^U)^{22} (1 + \alpha)}, \right. \\
\frac{e^{3A+U} (e^S - e^U)^{18}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha)}, \frac{e^{4A+U} (e^S - e^U)^{17}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha)}, \\
\left. \frac{e^{5A+U} (e^S - e^U)^{16}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha)}, \right. \\
\frac{e^{6A+U} (e^S - e^U)^{15}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha)}, \\
\frac{e^{7A+U} (e^S - e^U)^{14}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha)}, \\
\frac{e^{8A+U} (e^S - e^U)^{13}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha)}, \\
\frac{e^{9A+U} (e^S - e^U)^{12}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha)}, \\
\frac{e^{10A+U} (e^S - e^U)^{11}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha)}, \\
\frac{e^{11A+U} (e^S - e^U)^{10}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha)}, \\
\frac{e^{12A+U} (e^S - e^U)^9}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha)}, \\
\frac{e^{13A+U} (e^S - e^U)^8}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha)}, \\
\frac{e^{14A+U} (e^S - e^U)^7}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha)}, \\
\frac{e^{15A+U} (e^S - e^U)^6}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha)}, \\
\frac{e^{16A+U} (e^S - e^U)^5}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha) (1 + 15\alpha)}, \\
\frac{e^{17A+U} (e^S - e^U)^4}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha) (1 + 15\alpha) (1 + 16\alpha)}, \\
\frac{e^{18A+U} (e^S - e^U)^3}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha) (1 + 15\alpha) (1 + 16\alpha) (1 + 17\alpha)}, \\
\frac{e^{19A+U} (e^S - e^U)^2}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha) (1 + 15\alpha) (1 + 16\alpha) (1 + 17\alpha) (1 + 18\alpha)}, \\
\frac{e^{20A+U} (e^S - e^U)}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha) (1 + 15\alpha) (1 + 16\alpha) (1 + 17\alpha) (1 + 18\alpha) (1 + 19\alpha)}, \\
\left. \frac{e^{21A+U}}{(-e^S + e^U)^{22} (1 + \alpha) (1 + 2\alpha) (1 + 3\alpha) (1 + 4\alpha) (1 + 5\alpha) (1 + 6\alpha) (1 + 7\alpha) (1 + 8\alpha) (1 + 9\alpha) (1 + 10\alpha) (1 + 11\alpha) (1 + 12\alpha) (1 + 13\alpha) (1 + 14\alpha) (1 + 15\alpha) (1 + 16\alpha) (1 + 17\alpha) (1 + 18\alpha) (1 + 19\alpha) (1 + 20\alpha)} \right\}$$

- The normalized frequency of asexual species can be described by the analytical function: $fx =$

$$e^U e^A x (e^S - e^U)^{-(x+1)} \frac{\left(\frac{1}{\alpha}\right)^{-1+x} \text{Gamma}\left[1 + \frac{1}{\alpha}\right]}{\text{Gamma}\left[\frac{1}{\alpha} + x\right]}$$

$$fx[x_] := \text{Exp}[U] \text{Exp}[A x] (\text{Exp}[S] - \text{Exp}[U])^{-(x+1)} \frac{\left(\frac{1}{\alpha}\right)^{-1+x} \text{Gamma}\left[1 + \frac{1}{\alpha}\right]}{\text{Gamma}\left[\frac{1}{\alpha} + x\right]}$$

```
AnalyticalAsexFrequency21Classes = Table[fx[x], {x, 0, 21}] // Simplify;
AnalyticalAsexFrequency21Classes == AsexFrequency21Classes // FullSimplify
True
```

- Extension to k age-classes to approximate system with infinite age-classes

We can approximate a system with infinite age-classes using one with a large finite number of age-classes, k , by ensuring that asexual lineages will eventually decrease to negligible frequencies at same age (relative to the total abundance of asexuals). In our model, this condition is met when asexual species diversify at lower rates than sexuals, $e^A / (e^S - e^U) < 1$, or when diversification rates senesce with age, $\alpha > 0$. Given that the k -th age-class is negligible in frequency, their descendants will also be negligible in frequency. We make the simplifying assumption that they leave no descendants and so truncate the matrix at the k -th age-class.

Under these conditions, we can approximate an infinite age-class model with a k age-class model by taking the limit of k approaching infinity. We can still utilize the analytical function shown above to describe the frequency of asexual species in age-class x because of our truncation at the k -th age-class.

- Total frequency of asexual species (F)

- Classic model with no senescence in diversification rate, $\alpha = 0$, and $e^A / (e^S - e^U) < 1$; Equation [3]

Without senescence in diversification rates, $\alpha = 0$, coexistence between sexual and asexual species require that the diversification rate of all asexual species be lower than that of sexuals, $e^A / (e^S - e^U) < 1$. If $e^A / (e^S - e^U) \geq 1$, asexual species will diversify faster than sexuals, thus dominating the system. Note that we use the equivalent formula $fx[x] = \text{Exp}[U] \text{Exp}[A x] (\text{Exp}[S] - \text{Exp}[U])^{-(x+1)}$ here, when $\alpha = 0$, instead of

$$fx[x] = \text{Exp}[U] \text{Exp}[A x] (\text{Exp}[S] - \text{Exp}[U])^{-(x+1)} \frac{\left(\frac{1}{\alpha}\right)^{-1+x} \text{Gamma}\left[1 + \frac{1}{\alpha}\right]}{\text{Gamma}\left[\frac{1}{\alpha} + x\right]}$$

because substituting $\alpha = 0$ directly into the latter would result in indeterminate values.

$$F_{\text{Const}} = \frac{e^U}{-e^A + e^S - e^U}$$

$$\text{Sum}[\text{Exp}[U] \text{Exp}[A x] (\text{Exp}[S] - \text{Exp}[U])^{-(x+1)}, \{x, 0, \text{Infinity}\}]$$

$$\frac{e^U}{-e^A + e^S - e^U}$$

- Strong senescence model, $\alpha \gg 1$; Equation [4]

With sufficiently strong senescence in diversification rates, $\alpha \gg 1$, only age-class 0 and 1 contribute significantly to the total frequency of asexual species. All sub-sequence age-classes have negligible rates of diversification.

$$F_{\text{Senesce}} = \frac{e^U (e^A + e^S - e^U)}{(e^S - e^U)^2} = \frac{e^U}{e^S - e^U} \left(1 + \frac{e^A}{e^S - e^U}\right)$$

$$\text{Sum}[fx[x], \{x, 0, 1\}] // \text{FullSimplify}$$

$$\frac{e^U (e^A + e^S - e^U)}{(e^S - e^U)^2}$$

- Weak senescence model, $1 > \alpha > 0$; Equation [5]

We take the sum from age class 0 to Infinity to obtain an analytical expression for F_{Senesce} .

$$F_{\text{Senesce}} = - \frac{1}{(e^S - e^U)^2 \alpha^2} e^{A+U+\frac{e^A}{e^S \alpha - e^U \alpha}} (-1 + \alpha) \left(\frac{e^A}{e^S \alpha - e^U \alpha} \right)^{-1/\alpha} \left(\text{Gamma} \left[-1 + \frac{1}{\alpha} \right] - \text{Gamma} \left[-1 + \frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right)$$

FullSimplify[Sum[fx[x], {x, 0, Infinity}], Assumptions -> Re[α] > 0]

$$- \left(e^{A+U+\frac{e^A}{e^S \alpha - e^U \alpha}} (-1 + \alpha) \left(\frac{e^A}{e^S \alpha - e^U \alpha} \right)^{-1/\alpha} \left(\text{Gamma} \left[-1 + \frac{1}{\alpha} \right] - \text{Gamma} \left[-1 + \frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right) \right) / ((e^S - e^U)^2 \alpha^2)$$

If $e^A / (e^S - e^U) > 1$, asexual species initially possess higher diversification rates than sexual species. With senescence, asexual lineages will reach an age-class, x^* , possessing a diversification rate equal to that of sexual species (i.e. $e^A / (1 + \alpha x) = e^S - e^U$). That is, asexual species in age-classes younger than $x^* = (e^A / (e^S - e^U) - 1) / \alpha$ all diversify at higher rates than sexual species.

We solve for the proportion of asexual species that possess diversification rates higher than sexual below

FullSimplify[Sum[fx[x], {x, 0, (Exp[A] / (Exp[S] - Exp[U]) - 1) / α}] / (Sum[fx[x], {x, 0, Infinity}]), Assumptions -> Re[α] > 0]

$$1 + \left(e^{-A \left(-1 + \frac{1+e^A}{e^S \alpha - e^U \alpha} \right)} (e^S - e^U)^{-1 + \frac{1+e^A}{e^S \alpha - e^U \alpha}} \alpha^{\frac{1+e^A}{e^S \alpha - e^U \alpha}} \left(\frac{e^A}{e^S \alpha - e^U \alpha} \right)^{\frac{1+e^A}{e^S \alpha - e^U \alpha}} \right. \\ \left. \text{Gamma} \left[\frac{1}{\alpha} \right] \left(\text{Gamma} \left[\frac{e^A}{e^S \alpha - e^U \alpha} \right] - \text{Gamma} \left[\frac{e^A}{e^S \alpha - e^U \alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right) \right) / \\ \left((-1 + \alpha) \text{Gamma} \left[1 + \frac{e^A}{e^S \alpha - e^U \alpha} \right] \left(\text{Gamma} \left[-1 + \frac{1}{\alpha} \right] - \text{Gamma} \left[-1 + \frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right) \right)$$

■ Mean diversification rate of asexual species relative to sexual species when $1 > \alpha > 0$, (\bar{R}) ; Equation [7]

Here we find the average diversification rate of asexual species relative to that of sexual species when senescence is present but weak.

$$\bar{R} = \frac{1}{e^S - e^U} \sum_{x=0}^{\infty} \frac{f_x D_x}{F_{\text{Senesce}}} = \frac{\alpha \left(-\text{Gamma} \left[\frac{1}{\alpha} \right] + \text{Gamma} \left[\frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right)}{(-1 + \alpha) \left(\text{Gamma} \left[-1 + \frac{1}{\alpha} \right] - \text{Gamma} \left[-1 + \frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right)}$$

FullSimplify[Sum[DivRateAsex[x] fx[x], {x, 0, Infinity}] /

$$\left(- \left(e^{A+U+\frac{e^A}{e^S \alpha - e^U \alpha}} (-1 + \alpha) \left(\frac{e^A}{e^S \alpha - e^U \alpha} \right)^{-1/\alpha} \left(\text{Gamma} \left[-1 + \frac{1}{\alpha} \right] - \text{Gamma} \left[-1 + \frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right) \right) \right) / \\ \left((e^S - e^U)^2 \alpha^2 \right) * 1 / (e^S - e^U), \text{Assumptions -> Re[α] > 0} \\ \left(\alpha \left(-\text{Gamma} \left[\frac{1}{\alpha} \right] + \text{Gamma} \left[\frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right) \right) / \left((-1 + \alpha) \left(\text{Gamma} \left[-1 + \frac{1}{\alpha} \right] - \text{Gamma} \left[-1 + \frac{1}{\alpha}, \frac{e^A}{e^S \alpha - e^U \alpha} \right] \right) \right)$$

Here we show that \bar{R} is always less than 1 when there is senescence in asexual diversification rates (i.e. $\alpha > 0$).

$$\text{Let } R = \frac{e^A}{e^S - e^U}$$

```

g[α_, R_] = (α (-Gamma[1/α] + Gamma[1/α, 1/α R])) / ((-1 + α) (Gamma[-1 + 1/α] - Gamma[-1 + 1/α, 1/α R]));
Plot3D[{g[a, R]}, {a, 0.0001, 0.1}, {R, 0.94, 1.5}, AxesLabel → Automatic]

```

